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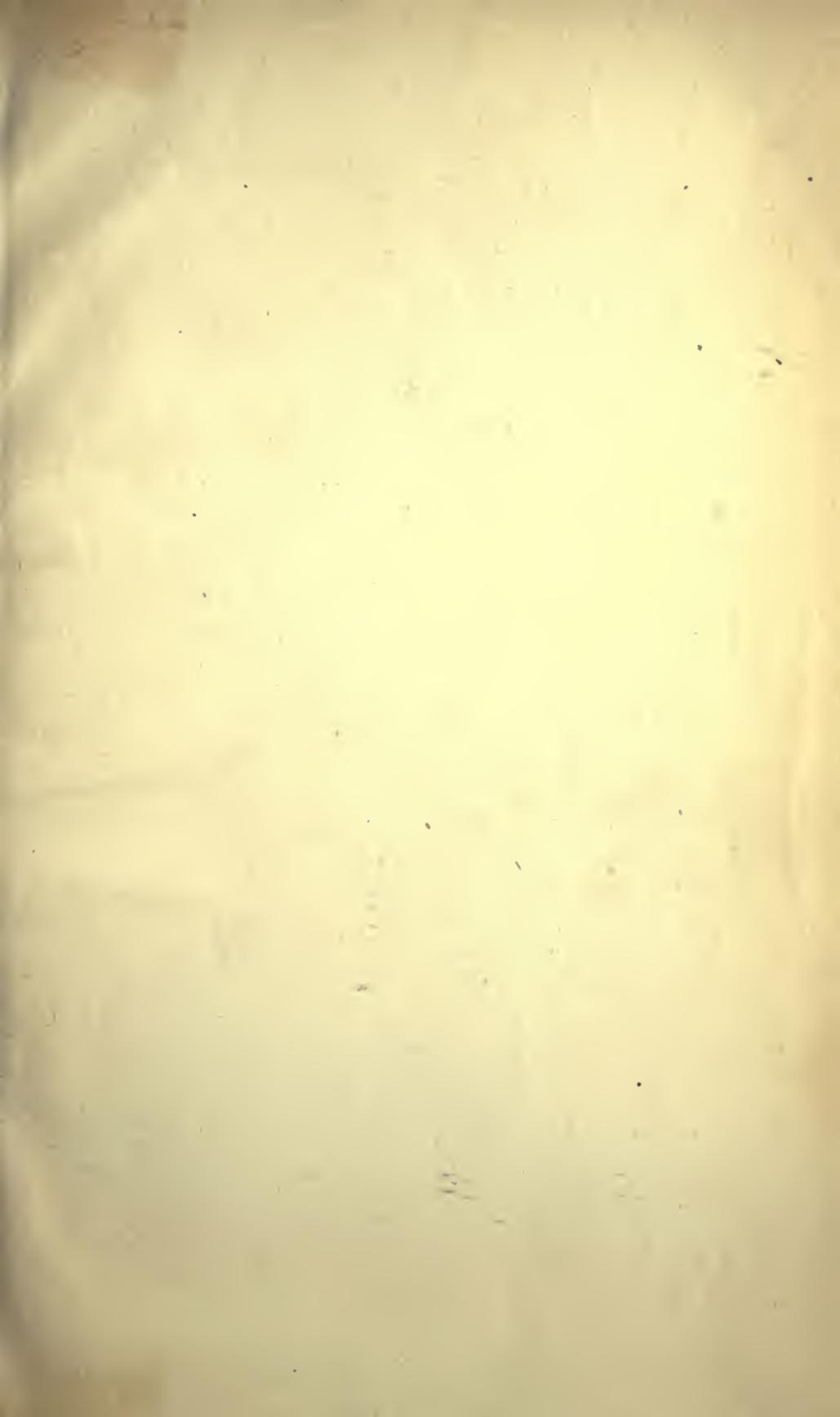
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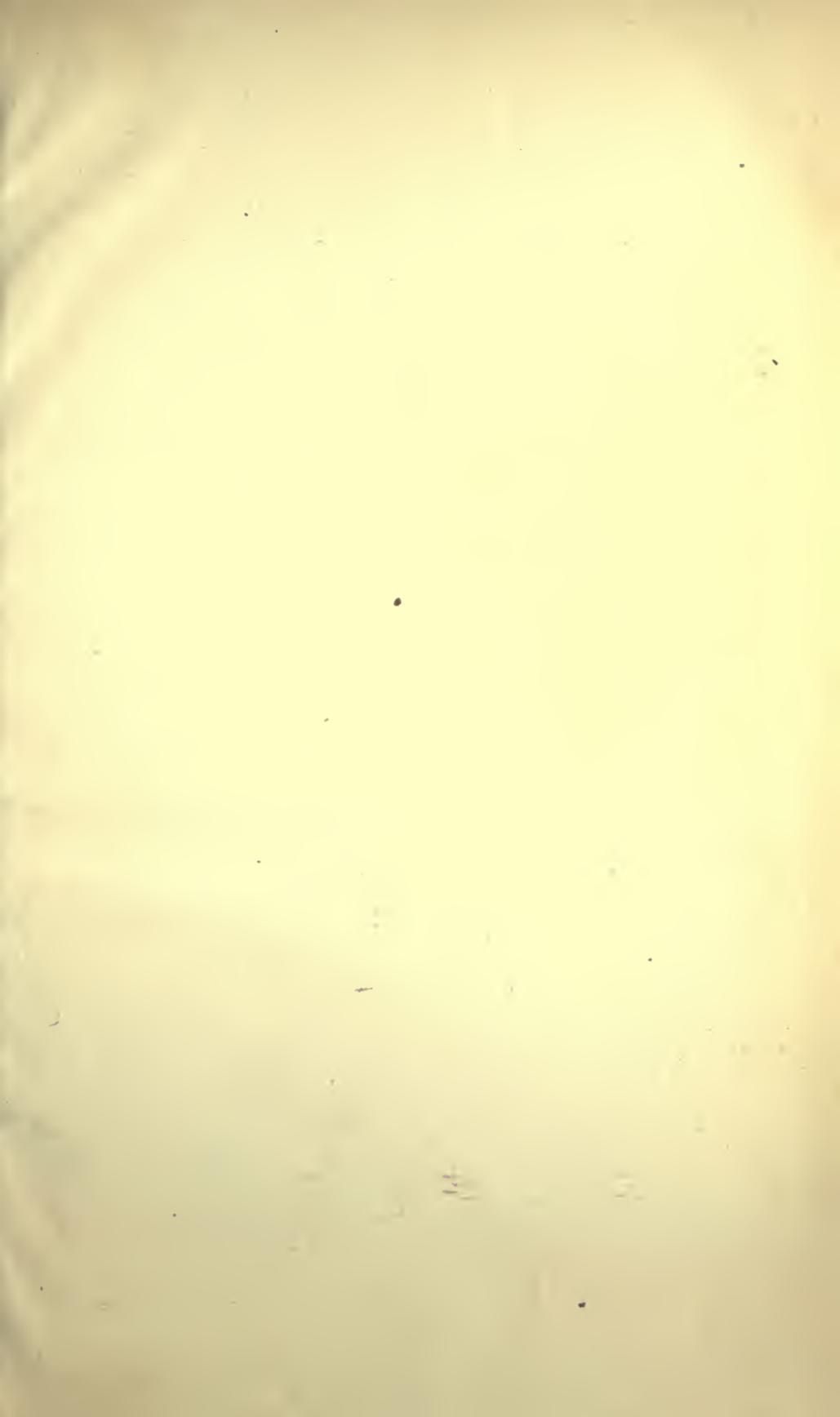
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LECTURES
ON THE
PHYSIOLOGY OF PLANTS

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Botany

LECTURES

ON THE

PHYSIOLOGY OF PLANTS

BY

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PREFACE.

THE absence of any text-book in the English language treating at all fully of the Physiology of Plants, so as to meet the requirements of advanced students, suggested to me, at an early stage in my career as a teacher of the subject, that I should publish my own lecture-notes just sufficiently expanded to make them readable. Of this suggestion, this volume is the outcome. The work of preparation began in 1877, but, on account of the pressure of other duties, it was not until 1882 that it had proceeded far enough to warrant going to press. I hoped at that time to have completed the Lectures within a twelvemonth at longest, but failing health and increasing demands upon my time have extended the period to four years. In consequence of this delay, it will be found that in the earlier Lectures the most recent researches have not been noticed. There will, I hope, be an opportunity to remedy this defect in a subsequent edition.

There is one point to which I would especially draw the attention of the reader, namely, to the use of the terms "dorsal" and "ventral" in speaking of the

positions taken up by dorsiventral organs. It is the general custom of those who have written on this subject to speak of the normally lower surface of the organ as the ventral, and of the upper as the dorsal. Morphologists, however, term the normally upper surface of dorsiventral leaves the ventral, and the lower the dorsal. I have adopted the former use of these terms with regard to leaves, so that in discussing the positions of these organs, I mean by dorsal the normally upper surface, and by ventral the normally lower surface.

I have to thank many friends for valuable hints and kindly criticisms, more especially Prof. Michael Foster, Sec. R.S., and Mr W. T. Thiselton Dyer, C.M.G., F.R.S., Director of the Royal Gardens, Kew, to both of whom I am much indebted.

CAMBRIDGE,

May, 1886.

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LECTURE I.

INTRODUCTORY.

IF a drop of the rain-water which has collected in a water-butt be examined under the microscope, a number of minute somewhat pear-shaped bodies of a green colour will be seen actively swimming in it. These bodies are what are termed the *zoospores* of a small Alga, *Hæmatococcus pluvialis*, better known as Protococcus. The rapidity of the movements of these bodies makes it difficult to observe their structure, but, if a trace of iodine be added to the drop of water, they will be brought to rest. It will then be seen that they are not all quite alike, some being smaller and others larger. The smaller ones consist of a minute mass of a jelly-like substance, granular and coloured green for the most part, but clear and colourless at the more pointed end where it is prolonged into two delicate filaments termed *cilia*: the larger ones have the same structure, but they possess in addition a membrane through which the cilia protrude (Fig. 1. *A.*). To this jelly-like substance the name of *protoplasm* has been given, and,

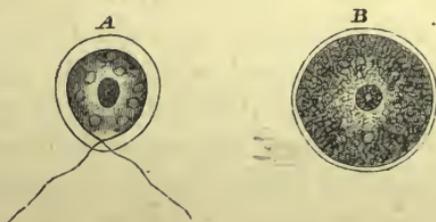


FIG. 1. *A*, Zoospore of *Hæmatococcus pluvialis*: *B*, Hæmatococcus cell.

on account of its universal presence in living organisms, it has been described as the *physical basis of life*. It usually occurs, as in these cases, in the form of minute individualised masses, each such mass being termed a *cell*. The membrane which surrounds the protoplasm of the larger zoospores is the *cell-wall*, and it may be shewn by appropriate tests that it consists of a substance known as *cellulose*: an investing membrane of this kind is present in the great majority of plant-cells, its presence is, in fact, the general rule, but it is not absolutely essential. The essential part of a living cell is its protoplasm, the cell-wall being a secondary formation, a product of the vital activity of the protoplasm. This relation between protoplasm and cell-wall can be well made out by observing the subsequent changes which these zoospores undergo. After moving actively for a time they come to rest, lose their cilia, acquire a spherical form, and the protoplasm surrounds itself with a firm cellulose membrane, each such non-motile cell constituting a Hæmatococcus plant (Fig. 1. B). After a time, if the external conditions are favourable, the protoplasm divides into a larger or smaller number of segments, the cell-wall is ruptured, and the segments of protoplasm are set free as actively moving ciliated cells (zoospores), destitute of a cell-wall, that is, as *primordial cells*. It is during their motile period that the larger zoospores clothe themselves with a cell-wall as described above.

In considering the life-history of Hæmatococcus we observe that it maintains itself, that it reproduces its kind, and that at one period of its life it is endowed with the power of active motion; phenomena which necessarily imply that the organism is constantly obtaining supplies of matter and of energy from without. The organism exhibits these phenomena, or rather it performs certain *functions* of which the phenomena are the outward and visible sign, in virtue of certain fundamental properties with which its protoplasm is endowed, properties which are possessed likewise, some in a higher some in a lower degree, by the protoplasm of all living plant-cells. It is necessary therefore, in commencing the study of the Physiology of Plants, the study, that is, of their

functions, to ascertain what are the fundamental properties of their protoplasm.

An acquaintance with the fundamental properties of protoplasm in virtue of which the processes of nutrition are effected may be perhaps most readily acquired by making a series of observations upon some small simple plant which can be obtained in quantity and of which the structure is known. The Yeast-plant (*Saccharomyces Cerevisiæ*) may be conveniently taken for this purpose. A drop of yeast placed under the microscope will be found to contain a great number of minute, more or less oval cells (Fig. 2, *a*), to the presence

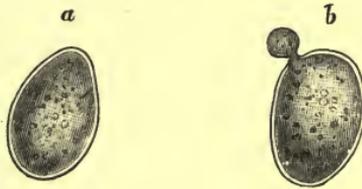


FIG. 2. *a*, A Yeast-cell: *b*, a Yeast-cell budding.

of which the turbidity of the liquid is due. In its structure a yeast-cell resembles a resting Hæmatococcus-cell, but the yeast-cell is much smaller and is uncoloured. If now a drop of yeast be added to a quantity of a liquid known as Pasteur's solution, which consists of distilled water holding a small percentage of certain inorganic salts and a larger percentage of certain organic substances in solution, it will be found that the Pasteur's solution, which is clear at first, becomes turbid, if allowed to stand for a few hours in a warm place. A drop of it examined under the microscope will be seen to contain a great number of yeast-cells, and it will also be seen that the cells are actively multiplying by the formation of small outgrowths (Fig. 2, *b*), which gradually enlarge until they attain nearly to the size of the parent-cell, when they become detached and constitute new individuals. It is evident that an enormous multiplication of the yeast-cells originally introduced into the Pasteur's solution has taken place, and this necessarily implies that a considerable quantity of protoplasm and of cell-wall has been formed. If, in a

second experiment, a drop of yeast be added to a quantity of pure distilled water, the liquid will not become turbid, that is, there will be no indication of any increase in the number of yeast-cells present; and not only so, but it will be found, after a time, that their protoplasmic contents have perceptibly diminished, so that an actual loss of substance has taken place.

The inferences to be drawn from the observations are (1) that the substances contained in the Pasteur's solution are of such a nature as to supply the yeast-cells with the materials necessary for the formation of protoplasm and of cell-wall, that is, to serve as *food* to the plant; (2) that the yeast-cell is capable of absorbing these substances and of elaborating from them protoplasm and cell-wall, and that it does so to such an extent as not only to provide for its own maintenance but also for the formation of new yeast-cells; and (3) that there are processes going on in the yeast-cell which tend to diminish its substance.

The protoplasm of the yeast-cell, and this is true of every living organism, is the seat of active chemical processes which are inseparably associated with the vital activity of the protoplasm. These collectively may be termed the *metabolism* of the organism. We may conveniently distinguish as *constructively metabolic* those processes which tend to form more and more complex compounds in the organism, and as *destructively metabolic* those processes which tend to break down the complex compounds with the formation of others of simpler composition. Some of the products of destructive metabolism are such that they cannot enter into the constructive metabolism of the organism; they are accordingly thrown off, and so, just as constructive metabolism is connected with the absorption of comparatively simple chemical compounds which constitute the food of the organism, destructive metabolism is connected with the elimination of comparatively simple chemical compounds which are the *excreta* of the organism.

The accumulation and dissipation of matter are not, however, the only results of the metabolic activity of the protoplasm of the yeast-cell. If a drop of yeast be dried and

the solid residue burned, a small but definite amount of heat will be evolved. But if a similar drop of yeast be added to a quantity of Pasteur's solution, and after having been left for some time, the turbid liquid be evaporated to dryness and the solid residue of yeast-cells burned, the amount of heat evolved will be considerable. In virtue of their constructive metabolic activity the cells contained in the drop of yeast added to the Pasteur's solution have formed a number of new cells, or, in other words, a considerable quantity of protoplasm and of cell-wall, and in the process of building up the complex chemical molecules of the substances which constitute protoplasm and of cellulose a considerable amount of energy has been accumulated. The heat given off when the dried yeast is burned is due simply to the conversion of this accumulated energy from the *potential* into the *kinetic* condition. The processes of destructive metabolism, on the other hand, involving as they do the breaking-up of complex chemical molecules into others of simpler composition, are accompanied by a conversion of potential into kinetic energy. That this is the case can be readily ascertained by comparing the temperature of a large quantity of Pasteur's solution in which the yeast is actively growing with that of the surrounding air; it will be found that the former is several degrees higher than the latter.

The results of the constructive metabolism of the yeast-cell are then an accumulation of organic matter and of energy, the results of its destructive metabolism are a diminution of organic matter and a dissipation of energy. Inasmuch as in the experiment before us we have found that a large quantity of yeast is formed from a small quantity, we learn that the constructive metabolism of the yeast-cell considerably exceeds its destructive metabolism, the weight of the dried yeast at the end of the experiment and the amount of heat given off when it is burned being the measure of the excess.

We are now in a position to make some definite statements as to the fundamental properties with which the protoplasm of the Yeast-plant is endowed :

1. it is *absorptive*, in that it is capable of taking up into itself the substances which constitute its food :

2. it is *metabolic*, in that it is capable of building up from the relatively simple chemical molecules of its food the complex chemical molecules of the organic substances present in the cell ; and in that it is capable of decomposing the complex molecules of these substances into others of simpler composition :

3. it is *excretory*, in that it gives off certain of the products of its destructive metabolism :

4. it is *reproductive*, in that portions of it can become separate from the remainder and lead an independent existence as distinct individuals.

These are, however, by no means all the fundamental properties with which the protoplasm of plants may be endowed. The observation of the zoospores of *Hæmatococcus* naturally suggests that their motility is due to some peculiar property possessed by their protoplasm, and this is in fact the case. When a zoospore is actively moving, its pointed hyaline end bearing the cilia is directed forwards, and at the same time the cell revolves round its long axis, so that it advances in a screw-like manner. The movement is entirely due to the cilia. So long as the organism is in motion, the cilia are vibrating so rapidly that it is difficult to see them. The lashing movement of the cilium is probably effected by the alternate rapid shortening of each longitudinal half. To this rapid shortening the term *contraction* has been applied, and the body exhibiting it is said to be *contractile*. Since the cilia are merely specialised portions of it, we may attribute to the protoplasm of these cells the fundamental property of *contractility*. It is obvious that the movements of the zoospores involve the performance of a certain amount of work ; the necessary energy is obtained from the destructive metabolism going on in the organism, which, as we have seen, is necessarily accompanied by a conversion of potential into kinetic energy.

Further, it appears that the movements of the cilia originate independently of any external conditions which might

act as exciting causes or *stimuli*: this being so, it must be concluded that the movements are the result of exciting causes existing within the organism itself, and therefore the protoplasm is to be regarded as being *automatic*, that is, as giving rise to the internal stimuli which cause the contraction of the cilia.

Although there is no reason to believe that stimuli acting from without *cause* the movement of the zoospores, yet there is evidence to shew that they may modify it. It has been found by various observers that the movement of the zoospores is affected by light: when exposed to light, the zoospores arrange themselves so that their long axes are parallel to the incident ray, and they move either towards or away from the source of light according to circumstances. It is evident, therefore, that the protoplasm is sensitive to the action of this stimulus, and it will be shewn hereafter that other external stimuli may also affect the protoplasm of the cells of plants. This sensitiveness to the action of external stimuli may be expressed in a general form by attributing to the protoplasm the fundamental property of *irritability*.

The protoplasm of the zoospore of *Hæmatococcus* is endowed, then, with the following fundamental properties, in addition to those which have been already enumerated with reference to the Yeast-plant:

5. it is *contractile*, as evidenced by the movements of the cilia:
6. it is *automatic*, in that the exciting cause or stimulus which produces the contraction originates in the organism itself:
7. it is *irritable*, inasmuch as the movements of the organism may be modified by the action of external stimuli.

These are, so far as can be ascertained, the fundamental properties with which the protoplasm of the cells of plants may be endowed, and in virtue of which it performs the functions which together make up its life. Of these properties, some, such as those of absorption, metabolism, and excretion, are found to be possessed by the protoplasm of all living cells, whereas the others do not appear to be so universally dis-

tributed. It occurs comparatively rarely that, as in the case of the zoospore of *Hæmatococcus*, all these properties are exhibited by the protoplasm of one cell.

Hæmatococcus and *Saccharomyces* are good examples of those lowly-organised plants in which the individual consists of a single cell; and yet, simple as is their structure, they present a distinction of parts, in other words, they exhibit *differentiation*. In the resting *Hæmatococcus* and in *Saccharomyces* we can distinguish between protoplasm and cell-wall, and in the *Hæmatococcus*-zoospore between the part of the protoplasm which is granular and coloured green and that which is hyaline and is produced into the cilia. It is possible, therefore, to imagine that still simpler forms might be met with, forms entirely undifferentiated, and this is in fact the case. In certain Fungi (*Myxomycetes*), for example, cells occur which consist merely of a minute mass of colourless and apparently homogeneous protoplasm. We are forced to conclude that in such an undifferentiated unicellular individual, all its functions are performed by all parts of its protoplasm alike, for there is no indication that any one part of it is especially charged with the performance of any one particular function. In a differentiated unicellular plant, however, there is an adaptation of certain parts of the protoplasm to the performance of certain functions; thus in *Hæmatococcus* and in *Saccharomyces* the peripheral layer of the protoplasm is especially concerned in the formation of the cell-wall, and in the zoospore of *Hæmatococcus* the cilia are the parts of the protoplasm which effect the movement of the organism. In the more highly organised unicellular plants, such as *Vaucheria* and its allies, the differentiation is carried still further: in those which are green, for instance, the colouring-matter is not distributed throughout the protoplasm but is associated with certain specialised parts of it, forming with them the *chlorophyll-carpuscles*; further, we find that in many cases the function of reproduction is performed by certain parts of the cell only. In ascending, then, from the lowest to the highest unicellular plants we find that whereas in the simplest forms all parts of the cell appear to be equally concerned in all the

functions of its life, in the higher forms there is a gradually increasing distinction of the functions and a localisation of them in certain parts of the cell, in other words, there are indications of *differentiation of function* and of *physiological division of labour*.

In highly organised unicellular plants we also find indications of a differentiation of another sort, of a differentiation of form or *morphological* differentiation. The simplest expression of this is the distinction of two regions in the body of the plant, both lying in the line marking the direction of most active growth, the *base* and the *apex*. In some forms this morphological differentiation goes so far as to indicate that marking-out of the plant-body into members, which, as we shall soon learn, finds its full expression in the higher plants: this is well seen in such forms as *Caulerpa* and *Bryopsis*.

In the majority of instances plants consist of a number of cells connected together. Some multicellular plants consist of cells which appear to be all exactly alike, and, although they are connected together, it seems that each cell, the protoplasm of which is usually highly differentiated, performs all the functions of its life independently of the others; this is the case, for example, in the *Confervaceæ* and *Ulvaceæ*. The functional or physiological differentiation of such multicellular plants cannot, therefore, be considered to be higher than that of a differentiated unicellular plant such as *Hæmatococcus*.

In most multicellular plants, however, it is readily seen that the constituent cells are by no means all alike, and further that each different kind of cell is connected with the performance of some particular function; thus, in such a plant, there are cells which are especially charged with the absorption of the food, others in which the constructive metabolism of the plant is especially performed, others again which are reproductive in function, and so on. Further, it is usually the case that cells of some one kind are characteristic of some particular part of the plant; that part is then said to be the *organ* for the performance of the function for which the cells in question are especially adapted, a term which is also applied to any part of the protoplasm of a differentiated

unicellular plant which has a particular function to discharge ; thus the cilia of the zoospore of *Hæmatococcus* are its motile organs.

In these plants, in which, as we have seen, the physiological division of labour finds its fullest expression, there is necessarily a mutual dependence between the various organs ; no one organ can discharge its function unless the others discharge theirs in an adequate manner. It is important therefore that there should be some means by which the organs, which are often widely separated, may be placed in direct communication with each other, and we find accordingly that certain cells are especially adapted for this purpose, such as the laticiferous cells and vessels which are present in many plants, and the cells constituting the fibro-vascular tissue, and it is further effected by the intercellular spaces.

We will now briefly consider the mode in which these different kinds of cells are developed. In these differentiated multicellular plants the formation of new cells is confined to certain definite regions, and at first the cells are very similar to each other. A group of cells in this stage corresponds to an undifferentiated multicellular plant, but important differences soon make themselves apparent. In the first place, it becomes evident that the growth of each of the constituent cells of the group does not proceed independently, but that it exhibits a certain correlation with that of the others ; such a group of cells we term a *tissue*. Secondly, the cells in their growth come to differ more or less widely from each other, the form assumed by each cell bearing a definite relation to the function which it is destined to perform in the economy of the plant. Of the various forms which the cells assume, those which resemble each other are connected together, so that several *tissue-systems* can be distinguished in the body of the plant. The plant is then said to exhibit *differentiation of tissues* or *histological differentiation*, and this is the expression of the adaptation in different directions which the originally similar cells have undergone for the due performance of the various functions of the plant.

It is in the multicellular plants also that the highest

degree of morphological differentiation is attained. In the simplest forms, such as the Confervaceæ and Ulvaceæ, the plant-body consists merely of a filament of cells in the one case and of a flattened expansion in the other. As we ascend we come first to forms, such as Oedogonium, in which, although the plant is a cellular filament, there is a distinction of base and apex; then to forms such as the Characeæ and many of the Florideæ in which the body consists of an axis bearing lateral appendages; finally to forms, such as the Ferns and the Flowering Plants, in which the body of the plant consists of parts which stand in definite and constant relation to each other; these parts are distinguished as stem, leaf, and root, and are termed the *members* of the plant.

Having now acquired some elementary general notions of the structure and physiology of plants, we may proceed to the detailed study of each of the functions. Before doing so, however, it will be well to become thoroughly acquainted with the structure of the living plant-cell such as we shall most frequently meet with, as well as with the properties of each of its constituent parts. This, therefore, will form the subject of the next lecture.

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LECTURE II.

THE STRUCTURE AND PROPERTIES OF THE PLANT-CELL.

FROM the preceding lecture we have learned that the cells of plants vary in their structure: the zoospores of *Hæmatococcus* afforded examples of naked or primordial cells consisting simply of protoplasm, and *Hæmatococcus* and *Saccharomyces* of cells possessing a cell-wall.

An examination of the tissues of a highly organised plant will shew that a third form of cell exists, cells, namely, which consist only of cell-wall. These cells are necessarily dead; they are merely the skeletons of cells which once contained protoplasm and were living. Still they are not useless; they give firmness and rigidity to the plant, and, as we shall see in detail hereafter, they are of importance in connexion with the conduction of water through the plant.

Since living cells are, in the vast majority of cases, provided with a cell-wall, our study of their structure and properties had better be made upon such as have this composition. For this purpose the cells of the cortical parenchymatous tissue of the stem of some succulent plant may be conveniently taken. When a section of this tissue is examined with the microscope it is seen (Fig. 3) that the cells are separated by cell-walls, that in each cell there is a layer of protoplasm which is in contact with the whole surface of the cell-wall; that either in this parietal layer or in a central mass of protoplasm which is connected by protoplasmic strands with the parietal layer there is a well-defined somewhat roundish

granular body, the *nucleus*; and finally, that the protoplasm and the nucleus do not completely occupy the whole cavity

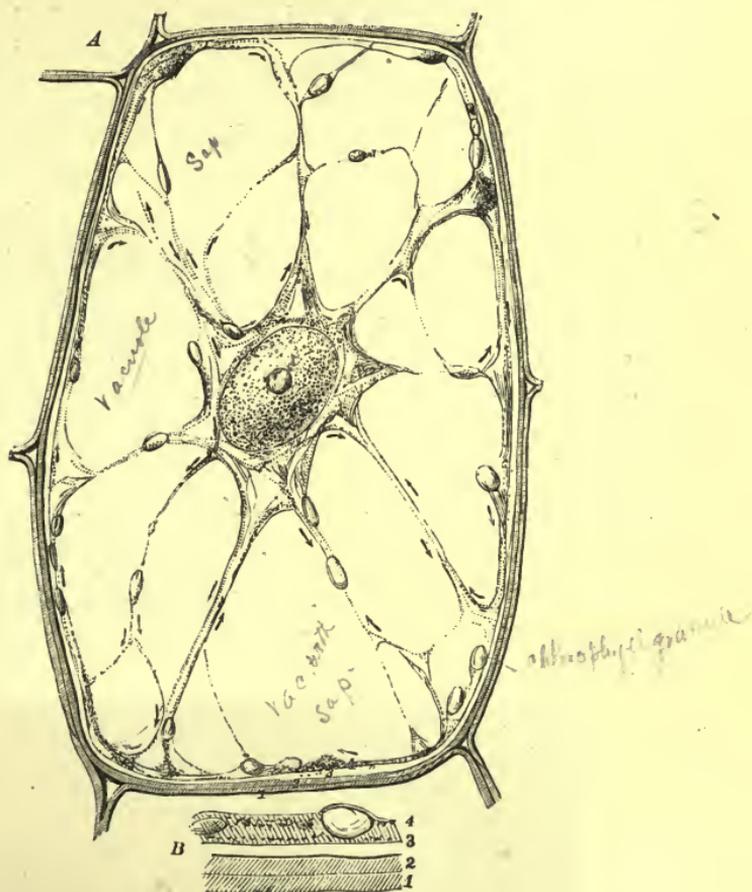


FIG. 3 (after Hanstein). *A*. A parenchymatous cell; at the exterior is the cell-wall (shaded); within this is the primordial utricle consisting of two layers, the ectoplasm (left clear) and the endoplasm which is granular and contains chlorophyll-corpuscles; the endoplasmic layer is connected by means of bridles which traverse the vacuole, with a central mass of endoplasm in which the nucleus, containing a nucleolus, is embedded. The arrows indicate the direction of currents in the protoplasm. *B*. A portion of the cell-wall and primordial utricle more highly magnified: 1, 2, the common cell-wall of two adjacent cells; 3, the hyaline ectoplasmic layer; 4, the granular endoplasmic layer, containing chlorophyll-corpuscles, of the primordial utricle.

of the cell, but that there is a large space, the *vacuole*, which is filled with watery fluid, the *cell-sap*. Let us now study each of these parts in detail.

The Cell-wall.

The wall of a parenchymatous cell such as that shewn in Fig. 3 will be seen to be a thin and apparently homogeneous membrane. If it be treated with solution of iodine it will assume a yellow colour, and if a drop of strong sulphuric acid be added the yellow will be replaced by a deep-blue colour. This reaction is characteristic of cellulose, and we may therefore conclude that the cell-wall consists, principally at least, of this substance which belongs to the group of the carbohydrates and to which the formula $x\text{C}_6\text{H}_{10}\text{O}_5$ has been assigned.

In the cell-wall, as in all organised structures—structures, that is, which have been formed by living organisms—a certain proportion of water is contained holding small quantities of various substances in solution. It has been found that the proportion of this water may be made to vary within certain limits without injury, but if these limits be overstepped disintegration of the cell-wall is the result. The variation in the amount of water present produces a corresponding variation in the volume of the cell-wall; hence the absorption of



FIG. 4 (after Dippel). Cell of *Equisetum* isolated and in transverse section, viewed with crossed Nicols.

water or *imbibition* by the cell-wall has come to be termed its "swelling-up."

The cell-wall possesses, further, well-defined optical properties. When examined with polarised light it is found to be doubly refractive, and, as von Mohl pointed out, its refraction is negative (Figs. 4 and 5).

FIG. 5.

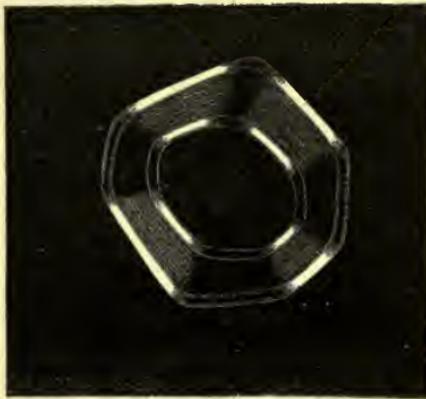


FIG. 6.



FIG. 5 (after Dippel). Transverse section of a tracheide of *Pinus sylvestris* viewed with crossed Nicols.

FIG. 6 (after Richter). Cystolith of *Ruellia picta* viewed with crossed Nicols.

Accepting for the present this brief statement of the chemical and physical properties of the cell-wall in its simplest form without explanation, we may pass on to consider firstly its formation, and secondly its growth and the chemical and physical changes which may accompany it.

With regard to the first formation of the cell-wall, it is usually considered that the cellulose is secreted by the protoplasm in the form of a membrane either over its whole surface, as in the case of isolated cells, or in the plane of division, as in the case of cells forming part of a tissue. Schmitz and Strasburger, however, are of opinion that the cell-wall is formed by the actual conversion of a layer of protoplasm into cellulose. Further details must be reserved until we have become acquainted with the structure of protoplasm.

The growth in surface of cell-walls is considered by Naegeli

to take place by the intercalation of new solid particles between those already in existence, a mode of growth which he has termed *growth by intussusception*. Strasburger is, however, of opinion that such an intercalation of new solid particles does not take place. He regards the subsequent increase in surface of the cell-wall to be either merely a phenomenon of imbibition, or to be due to stretching.

The growth in thickness of cell-walls, and, we may add, the increase in bulk of starch-grains, is brought about, according to Dippel, Schmitz, Strasburger, and others, by the repeated formation of laminae, of cellulose in the one case and of starch in the other, in the manner described above. These laminae are deposited, in the case of cell-walls, on the inside of those previously formed; in the case of starch-grains, on the exterior of the grain. This mode of growth is termed *growth by apposition*.

A thickened cell-wall always exhibits evident heterogeneity of structure. The wall of a bast-fibre, for instance, seen from the surface, presents a number of lines crossing it obliquely or even at right angles to its long axis; these con-

FIG. 7.

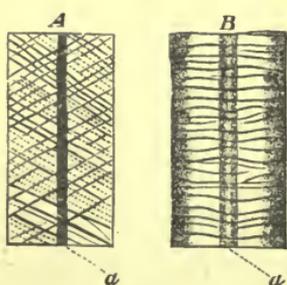


FIG. 8.

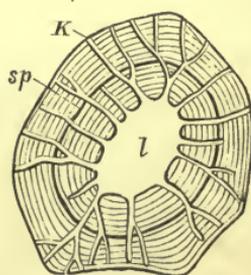


FIG. 7 (after Naegeli). Cell-wall seen from the surface, shewing striation :
A oblique, *B* transverse ; *a*, lumen of cell.

FIG. 8 (after Sachs). Transverse section of cell-wall, shewing stratification :
sp, split of the wall into two shells ; *K*, canals traversing its thickness ;
l, lumen of cell.

stitute what is known as the *striation* of the cell-wall (Fig. 7). Seen in transverse section the wall presents a number of concentric layers which constitute its *stratification* (Fig. 8). Naegeli

accounted for these appearances by ascribing them to an unequal distribution of water and of solid matter in the cell-wall, some parts containing a larger proportion of solid matter, others a larger proportion of water. On this view the striæ mentioned above are the expression of the alternation of more and less dense layers in planes inclined to its long axis, and the concentric layers of the alternation of more or less dense layers from within outwards. Dippel and Strasburger explain these appearances in altogether a different way. They have come to the conclusion that a cell-wall, or rather each of the concentric layers of a thickened cell-wall, consists of a number of spirally-wound bands, and that the striæ of the cell-wall are the planes of contact of these bands. With regard to the stratification, if the growth in thickness of the cell-wall by apposition be assumed, the concentric layers correspond to successive laminae.

It may be stated generally that the growth in thickness of cell-walls is accompanied by changes in their physical properties, or in their chemical composition, or in both. The formation of mucilage and of gum, for instance, depends upon an alteration of the cell-wall which increases its capacity for absorbing water, and this is so great in certain cases that the cell-wall becomes actually soluble: but this modification of its physical properties is not accompanied by any change in the ultimate chemical composition of cellulose, though doubtless by an alteration in its molecular constitution.

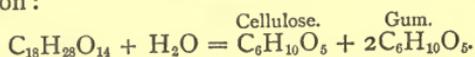
It must not be assumed, however, that a cell-wall always consists of cellulose at its first formation; it may consist from the beginning of a substance other than cellulose. This may be observed, for instance, in the extine of some pollen-grains, the exospore of spores, which give from the first the reactions of cuticle.

Mucilage is found in various parts of plants; in seeds, notably in those of the Quince and in Linseed; in the roots of the Marsh-Mallow; in the fruits, stems, and leaves of various plants. In seeds it is derived from the middle layers of the thickened walls of the epidermal cells. The various kinds of Gum are produced by the alteration of the whole wall of the parenchymatous cells which form the pith and medullary rays of certain plants, most of which belong to the Leguminosæ and Rosaceæ.

Frank considers that mucilage is not a definite chemical substance, but in some cases a form of cellulose, in others a form of gum; he is

also of opinion that gum is not necessarily a degradation-product, but that it may be a normal constituent of the cell-wall.

Kirchner has obtained from Quince seeds a substance which he believes to be pure mucilage. He regards it as a compound of gum and cellulose, and assigns to it the formula $C_{18}H_{28}O_{14}$. On boiling with dilute hydrochloric acid it decomposes into cellulose and gum according to the following equation :



The substance known as *Pectose* (Frémy), which is to be found in many parts of plants, more especially in unripe fruits and in bulbous roots, is allied to mucilage; it is probable that this substance is also derived from cellulose.

In most cases, however, the modification of the physical properties of the cell-wall is correlated with a considerable alteration in its ultimate chemical composition, inasmuch as it is due to the presence of substances, either organic or inorganic, which are chemically different from cellulose. The larger the proportion of these substances present, the more complete is the modification of the physical properties of the cell-wall; and conversely, inasmuch as a certain proportion of cellulose is always present in the chemically altered cell-wall, it always exhibits in some degree the physical properties which we have found to be characteristic of unaltered cell-walls.

The organic substances which occur in altered cell-walls are *suberin* and *lignin*, and cell-walls containing these substances are said to be *cuticularised* and *lignified* respectively. These substances have a larger proportion of carbon in the molecule than cellulose has. The cell-walls in which they are present in any considerable quantity do not give the blue colour when treated with iodine and sulphuric acid; their presence diminishes the capacity of the cell-wall for absorbing water, and, in the case of cuticularised cell-walls, their optical properties are modified.

It is not yet possible to account satisfactorily for the presence of these substances in cell-walls. They are probably the result of the modification of the cell-wall, and not of infiltration. It is not easy to connect their production with the metabolic activity of the protoplasm, for it has been observed that lignification takes place, in Conifers at least, after

the cells have lost their protoplasmic contents; but it must be borne in mind that their formation can only take place in a living plant.

The epidermal cells of leaves afford good examples of cuticularisation. If a section of a coriaceous leaf be treated with iodine and sulphuric acid, it will be found that the thickened external walls of the epidermal cells present a series of layers which have assumed a blue colour, the colour being most intense in the most internal layer, and becoming gradually less evident towards the free surface, the external layers shewing it scarcely at all. From this it appears that the proportion of suberin to cellulose gradually increases from the internal to the external layers. The cuticularised external layers of the walls of adjacent cells may be easily peeled off over considerable areas of the epidermis as a continuous membrane, interrupted only by the stomata; to this the name of *cuticle* is given. Cork also consists of cells the walls of which have undergone cuticularisation; but here the whole extent of the cell-wall is affected, and not merely a part of it as in the epidermal cells. In the case of cork cells which are in contact with other cells on all sides, the most external layer of the cell-wall is lignified to form the *middle lamella*. The effect of cuticularisation is to make the cell-walls more resistant both chemically and physically; thus the cuticle and the walls of old cork-cells are not affected by treatment with mineral acids, nor are they soluble in ammoniacal solution of cupric oxide; their double refraction is well marked, and, instead of being negative like that of unaltered cell-walls, it is positive; they are more elastic than ordinary cell-walls; their capacity for taking up water is very small, so small, in fact, that they may be regarded as almost impermeable to water. This impermeability to water doubtless depends to some extent upon the presence of wax or of resinous substances which prevent direct contact between the membrane and the fluid.

Frémy isolated the cuticle of various leaves; after he had removed foreign bodies as far as possible, a substance remained to which he gave the name of Cutin. Von Höhnel has recently found that the walls of

cork-cells contain a substance to which he gives the name of Suberin, and he points out that Cutin and Suberin are closely allied if not identical substances. This is shewn by their chemical composition and by their properties :

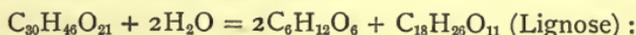
	Cutin (Frémy).	Suberin (von Höhnel).	Cellulose.
C.	73·66	74	44·44
H.	11·37	10	6·17
O.	14·97	16	49·38

both cuticle and cork give ceric acid (Doepping) (impure suberic acid, $C_8H_{14}O_4?$) when treated for a considerable time with nitric acid, or with nitric acid and potassic chlorate (Schultz's mixture); when heated with strong solution of caustic potash a soap is formed in both cases. It was thought, in accordance with de Bary's researches, that the presence of wax in or upon cuticularised epidermal cells was a feature which clearly distinguished *cuticularised* cells from *corky* cells, and a similar view was also held with regard to the presence of silica in the cell-wall: von Höhnel has, however, shewn that wax is present in the walls of the cork-cells in the Willow, and silica in those of a number of plants. There is, therefore, a considerable body of evidence in favour of von Höhnel's view as to the identity of cutin and suberin. It is of interest to note that suberin appears to be a substance intermediate between cellulose and vegetable wax.

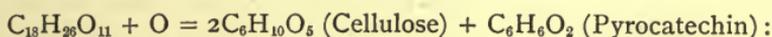
Cells with lignified walls occur very commonly in plants, not only in the wood, of which they are especially characteristic, but also in the bast (usually the bast-fibres) and in the ground-tissue (sclerenchyma). They can usually be readily distinguished in a section on account of the yellow or brown colour which is given to them by the lignin, but if the proportion of lignin is small, the cell-wall remains uncoloured. In this case the presence of lignin can be readily demonstrated by treating the section with a solution of anilin chloride acidified with hydrochloric acid; this reagent produces a bright golden-yellow colour in cell-walls which contain even a trace of lignin. As in cuticularised cells, so also in lignified cells the alteration of the cell-wall is most marked in its external layer, and least in its internal layer. The external layer of the cell-wall (forming the middle lamella) resists the action of strong sulphuric acid, but is dissolved by heating with Schultz's mixture, whereas the internal layer dissolves in the strong sulphuric acid but resists treatment with Schultz's

mixture; the intermediate layer is affected to some extent by both these reagents. The effect of lignification is to make the cell-wall harder and more elastic, and to diminish its capacity for absorbing water, without, however, rendering it impermeable: on the contrary, it is a characteristic property of a lignified cell-wall, as Sachs has shewn, that water readily traverses it. The importance of this property will become apparent hereafter when we are discussing the movement of water in plants.

Lignin cannot be regarded as a definite chemical compound: the name includes probably a number of different substances which are formed by the gradual alteration of cellulose in the process of lignification. Since treatment with solution of potash or with nitric acid does not disorganise the lignified cell-wall although it removes about one-tenth of its substance, there is reason to believe that the lignin substances are chemically combined with the cellulose. It has been suggested that cellulides are present, that is, compounds of cellulose with aromatic bodies: and since treatment of the cell-walls with hydrochloric acid or with chlorine sets free a substance which reduces cupric oxide, it seems probable that glucosides may be present also. Erdmann considers that he has obtained from pine-wood a definite substance to which he gives the name of Glycolignose. When boiled with dilute hydrochloric acid it is decomposed according to the equation



and when lignose is decomposed by long-continued boiling with dilute nitric acid the following change is effected:



thus glycolignose appears to be a glucoside, and lignose a cellulide.

The inorganic, or rather the mineral substances which are found deposited in cell-walls are principally silica and salts of calcium; iron, manganese, aluminium have also been detected. Cell-walls which contain these substances, leave, after combustion, a considerable ash; in some cases the ash forms a complete skeleton of the tissue.

Silica especially occurs in the cuticularised walls of epidermal cells, but, as we have already seen, it is not confined to them. The amount present is often very large; thus Struve found that it constitutes 99 per cent. of the dry epidermis of *Calamus Rotang*.

The exact form in which silicon is present in cell-walls is not yet ascertained; that is, whether it is present as particles of silica deposited between those of the organic substance, or whether it enters into the chemical composition of the organic substance, forming possibly a silicon cellulose. The silica may be removed from the cell-wall by treatment with hydrofluoric acid, without disorganising it.

The salts of calcium which are found in cell-walls are the oxalate and the carbonate. Calcium oxalate occurs either in the form of minute granules or as distinct crystals, in various parts of a great number of plants; for instance, in the walls of the epidermal cells of many Conifers and of species of *Sempervivum* and *Mesembryanthemum*, in the bast-fibres of many *Taxineæ* and *Cupressineæ*, in the cortex of many Gymnosperms and species of *Acer*, *Fagus*, *Salix*, and in all parts of *Welwitschia* and other *Gnetaceæ* (Solms-Laubach). Calcium carbonate is frequently present in the walls of hairs, but it is more especially deposited in the ingrowths of the cell-wall, known as *cystoliths*, which are found in the epidermal cells of the *Urticaceæ* and in almost all the tissues of the *Acanthaceæ*; it occurs either as granules or as small crystals.

It is still an open question whether calcium carbonate in *cystoliths* exists in an amorphous or a crystalline form. Weiss, and more recently Richter (see Fig. 6), have found that *cystoliths* are doubly refractive, and they conclude that the calcium carbonate is present in the crystalline form; but this observation has not been confirmed by other observers, such as Sachs and Melnikoff.

Calcium carbonate is often found as an incrustation on the surface of plants. In some cases it is evident that the incrustation has been formed by the evaporation of water, holding the salt in solution, which had been excreted by the plant: in the cases of submerged plants, it is possible that the calcium carbonate may be deposited on the surface in consequence of the absorption of carbonic acid from the water by the plant.

We have assumed, so far, that the cell-wall is a closed membrane, which shuts off the contents of one cell from those of adjoining cells; but this is by no means always the case. The *sieve-tubes*, for instance, consist of cells placed end to end, the transverse walls of which are perforated so that a

continuity of the protoplasm of the cells of the row can be readily observed; in the case of the vessels of the wood and of the laticiferous vessels, the separating walls have been entirely absorbed, so that these structures are spoken of as *cell-fusions*. Even in parenchymatous cells a communication of the protoplasm of adjoining cells has been observed; by Tangl, for instance, in the endosperm of certain seeds, by Gardiner, in the contractile organ at the base of the petiole of *Mimosa*, and by Frommann in epidermal cells. It is probable that this is the case far more commonly than is usually supposed, for the walls of most parenchymatous cells, when treated with appropriate reagents (potash or Schultz's solution), shew what are apparently thinner areas (pits) through which the protoplasmic filaments might be supposed to pass.

The Protoplasm.

The protoplasm of the cell under consideration (Fig. 3) forms, as has already been pointed out, a layer, formerly termed the *primordial utricle*, which closely lines the cell-wall, and which is connected by means of bridles with a mass towards the middle of the cell in which the nucleus is imbedded. Careful examination of the peripheral layer shews that it consists of two layers, an outer hyaline and firm, in close contact with the cell-wall, an inner granular and somewhat fluid; the former may be distinguished as the *ectoplasm* (*hautschicht*), the latter as the *endoplasm*. The granular appearance of the endoplasm is due to the presence of minute solid particles of organic and inorganic substances, drops of oil, etc., which may be distinguished from the protoplasm itself as *metaplasm* (Hanstein), and also to the presence of minute corpuscles, termed *microsomata*, which are probably to be regarded as part of the protoplasm. Very commonly the endoplasm is bounded towards the vacuole by a hyaline firm layer resembling the ectoplasm which bounds it towards the cell-wall.

This distinction of layers is all that can be made out as to the structure of the protoplasm when the cell is examined

under ordinary circumstances. Frommann, Schmitz, Strasburger and others have succeeded, however, by carefully hardening the tissue and staining the sections, in detecting a more intimate structure. In a young parenchymatous cell, for instance, which is entirely filled with protoplasm, the endoplasm, after hardening and staining, presents a deeply-stained fibrillar network, the meshes being occupied by an unstained more fluid substance; the ectoplasm presents, not a reticulate but a finely punctated appearance. As the cell increases in size, lacunæ are formed in the endoplasm which coalesce to form the vacuole, and the protoplasm (Fig. 3) constitutes the primordial utricle and the bridles, as mentioned above. The reticulate structure has, at this stage, almost entirely disappeared, but it may sometimes be observed in the endoplasmic layer of the primordial utricle; the more delicate bridles appear to be quite homogeneous, whereas the stouter ones present a finely punctated appearance.

The general conception of the structure of protoplasm which these observations enable us to form is this; that it consists of a reticulum of fibrillæ, enclosing a more fluid substance in its meshes, and that its consistency varies with the size of the meshes, that is, with the proportion of solid and fluid substance of which it is made up. It is probable that all actively living protoplasm possesses this structure.

With regard to its physical properties, protoplasm, like other organised bodies, is capable of swelling-up, but it has no effect upon polarised light.

Chemically considered, protoplasm, apart from the metaphasm and from the substances which are held in solution in the water which saturates it, consists of a mixture of substances which are known as *proteids*. If a cell which contains abundant protoplasm be treated with a dilute solution of potash, it will be found that a considerable quantity of the protoplasm has been dissolved, leaving a firm framework or reticulum behind, which is dissolved on boiling in strong potash. We may thus distinguish two groups of proteids in the protoplasm, namely, those which are and those which are not soluble in dilute potash. To the second of these two groups

belongs the substance (or mixture of substances) to which Reinke has given the name of *plastin*; to the first belong the proteids termed *globulins* (Hoppe-Seyler), which are also soluble in solutions of common salt, and the *peptones*, which are also soluble in water and are not precipitated from their solution on boiling. These proteids all consist of Carbon, Hydrogen, Nitrogen, Oxygen, and Sulphur, and, according to Reinke, plastin contains Phosphorus in addition.

Reinke studied the composition and properties of plastin obtained from the plasmodium of *Æthaliium*, a myxomycetous Fungus. The probable presence of phosphorus in its molecule is of interest, in that it suggests a relation between the plastin of the protoplasm and the nucleïn (see *infra*) of the nucleus. Globulins have been obtained by Hoppe-Seyler from buds and young shoots of plants, and they are especially abundant in seeds. Peptones have not been found in quantity in any parts excepting seeds, in which they are always present and are usually abundant.

This chemical analysis of the protoplasm in the cell throws some light also upon the physiological relation of the various proteids to each other. We find that whereas in a young growing cell the quantity of proteids present is considerable, it gradually diminishes as the cell grows older, until, when the cell has ceased to grow, the protoplasm consists of little more than the plastin-framework. The cell shewn in fig. 3 has reached this stage. It appears probable, therefore, that the plastin-framework is the actual living protoplasm, the *organised proteid* of the cell, whereas the globulins (and peptones, if present) are dead or *unorganised* proteid, the *enchylema* of Hanstein. Reinke found in his researches on *Æthaliium* that the unorganised proteid could be extracted from the plasmodium by simply squeezing it. A mechanical analysis of this kind takes place in the ripening of seeds. In a cell of a ripe seed it is found that the globulins and peptones are deposited in the form of granules (aleurone-grains) in the meshes of the plastin-framework.

In addition to the protoplasm, as described above, the cells of the higher plants commonly contain differentiated protoplasmic bodies, which may contain a colouring matter

(chlorophyll or etiolin) or may be colourless; the former are termed *chlorophyll-* (or *etiolin-*) *corpuscles*, the latter *starch-forming-corpuscles* or *amyloplasts*. Their structure and general chemical composition are probably the same as those of the protoplasm.

A few words may be added here with reference to the microsomata. These are minute particles of an irregularly rounded or somewhat elongated form; they stain readily, and are evidently of a protoplasmic nature. As already mentioned, they occur especially in the endoplasm, but they are to be found occasionally in the ectoplasm. Schmitz has observed that in protoplasm, which presents a distinct fibrillar reticulum, the microsomata appear to be attached to the fibrillæ: he compares them to the chromatin-granules of the nucleus (see *infra*). They play an important part in connexion with the formation of the cell-wall. When a mass of protoplasm is about to surround itself with a cell-wall, the ectoplasm becomes filled with microsomata, and similarly in cell-division the cell-plate, from which the wall is formed, is made up of microsomata. The microsomata coalesce laterally and become altered into cellulose. This is clearly shewn in the case of cell-walls which present oblique striation. Strasburger observed in the finely striated cells of *Pinus sylvestris* that the microsomata are arranged in spiral rows, corresponding to the planes of striation seen in the cell-wall, and it appears that, in the formation of a layer of the cell-wall, the microsomata of each row coalesce to form a spiral band of cellulose; in more coarsely striated cell-walls, several adjacent rows of microsomata coalesce laterally to form a single spiral band.

The Nucleus.

The nucleus (Fig. 3) is a body of a somewhat oval form which can be readily distinguished, on account of its being more highly refractive, from the protoplasm by which it is surrounded. Its outline is definitely marked owing to its structure being more firm towards the periphery. In the interior of the nucleus there is a distinct rounded body the *nucleolus*; it frequently happens that two or more nucleoli are present. Besides this, the ground-substance of the nucleus usually contains a number of granules, but in some cases it can be made out that it is traversed in all directions by trabecular fibres, which form a reticular frame-work within it, the meshes of which are larger towards the centre and smaller towards the periphery.

Flemming considers that isolated granules are never to be found in nuclei: he regards the apparent granules as being the transverse sections of the trabecular fibres. Strasburger is of opinion that the reticulum is in reality a single convoluted fibre, consisting of protoplasm (nucleoplasma) in which microsomata are imbedded; the nucleoli are large microsomata.

Chemically considered the nucleus appears to consist, principally at least, of a substance termed *nucleïn*, which is allied to the proteids, but differing from them in that it contains phosphorus but no sulphur. Miescher ascribes to it the formula $C_{229}H_{499}N_9P_3O_{222}$.

Flemming finds that there is a substance present in the nucleolus and in the frame-work which stains readily when treated with various colouring-matters (hæmatoxylin, safranin, nigrosin); to this he gives the name of *chromatin*, the substance which does not stain being termed *achromatin*. These substances, or at any rate chromatin, may be bodies of definite chemical constitution.

According to Zacharias, the more solid parts of the nucleus consist of plastin and of nucleïn; the nucleïn he considers to be the chromatin of Flemming.

The fact that a nucleus has now been found in almost all living cells seems to shew that the presence of such a body is of importance to the life of the cell, but it is not yet possible to ascribe to it any definite function. It is the general rule that, in the process of cell-division, the division of the nucleus precedes that of the protoplasm, and this, together with the fact that the granules in the protoplasm may frequently be seen to be arranged in lines radiating from the nucleus, would seem to indicate that the nucleus, is the centre of the molecular forces of the cell. Strasburger and Schmitz have however come to the conclusion that the protoplasm is the active agent in cell-division, and that the division of the nucleus is induced by that of the protoplasm. It has been suggested that the nucleus is of importance in connexion with the nutrition of the cell, a view which is supported by the fact that when cells attain a very great size (*e.g.* Vaucheria-filaments, hyphæ of Fungi, laticiferous cells) they become multinucleate. Strasburger is of opinion that it is especially connected with the formation of proteid-matter in the cell (see Lecture IX.).

The Vacuole and the Cell-Sap.

In a very young cell the protoplasm and the nucleus fill the whole cavity so that no vacuole is apparent. At an early period lacunæ containing watery fluid make their appearance in the protoplasm; then, inasmuch as the growth of the protoplasm does not keep pace with that of the cell-wall and inasmuch as the peripheral portion of the protoplasm always remains in direct contact with the cell-wall, these lacunæ become larger and fuse so as to form one continuous vacuole which is traversed here and there by bands of protoplasm which connect the peripheral layer (primordial utricle) with a more or less centrally placed mass. It occurs, not uncommonly, that ultimately the whole of the protoplasm is required to form the primordial utricle, and in such a case the nucleus is parietal.

The cell-sap, the watery fluid which saturates the protoplasm and the cell-wall and occupies the vacuole, consists of water holding in solution a number of both organic and inorganic substances, which have either been formed and thrown off by the protoplasm, or have yet to be absorbed and elaborated by it. The principal organic substances are the following; a substance which reduces alkaline cupric solutions, to which the general term "sugar" may be applied; organic acids, either free or in the form of acid salts, for the cell-sap reddens litmus-paper: colouring matters, in the cell-sap of many cells: crystallisable nitrogenous bodies, such as asparagin, leucin, tyrosin, especially in organs in which metabolism is active. The inorganic substances are probably salts of potassium and sodium, chiefly nitrates, chlorides and sulphates.

The principal forms of sugar and its allied bodies (carbohydrates) which occur in the cell-sap are: *cane-sugar* (sucrose or saccharose), $C_{12}H_{22}O_{11}$, which reduces the alkaline cupric solution only after prolonged boiling: *mannite* ($C_6H_{14}O_6$) and *inulin* ($C_6H_{10}O_6$) which do not reduce the alkaline cupric solution; inulin is deposited on treating the tissues with alcohol, in the form of sphaerocrystals: *glycogen* ($C_6H_{10}O_6$), which forms an opalescent aqueous solution, and does not reduce the cupric solution on boiling: *glucose* ($C_6H_{12}O_6$), which readily reduces the alkaline cupric

solution on boiling; of this there are two varieties, *dextrose* or grape-sugar, which rotates the plane of polarisation to the right, and *levulose*, which rotates it to the left.

Of the colouring-matters of plants some, such as the green (chlorophyll) and the yellow, are deposited in corpuscles of a protoplasmic nature, whereas the others, especially the red and blue, are dissolved in the cell-sap. It is to the presence of colouring-matters in solution in the cell-sap that the colours of petals etc. are principally due.

It has been found that the organic acid which is most commonly present in solution in the cell-sap is malic acid: tartaric and citric acids frequently occur.

Solid bodies are also commonly present in the vacuole; for instance, starch-grains, aleurone-grains (in seeds), and crystals of calcium carbonate or oxalate. Calcium oxalate frequently occurs in the form of a bundle of acicular crystals which have been termed *raphides*.

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LECTURE III.

THE STRUCTURE AND PROPERTIES OF THE PLANT-CELL (continued).

I. *The Molecular Structure of Organised Bodies.*

WE learned, in the preceding lecture, that cell-wall, protoplasm and nucleus all present indications of structure; the cell-wall in its stratification and striation, the protoplasm and the nucleus in their fibrillar network. But they possess beyond this a molecular structure which cannot indeed be detected with the microscope, but which can be inferred from their properties. As a conception of this molecular structure is of some importance in assisting us rightly to comprehend many of the phenomena which we shall meet with in the study of living plants, we will enter upon a somewhat detailed consideration of it.

In speaking of the properties of organised bodies the first and most conspicuous was their capacity of absorbing water, their power of "swelling-up" or imbibition as we termed it. When this was first observed it was thought to be peculiar to organised bodies, to bodies, that is, which had been formed by a living organism. It has been subsequently discovered, however, that bodies which had not been formed by a living organism possessed this property, such, for instance, as the acrylcolloid of Wagner and Tollens, and membranes of precipitation of cupric ferrocyanide, of ferric hydrate, etc. In order to include these bodies the meaning of the term

“organised” was extended, so as to include all bodies capable of swelling-up.

Now as to the explanation of this phenomenon. According to Naegeli it is the expression of the taking up of a number of particles of water between the solid particles (termed by him *micellæ*) of the organised body. That the absorption of water is not effected by capillarity is inferred from the fact that organised bodies are not porous. A perfectly dry cell-wall, for example, is transparent, and this could not be the case if any capillary interspaces existed between its micellæ, for, in the dry state of the wall, such interspaces would necessarily be filled with air, and the wall would therefore be opaque. In a dry cell-wall, then, the micellæ are in contact on all sides. When it takes up water, the water does not enter into already existing spaces between the micellæ, for there are none; it must therefore penetrate between the micellæ, forcing them apart against the opposing force of cohesion which tends to hold them together.

These micellæ of Naegeli's must by no means be confounded with chemical molecules; they are aggregates of larger or smaller numbers of chemical molecules. It must also be pointed out that in a case of ordinary swelling-up, the water does not penetrate into the micellæ: when this takes place the result is, as we shall find hereafter, that the micellar structure is disintegrated.

Upon these facts Naegeli founded a general theory of the structure of organised bodies. He conceives them as consisting of solid micellæ, each of which is, under ordinary circumstances, surrounded by a layer of water, the micellæ with their watery envelopes being held together by the following forces: (*a*) the attraction of the micellæ for each other, a force which varies inversely as the square of the distance between them; (*b*) the attraction of each micella for the water which surrounds it, a force which varies inversely as some higher power of the distance; and (*c*) the force which holds together the ultimate chemical molecules of which each micella consists.

From the fact that the swelling-up of organised bodies

does not take place equally in all three dimensions of space and from their double refraction Naegeli inferred the form of the micellæ. The unequal swelling-up, he considered, indicated that the micellæ were anisometric, the direction of least expansion corresponding to the direction of the longest axis of the micellæ, for it is in this direction that their attraction for each other would be greatest and for water least. As to the double refraction, he found that when the bodies exhibiting it (starch-grains, cell-walls, crystalloids), were subjected to strain or torsion, or were made to swell-up, they did not lose it. He argued that, since the optical properties of these organised structures are apparently not dependent, like those of a crystal or of a piece of glass, upon the relative position of their constituent particles, they must be inherent in the particles themselves. Each micella, then, possesses the optical properties of an anisotropic crystal. Naegeli concluded, therefore, that the micellæ are crystals, and from the interference colours observed with the polariscope, he inferred that they must be biaxial crystals, and assigned to them, as a probable form, that of parallelipedal prisms with rectangular or rhomboid bases.

Such is, very briefly, the "micellar theory" of the structure of organised bodies developed by Naegeli from his observations on cell-walls, starch-grains, and on the proteid crystalloids which are found more especially in seeds. He was unable, however, to apply it in its entirety to protoplasm, for the optical properties of protoplasm are not such as to indicate that its micellæ are crystalline.

Strasburger has given an altogether different account of the various phenomena described above. In the first place he rejects the idea of the aggregation of the chemical molecules into micellæ. He is of opinion that the force which binds together the molecules is of a chemical as opposed to a physical nature, that they are held together not by cohesion but by chemical affinity: he regards them as being linked together, probably by means of multivalent atoms, into molecular networks, the water present being retained in the meshes by intermolecular capillarity.

Let us now see how imbibition can be explained from this point of view. Strasburger points out that there is reason to believe that the feeble diffusibility of all colloids is due to the connexion of their molecules in the manner described above. Some colloids, such as the acrylcolloid mentioned above, gum, gelatine and others, are capable, whereas others, such as gelatinous silicic acid, are incapable of swelling up. The conclusion from this is that the molecular network is in some cases extensible, in others inextensible, that is, that the molecules may or may not be mobile about their position of equilibrium. Inasmuch as the proportion of water in a colloidal substance depends upon the size of the intermolecular meshes, swelling-up, that is, the absorption of water, must be due to the increase in size of the meshes of an extensible molecular network. The limit of swelling-up is reached when the capillary attraction is equal to the chemical affinity; when the former exceeds the latter the molecules become dissociated and the organised structure is destroyed.

But certain facts yet remain to be explained. How are we to account, from this point of view, for the fact that different parts of an organised body contain different proportions of water, and for the fact that the swelling-up of such a body is unequal in different directions? With regard to the first of these, Strasburger points out that the amount of water which a colloid which does not swell up, such as silicic acid, can absorb, is just that which it contained at its first formation; in other words, that the size of the meshes of the molecular reticulum is determined by the amount of water present in them when the reticulum is formed. Thus the unequal distribution of water in an organised body may be ascribed to the unequal size of the intermolecular meshes in different parts. This affords also some explanation of the unequal swelling-up of organised bodies, but not a complete one. The important feature in the swelling-up of organised bodies to which Strasburger draws attention, a feature which distinguishes these bodies which have been formed by living protoplasm from the unorganised colloids which are capable of swelling, is that it bears a definite relation to their anatomical structure. This relation is that

the direction of greatest swelling is at right angles to the indications of structure: thus, in a starch-grain or in a cell-wall, the direction of greatest swelling is at right angles to the layers of stratification.

Before leaving this part of the subject it will be well to say a few words concerning the proteid crystalloids which have been already mentioned more than once. These are true crystals which differ from other crystals only in that they are capable of swelling-up. They are usually considered to be organised bodies, but it appears from the researches of Van Tieghem on the Mucorini that they are not formed by the organising activity of living protoplasm, but by simple crystallisation, and Schimper has shewn that their swelling-up is regulated by the same laws which govern the expansion of other crystals when heated.

We will now turn to Strasburger's explanation of the optical properties of organised bodies. He points out that, on the micellar theory, organised structures such as cell-walls and starch-grains should not lose their optical properties when their organisation is destroyed, for the particles of the disintegrated micellæ would, like particles of broken crystals, still retain their double refraction, and they would therefore also continue to exert a depolarising effect. But this is not the case. Organised structures cease to be doubly refractive at the moment when their organisation is destroyed. Naegeli himself states that when starch-grains and cell-walls are made to swell excessively by treatment with acids or alkalis, or by heating, they soon completely lose their double refraction.

It appears, then, that the optical properties of organised structures are dependent upon their organisation. They may be chemically altered by treatment with reagents, their form may be changed by physical forces, but their optical properties remain, provided that their organisation is not affected. Strasburger's account of the nature of this organisation is to the following effect. Cell-walls and starch-grains consist of successive lamellæ which are in different states of tension and are firmly adherent; and just as a piece of glass becomes doubly refractive when differences of tension are set up within

it, so the double refraction of a cell-wall or of a starch-grain is due to the differences of tension in the lamellæ of which it is composed. If from any cause the differences are increased or diminished, the double refraction will correspondingly vary; thus the double refraction of a thick cell-wall is more marked than that of a thin one, and that of one which contains a small proportion of water than that of one which contains a larger proportion.

Strasburger's view is borne out in a striking manner by the fact, first observed by von Mohl, that the interference colours presented by starch-grains when examined with a polarising microscope are precisely complementary to those presented by unaltered cell-walls; where the one is coloured yellow, for instance, the other is coloured blue, and *vice versa*. The position of the colours in starch-grains corresponds to that in a piece of glass which is under traction, the position of the colours in the cell-wall to that in a piece of glass which is under compression. The former arrangement of the colours is said to be *positive*, the latter *negative*. Strasburger has shewn that a starch-grain tends to increase in size, whereas a cell-wall tends to contract: the tension of the one is of the nature of traction, of the other compression. The inference is that the different position of the interference colours is due, as is the case with glass, to the difference of tension. The correctness of this inference is confirmed by Strasburger's observation that when a cell-wall is becoming cuticularised its optical properties become reversed. Von Mohl had observed that cuticularised cell-walls are, like starch-grains, optically positive, but Strasburger was, I believe, the first to trace the gradual change in the optical properties of the cell-wall which accompanies its cuticularisation. This change is due, according to Strasburger, to the fact that the lamellæ which are undergoing cuticularisation increase somewhat in volume, and consequently the tensions existing in the unaltered cell-wall, and with them its optical properties, become reversed.

In discussing the molecular structure of organised bodies we have confined our attention almost entirely to cell-walls and starch-grains; in concluding the subject we may briefly

consider protoplasm. Of all organised bodies protoplasm is the one which most nearly approaches a fluid, as is shewn by the fact that it tends to assume a spherical form when in a state of equilibrium. But it is, nevertheless, not a fluid; it is a semi-fluid. We may define such a body, as Pfaundler has done, by saying that it consists of an intermixture of groups of solid and of fluid molecules. Assuming Strasburger's theory of the molecular structure of organised bodies, we must regard the molecular structure of protoplasm as capable of undergoing constant modification, the grouping of the molecules being in a state of perpetual change, the result of this molecular activity being the phenomena which we term vital, and which distinguish protoplasm, as living, from all other organised bodies.

II. *The swelling-up of Organised Bodies (Imbibition).*

We have already become familiar with this phenomenon, and we have discussed in detail the explanations of it which have been offered. We will now briefly consider its broader features which are independent of any theory as to the actual mode in which it is effected.

The force with which water is thus absorbed is very considerable; it is not only sufficiently great to overcome the elastic resistance which is offered by the molecules of the body itself, but it can overcome a great external pressure in addition. This is well shewn by an experiment of Hales. He filled an iron pot nearly full with peas and water, and placed on the peas a leaden cover bearing a weight of 184 lbs.; as the peas began to swell, they raised the cover and the weight.

The absorption of water by an organised body has been found to be accompanied by an evolution of heat. This fact appears to have been first definitely stated by Pouillet, but it has since been observed by many investigators. Naegeli found, for instance, that when 40 grms. of perfectly dry wheat-starch were mixed with an equal weight of water, the temperature rose from 22° C. to 32.5° C. This evolution of heat indicates that the absorption of water is accompanied by con-

densation, and this has been found to be the case. Reinke ascertained that the thallus of *Laminaria* absorbed 230 per cent. by weight of water, and that the water underwent a condensation of 0·2 per cent.

The maximum amount of water which a cell-wall may absorb varies with the constitution of the membrane and with various external conditions. Naegeli found that the gelatinous cell-walls of Nostocaceæ and Palmellaceæ may contain as much as 200 parts of water to 1 of solid substance; on the other hand Sachs has estimated the amount of water which 100 c. cm. (156 gm.) of dry wood of *Pinus sylvestris* may take up to be about 50 c. cm. Temperature has an important influence; the amount of water absorbed in a given time is greater at a higher than at a lower temperature. Further, the presence of a substance in solution in the water may affect absorption. Thus Reinke found that peas placed in distilled water for three hours increased 43·2 per cent. in volume, whereas when placed in a mixture of 100 parts of water and 30 of alcohol the gain was only 22·5 per cent.: in another experiment some peas placed for 2½ hours in water increased 54·5 per cent. in volume, and others in a solution of 20 parts of calcium chloride in 100 of water increased only 19·1 per cent. On the other hand it is well known that the presence of acids or alkalis in the water increases the swelling-up of organised bodies. If, however, the acid or the alkali be present in large proportion so that the solution is tolerably concentrated (and this is also true in many cases of the action of water at a high temperature), the swelling-up becomes excessive, and the body cannot be restored, as it can under ordinary circumstances, to its normal size by washing out the acid or the alkali. Evidently some permanent alteration in its constitution has been effected, for if it be dried, and be then placed in water, it will not again swell up. It has lost the power of absorbing water as well as any special optical properties which it may have possessed. Its organised structure has been destroyed.

We may note here two facts which will be found useful hereafter in discussing the movement of water in plants.

Reinke has ascertained, firstly, that the amount of evaporation from an organised structure depends upon the degree of its saturation ; it is greatest when the body is fully saturated : secondly, that the pressure which is necessary to force water out of an organised body is at its minimum when the body is at its maximum degree of saturation or imbibition.

III. *The Osmotic Properties of the Cell.*

It has been already pointed out in the case of Yeast, that the cell is capable of absorbing water containing various substances in solution, and, now that we have learned something as to the structure of the cell, we are in a position to study this process in detail. If a section of a succulent stem, mounted in distilled water, be examined under the microscope, it will be seen that the parenchymatous cells are fully expanded, that they evidently contain as much water as they

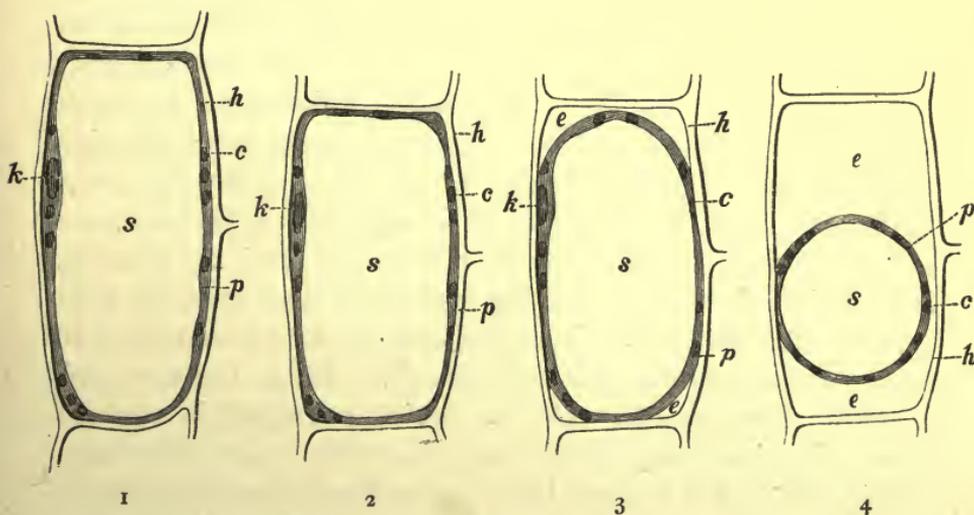


FIG. 9 (after de Vries). Young parenchymatous cell from the peduncle of *Cephalaria leucantha*: 1, Turgid cell ; 2, the same cell in 4 per cent. nitre solution ; 3, in 6 per cent. solution ; 4, in 10 per cent. solution, shewing complete plasmolysis : *h*, cell-wall ; *p*, primordial utricle ; *k*, nucleus ; *c*, chlorophyll-corpuscles ; *s*, cell-sap ; *e*, nitre solution which has entered the cell.

possibly can. Cells in this condition are said to be *turgid*. If now a 4 per cent. solution of nitre be substituted for the distilled water, it will be observed that the cells become

smaller without, however, undergoing any other perceptible change (Fig. 9, 2). This diminution in size can only mean that water has been withdrawn from the cells, the withdrawal being accompanied by an elastic contraction of the cell-wall. The nitre solution has withdrawn water until its attraction for water has come to be equal to that of the cell-sap, and this state of equilibrium having been reached, the withdrawal has ceased. On replacing the nitre solution by distilled water, the cells will regain their original size. From these very simple experiments we learn that the cell is capable of absorbing water in such quantity as to cause considerable stretching of the cell-wall and of the primordial utricle, that is, to set up a considerable hydrostatic pressure in the cell. This state of tension between the hydrostatic pressure on the one hand and the elasticity of the cell-wall on the other is designated as *turgidity*.

The diffusion of liquids through membranes is termed *osmosis*, and we may now enquire into the conditions of its accomplishment. They are briefly these. When two different liquids are separated by a membrane which they are both capable of wetting, currents are set up between the two liquids which traverse the membrane. Thus when an ordinary osmometer (the membrane of which consists of a piece of ox-bladder with the muscular coats removed) containing a liquid, is placed in a vessel containing another liquid, currents pass through the membrane into and out of the osmometer, the former being termed the *endosmotic* the latter the *exosmotic* current. The quantity of the liquids conveyed in each of these directions may be the same, or they may differ very considerably, for it has been ascertained that that liquid traverses the membrane in greatest quantity which wets it most readily, and further, that the chemical nature of the liquids is of great importance in the process. Thus Graham observed that when an osmometer, with a bladder-membrane, containing alcohol was introduced into a vessel containing distilled water, the level of the liquid in the osmometer-tube rose rapidly in consequence of the endosmose of water, whereas, when a film of collodion was substituted for the bladder

the contrary took place; and again, that when an osmometer containing a 1 per cent. solution of potassium chloride was placed in distilled water the liquid in the tube rose 18 mm., whereas when a 1 per cent. solution of potassium carbonate was used, it rose 439 mm.

The absorption of water by the cell is doubtless subject to the same conditions as those which we have found to determine the osmosis in the osmometer, the cell-sap corresponding to the fluid contained in the osmometer. The question now arises as to the determination of the osmotically active substance. It must be borne in mind that the concentration of the cell-sap is slight, its specific gravity being but little higher than that of distilled water; the osmotically active substances which it contains must therefore possess a strong affinity for water. That sugar is not the substance which is active in the process is evident; for, inasmuch as its affinity for water is comparatively slight, a much larger quantity of it would have to be present than can be inferred from the concentration of the cell-sap, in order to account for the amount of water absorbed. This objection applies also to the other organic substances present which have only a slight affinity for water. The mineral salts in the cell-sap have a much greater affinity for water than sugar has, and they are doubtless osmotically active. It must be remembered, however, that these salts are not produced in the cell, but are absorbed from without; hence there is a limit to their osmotic activity. The osmotically active substances which we seek must be such as have a great affinity for water and are constantly being produced in the metabolism of the cell. De Vries has pointed out that the organic acids and acid salts fulfil these requirements. They are present in all living cells which are capable of becoming turgid, their formation is doubtless a necessary part of the metabolism of the cell, and their affinity for water is considerable.

Assuming then that the organic acids and acid salts are the substances which bring about the absorption of water by the cell, we may go on to enquire into the conditions upon which the turgidity of the cell depends. A closed bladder containing syrup will soon become turgid when immersed in a

vessel of water: can we then directly compare a turgid cell to a turgid bladder, the cell-wall corresponding to the membrane of the bladder, the cell-sap to the syrup? The answer to the question is that such a comparison is inaccurate, for it has been found that the cell-wall is not able, like the membrane of the bladder, to hinder the escape by exosmosis of the contained liquid to such an extent as to become turgid. It is the lining layer of protoplasm, the primordial utricle as we have termed it, which offers the necessary resistance and prevents the escape of liquid by exosmosis: it is to this that the turgidity of the cell is to be ascribed. We can now compare the turgid cell to the turgid bladder: the cell-wall and the primordial utricle together correspond to the membrane of the bladder, the cell-wall supplying the necessary elasticity, the primordial utricle the necessary resistance to exosmosis.

We will consider, in conclusion, the absorption into the cell of substances in solution. Speaking generally, we may say that the passage of any dissolved substance through a membrane is determined by the size of its molecules; if the molecules of the substance are smaller than the intermolecular interstices of the membrane then they will be able to traverse the membrane. It is upon this that the formation of Traube's artificial cells depends, the formation of a membrane of precipitation being due to the fact that the intermolecular interstices of the precipitate are smaller than the molecules of the substances producing it. Further it has been observed that membranes of precipitation are permeable to some salts and not to others; for instance, water and potassic chloride will traverse a membrane of cupric ferrocyanide, but the chlorides of barium and of calcium, the sulphates of potassium and ammonia, and barium nitrate, will not traverse it. The most conclusive proof is afforded by the possibility of diminishing the size of the intermolecular interstices of a membrane, and of thereby modifying its permeability. Thus when a solution of gelatin comes into contact with a solution of tannic acid, a membrane is formed which is permeable to ammonium sulphate. If ammonium sulphate be added to the solution of gelatin, and a soluble salt of barium to the solution of

tannic acid, a membrane of precipitation is formed which is infiltrated with barium sulphate. This membrane, unlike the former, is impermeable to ammonium sulphate, and will only allow the smaller molecules of such substances as ammonium chloride and water to pass through it. This consideration affords an explanation of the fact that colloidal substances cannot diffuse through membranes. According to Strasburger's hypothesis, these substances consist of groups of molecules linked together by multivalent atoms; when such a group is larger than the intermolecular interstices of a membrane, it cannot diffuse through it.

In discussing the absorption of substances in solution by cells, we must bear in mind that they have to pass through, firstly, the cell-wall, and secondly, the primordial utricle. If a substance cannot traverse the cell-wall it is impossible for it to be absorbed by the cell, but this is a matter of only secondary importance. The matter of primary importance is the passage of substances through the primordial utricle. We shall see that of the many substances which readily pass through the cell-wall, some cannot traverse the primordial utricle at all, and others only in small quantity, and the conclusion that we shall arrive at will be that it is the primordial utricle which determines what substances and what quantity of them shall enter the cell.

If a section of parenchymatous tissue be treated with a 6 per cent. nitre solution, it will be seen that the cells undergo a diminution in size, and that the primordial utricle becomes detached from the cell-wall at the angles of each cell (Fig. 9, 3); if a 10 per cent. solution be used, the primordial utricle will assume the form of a spheroidal vesicle almost entirely free from the cell-wall, the space between the primordial utricle and the cell-wall being filled with the nitre solution (Fig. 9, 4). A cell in this condition is said to be *plasmolytic* (de Vries). This behaviour of the primordial utricle is the expression of the fact that water has been withdrawn from the cell-sap, and it appears that none, or at most a very small quantity of the nitre solution has penetrated through the primordial utricle into the vacuole, although it readily passes

through the cell-wall. This is an instance, then, of the resistance which the primordial utricle offers to the passage of substances through it. More striking instances are however afforded by cells which contain colouring matters in solution in their cell-sap. Naegeli pointed out that certain colouring matters (anthocyanin, erythrophyll) do not pass through the primordial utricle of living cells. De Vries repeated Naegeli's observations upon the parenchymatous cells of the Beet-root, and found that after they had been left for as many as fourteen days in water, neither the colouring-matter nor the sugar which their cell-sap holds in solution had escaped from them. He further shewed that a solution of sugar will readily pass through the cell-wall, for when the cells of the Beet-root are placed in syrup they become plasmolytic. When the cells are killed, for instance by heating them above 60°C ., or by immersing them in alcohol, the cell-sap readily escapes from them. This is in accordance with the well-known fact that it is impossible to stain living protoplasm: it is when protoplasm is dead that colouring-matters can penetrate into it.

When we compare the osmotic properties of the primordial utricle with those of the cell-wall, the explanation of the difference between them which at once suggests itself is that the intermolecular interstices of the former (at least of the outer firmer layer which we have termed the ectoplasm) are smaller than those of the latter, so that substances which can readily traverse the one cannot traverse the other, but this explanation cannot be regarded as complete. It still remains difficult to understand, as we shall see more fully in the next lecture, how it is that a sufficient quantity of nutritive salts can be taken up by the plant, and how such substances as sugar can pass from cell to cell in the plant. Possibly, as Pfeffer suggests, the osmotic properties of the primordial utricle may vary from time to time, and possibly the saccharine substances which are certainly transferred from one part of the plant to another, travel in other chemical forms. But we must bear in mind that we have here a living and not a dead membrane to deal with, and consider that the laws which regulate osmosis through the latter may be, and probably are,

profoundly modified in the former by the vital forces which are active in it.

But the passage of substances from cell to cell may doubtless take place otherwise than by osmosis. Where the protoplasm of adjoining cells is continuous, a condition which we saw in the last lecture is probably not uncommon, substances both soluble and insoluble (proteids and fats) in water may be directly conveyed from one cell to another. Again, it frequently happens, as we shall learn in a subsequent lecture, that the hydrostatic pressure which is set up in cells by endosmosis is so great as to cause an escape, a filtration under pressure, of liquid from them. This is probably of importance in the transmission of substances which, though soluble in water, diffuse but slowly.

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LECTURE IV.

ABSORPTION.

IN the first lecture we met with a very simple case of this function. We found that the yeast-cell, floating in Pasteur's solution, is capable of absorbing water and dissolved substances, and it is in this way that all plants obtain the materials of their food. It is characteristic of plants that they can only absorb their food in the fluid form, for everything that they take up has to pass through closed cell-walls. In the higher plants absorption does not take place to an equal extent at all points of their surface, as is apparently the case with the Yeast-plant, but we find certain members of these plants exhibiting special adaptation for the performance of this function. These absorbent organs are the *roots*, as regards water and substances in solution, and the *leaves*, as regards gases.

In thallophytic plants there are no roots or leaves : water and substances in solution are absorbed either directly by the cells of the thallus or by root-hairs (*rhizoids*) ; gases are absorbed by the cells of the thallus. The Muscineæ also have no true roots, but only root-hairs.

I. *Absorption of Water and of Substances in Solution.*

The parts of the roots of the higher plants which are active in absorption are the *root-hairs* and the uncuticularised epidermal cells of the younger roots. The root-hairs of these

plants are thin-walled, unicellular, unbranched filaments, which are developed from the epidermal cells of the root at some little distance behind its growing-point; they are of short duration, and leave after their death no trace of their existence. In many of the lower plants the root-hairs are multicellular and branched, and in the Muscinæ the cell-wall is frequently thickened and of a brown colour.

The plants which we shall more especially consider are land-plants, plants, that is, which have their roots imbedded in the soil. It will therefore be advantageous to give here a

FIG. 10.

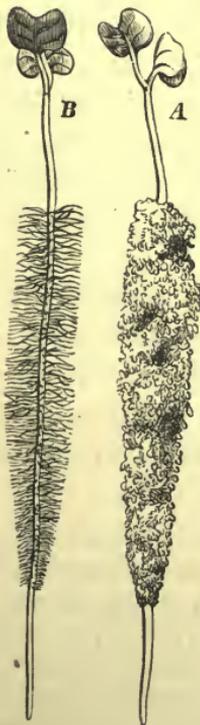


FIG. 11.

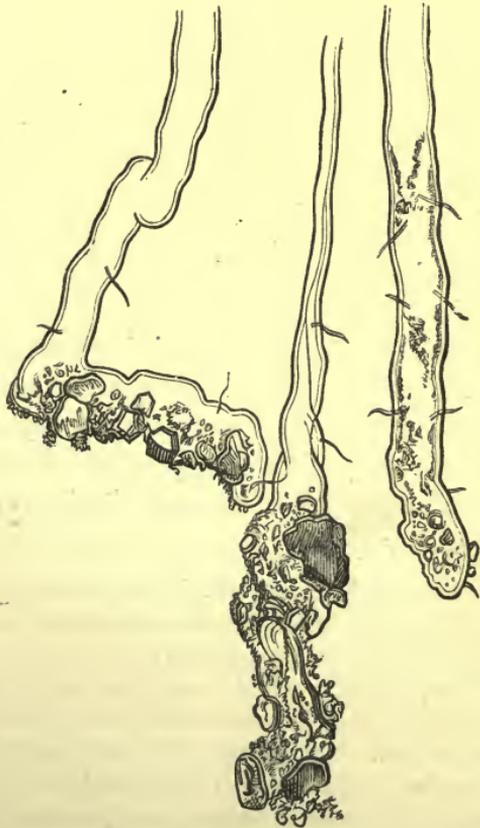


FIG. 10 (after Sachs). Seedling of *Sinapis alba*: A, after removal from the soil; B, after washing in water.

FIG. 11 (after Sachs). Ends of root-hairs of a seedling of *Triticum vulgare*, shewing their intimate connexion with particles of soil.

brief account of the general nature and properties of the soil. The soil may be regarded as consisting of a mixture of irregular particles of mineral and of organic matter (*humus*). The interspaces between the particles are usually filled with air, but even when it is very dry, each particle is covered with a film of water, *hygroscopic water* as Sachs terms it, which adheres to it with considerable force. The root-hairs make their way into these interspaces, and, in the course of their growth, their cell-walls come into very close contact with the particles of the soil. In consequence of this intimate connexion, they can readily absorb the hygroscopic water of the particles, although they have to overcome the force of adhesion existing between the particles and the water which invests them. Inasmuch as the particles with their films of water form a sort of capillary system in the soil, the withdrawal of water by a root-hair at any point causes a flow of water towards that point from adjacent particles: in this way a plant with a well-developed root-system drains a considerable area. The roots, as they grow and branch, form root-hairs at new points, so that fresh sources of supply are continually being opened up.

This property of retaining water is not possessed equally by all kinds of soil: it is possessed, for instance, to a high degree by clay and to a low one by sand. Moreover, the soil can not only retain a portion of the water which enters and passes through it in the liquid form, but it can condense aqueous vapour.

The importance of this latter property of the soil is well shewn by an experiment of Sachs. A scarlet-runner was grown in a flower-pot, and, after having been left unwatered for some time, the pot was placed in a receiver, the air in which was saturated with aqueous vapour, the stem and leaves projecting into the external air through an aperture in the lid of the receiver. The plant, which was beginning to wither, soon recovered a healthy appearance. From this it is evident that the plant must have been supplied with water; and since no water in the liquid form was poured on to the soil, and since, as Sachs had previously shewn, roots cannot directly absorb aqueous vapour, it is evident that the water with which the plant was supplied had been derived from the watery vapour with which the atmosphere of the receiver was saturated, and had been condensed on the surface of the particles of soil.

Another important property of the soil is that it can withdraw from their solutions salts, and other substances, and can retain them. Way found, for instance, that when solutions of the chloride, nitrate or sulphate of potassium were poured over portions of clay-soil, the water which drained off contained a smaller proportion of the base than the original solution, whereas the proportion of the acid was the same, the acid being combined with a new base, generally lime. He also found that free potash and ammonia are thus absorbed by soil, as also phosphoric acid. This property is one of great practical importance, inasmuch as it is in virtue of it that the soluble salts of nutritive value which the soil contains are not entirely washed out of it by excessive rain. Further, in consequence of this retention of soluble salts by the soil, the solutions of them which are presented to the root-hairs are rendered very dilute, a condition which is favourable to the process of absorption.

The following results of Henneberg and Stohmann will serve to illustrate the preceding statements. In each case 100 grms. of soil were treated with 200 c.c. of a solution of ammonium phosphate for six hours.

1.	Amount of H_3PO_4 in the solution,	0'144	grm. :	amount absorbed,	0'072	grm.
2.	„	„	0'720	„ :	„	0'244
3.	„	„	1'440	„ :	„	0'396

Sachs has pointed out that it is the hygroscopic water in the soil which is of importance to plants, and that any water which may be present in the interspaces and which is not affected by the force of adhesion—free water, we may term it—is not only of no use to plants but may be even hurtful, in that it prevents the free access of air to the roots. It is in fact the object of draining, to remove from the land the free water. And yet there are plants whose roots are permanently immersed in water, and these do not appear to suffer. This leads us to consider the modifications which are presented by roots, and which are an expression of the adaptation of plants to their environment. We may distinguish, from this point of view, four kinds of roots; land-

roots, water-roots, air-roots, and the roots of parasitic plants which penetrate into their hosts. The difference of organisation between land- and water-roots depends upon the fact that the former have to absorb water in opposition to the force with which it is retained by the soil, whereas the latter absorb only free water. The experiments of Sachs clearly indicate this difference. He found that if the roots of a land-plant be kept immersed in water, they will persist for a time and supply the plant with water; sooner or later new roots are developed which are adapted for the absorption of water under these conditions—which are, in fact, water-roots—and the original roots, at least the younger ones, die. When a land-plant is grown from the first under these conditions, it forms only water-roots. If such a plant be now transferred to soil it will wither, doubtless because its roots are incapable of taking up the hygroscopic water.

Air-roots are found principally in monocotyledonous plants, such as Orchids and other Epiphytes. That they can absorb water is shewn by the fact that plants which have no other means of supply, continue to grow. They present evident peculiarities of structure. In Orchids the air-root is invested by a membrane, the *velamen*, consisting of several layers of cells containing air, the irregularly thickened walls being perforated; in other cases the cortical parenchyma of the root is loose and spongy, and the epidermal cells are produced into a number of long hairs. These roots are thus enabled to retain any drops of water which may fall upon them. This water will dissolve, or at least assist in the solution of any mineral substances which may have been deposited on the surface of the roots in the form of dust, and thus it is that the plant obtains its supplies.

From the researches of Unger and of Sachs it would appear that the velamen of Orchids can condense watery vapour, and thus make it available for absorption.

Air-roots cannot adapt themselves to an existence in soil or in water; according to Chatin, they die if they penetrate into the one or the other; and conversely, if the root of a

normally epiphytic plant be caused to develop first in soil, it rapidly perishes if it is subsequently exposed to the air.

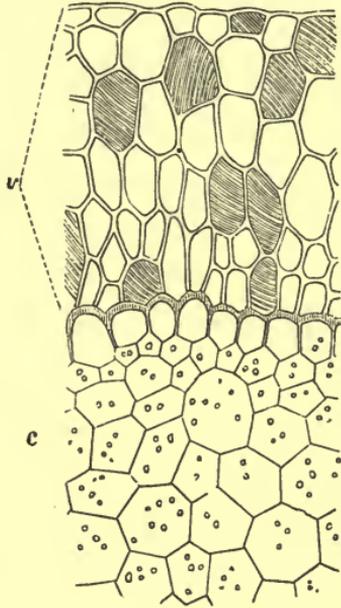


FIG. 12 (after Unger). Transverse section of part of the air-root of an Orchid: *v*, the velamen; *c*, the cortex.

The roots of parasitic plants penetrate the tissues of their hosts and fuse with them; in this way a communication is established by means of which the parasite obtains its supplies of water and of substances in solution.

A few words may be said here with reference to the distribution of the roots in the soil. It has been already pointed out that roots, as a rule, branch freely, and that in consequence of their continuous apical growth they are always entering new areas of soil from which the plant can obtain fresh supplies of water and of nutritive substances. Their distribution may, however, be materially affected by the nature of the medium into which they penetrate. If a root passes out of soil into water it becomes excessively elongated, but if it enters a moderately strong solution of some salt this rapid growth in length is checked, as Sachs first pointed out. Nobbe studied this subject in detail, and found that the roots of Barley and of Buckwheat attained their greatest develop-

ment in solutions containing from $\frac{1}{2}$ to 2 per thousand of inorganic salts. The branching of roots is affected by the proportion of water in the soil, the number of branches being greater, according to Unger, when the soil is moist than when it is dry; in the latter case the development of root-hairs is more considerable. It is also a well-known fact that roots always tend to grow towards moisture, a fact which cannot be satisfactorily explained at present. An interesting experiment of Nobbe's has brought another fact of this kind to light. He cultivated Maize and Clover plants in pots containing layers of soil of which some had been previously soaked in solutions of nutritious substances, and he found that the roots branched much more freely in the layers which had been thus treated than in the others.

Of the external conditions which materially affect the absorption of water by roots an important one is the temperature of the medium in which they are. From the experiments of Sachs we learn that roots absorb water more actively at a higher than at a lower temperature. For this function, as for all others, there is an optimum temperature at which it is performed with the greatest activity, and above or below which the activity diminishes.

But the absorption of water by roots is not affected only by the temperature of the medium in which they themselves may be, but also by that of the medium which surrounds the other parts of the plants. Thus roots absorb with greater activity when the air is at a high than when it is at a low temperature.

Vesque has found that, under certain conditions, a *sudden rise* in the temperature of the soil, but more especially in that of the air, has the effect of temporarily diminishing the absorption, and a *sudden fall* of increasing it. The explanation of this will be given in connexion with the subject of transpiration (p. 118).

The explanation of the effect of the temperature of the air upon the absorbent activity of the roots depends upon the fact that, under ordinary conditions, the leaves of a plant exhale a considerable quantity of watery vapour (Transpiration). Inasmuch as the degree of humidity of the

air is usually lower at a high than at a low temperature, the loss of water from the leaves is greater when the temperature of the air is higher. This drain upon the water in the plant leads to an increased absorbent activity of the roots. But although increase or diminution of transpiration produces a corresponding change in the activity of absorption, yet the two functions are not directly proportional. Nor does absorption necessarily depend upon transpiration, for, as we shall see hereafter, absorption takes place with considerable activity at times when the plant is not transpiring. This point will be fully discussed in a subsequent lecture when the subject of transpiration is being considered.

We will now consider more particularly the absorption of substances in solution, and, inasmuch as these substances are usually inorganic chemical compounds, we may briefly designate them as *salts*. We may very well begin by studying the process of absorption as it takes place in the Yeast-plant. In the first place it is obvious that the substances absorbed by it are dissolved in water; that the substances absorbed are of such a nature that they can not only diffuse through the cell-wall, but also pass through the primordial utricle; and further, that the continued absorption of any substance depends upon the fact that the proportion of it in the Pasteur's solution is greater than the proportion of it in the cell-sap of the Yeast-plant, for this, we have already seen, is a necessary condition of osmosis. In the case of a substance contained in the Pasteur's solution and used by the Yeast as food, this inequality is maintained by the metabolism of the organism. When a quantity of the substance is absorbed, it undergoes chemical change: the effect of this is to diminish the amount of the substance in the cell-sap, and thereby to cause the absorption of a further supply of it.

The process of absorption is essentially the same in the root-hairs of the higher plants. Only such substances are taken up as are soluble and can pass through the cell-wall and primordial utricle, and the continued absorption of any substance depends upon the fact that the proportion of it in

the cell-sap is smaller than that in the external fluid. In the case of root-hairs, this inequality is maintained not only by the metabolism of the absorbing cell, as in Yeast, but, inasmuch as the plants now under consideration are multicellular, the substances in solution in the cell-sap of the root-hairs are being constantly withdrawn by the more internal cells of the root and are transmitted throughout the plant. In fact, as far as the process of absorption is concerned, the cell-sap of one of these internal cells stands in the same relation to the cell-sap of the root-hair as the cell-sap of the root-hair does to the external fluid. This relation exists likewise between the successive layers of cells of the root, and thus there is set up a current of water holding substances in solution, passing from the surface towards the interior.

Although the root-hairs can only absorb salts in solution, it must not be thought that the root-hairs of land-plants are immersed in water like a yeast-cell in Pasteur's solution. This is true indeed of floating water-plants, but in the case of land-plants the root-hairs are imbedded in soil which frequently contains a relatively small amount of water, and in which many of the salts to be absorbed are present in an insoluble form. The salts, soluble in water, which the particles of the soil may contain, are dissolved by the hygroscopic water, and are thus prepared for absorption by the root-hairs. That salts which are insoluble in water, are, however, absorbed, is quite certain, and we will now proceed to enquire into the means by which their solution is brought about.

In the first place, a soil which is rich in humus contains a considerable quantity of carbon dioxide, and this gas is also given off by the roots of living plants; and it is well known that water charged with carbonic acid is capable of dissolving substances, such as calcium carbonate and certain silicates, which are insoluble in pure water. In the second place, the presence of certain soluble salts in the soil, involving as it does chemical decompositions, brings into the soluble form substances which were originally insoluble, and increases in some cases the solubility of those which are only slightly soluble. ✓

These statements are borne out by the experiments of Beyer, to which the following figures refer. In each case one kilogramme of felspar was treated with $2\frac{1}{2}$ litres of water, or of a watery solution of one of the salts enumerated: the figures give the amount, in grammes, of the substances dissolved.

	Potash	Soda	Lime	Magnesia	Silica	Total
Distilled water	0'051	0'078	0'058	0'006	0'049	0'242
Distilled water, with CO ₂	0'071	0'114	0'067	0'004	0'069	0'325
Lime, $\frac{1}{10}$	0'209	0'174	—	0'003	0'061	0'447
Ammonium sulphate, $\frac{1}{5}$	0'161	0'094	0'122	0'035	0'066	0'478
Sodium nitrate, $\frac{1}{5}$	0'089	—	0'049	0'003	0'060	0'201
Sodium chloride, $\frac{1}{5}$	0'163	—	0'091	0'008	0'032	0'294
Sodium chloride, $\frac{1}{5}$, and CO ₂	0'183	—	0'123	0'006	0'057	0'369

Finally the constituents of insoluble salts are brought into solution by means of the acid sap which saturates the cell-walls of the root-hairs. That the root-hairs are acid is easily demonstrated by means of litmus-paper, or, as Sachs suggested, by placing a root in a solution of potassium permanganate, when the salt is decomposed and a precipitate of the hydrated dioxide is formed upon the surface of the root, a reaction which does not take place when a leaf or a stem is placed in the solution. This acid reaction is shewn not to be merely due to carbonic acid, by the fact that the reddening of the litmus-paper is permanent.

The important part played by this acid sap in the absorption by roots of salts which are insoluble in pure water is indicated by means of the following experiment devised by Sachs. If a well-polished slab of marble be placed in a flower-pot and a Bean or a Sunflower be planted in the soil above it, the roots will penetrate through the soil until they reach the surface of the marble. They will then grow along it, in close contact with it. If, after some time, the slab of marble be taken out, its surface will be found to be corroded wherever the roots have been in contact with it; in fact, in a successful experiment, the root-system is etched upon it. This corrosion is the expression of the fact that the acid roots have dissolved and removed particles of the marble, and the

fact that the surface of the marble is corroded only at those points at which it was in contact with the roots shews that the corrosion is not due to the action of carbonic acid, for that is everywhere present in the soil, but to the acid sap in the walls of the root-hairs. Similar experiments made with dolomite, magnesite, and osteolith, give the same results. When a slab of gypsum is used, the result is different. In this case it is the general surface of the slab which is corroded, the parts in contact with the roots being preserved and forming therefore projections: the roots appear to protect the gypsum from the solvent action of the water in the soil.

It has been pointed out that insoluble salts present in the soil may be converted into soluble compounds by decompositions taking place between them and soluble salts which the soil already contains or which have been supplied to it, and there is reason to believe that the action of the acid sap of the cell-walls is of this nature also. It has been found, for instance, that when the roots of a plant are made to grow in a solution in which calcium phosphate and potassium nitrate are present, the solution becomes alkaline (Boussingault): if, however, the solution be one of the chloride of an alkaline metal or earth, the solution becomes strongly acid (Rautenberg and Kühn). The most probable explanation of these facts is that the salts are decomposed by the acid sap of the roots, the acid being absorbed in larger proportion in the first case, the base in the second. We learn also from this that the chemical elements are not necessarily absorbed by roots in the combinations in which they are present in the soil.

We see, then, that in all cases the salts which are absorbed by the roots of plants are absorbed in solution, and we have now to enquire into the relation between the amount of salts and the amount of water absorbed, to enquire, that is, if a salt in solution is absorbed in the same proportion as the water in which it is dissolved. For example, let us suppose the roots of a plant to be immersed in a solution which contains say 0.1 per cent. of a particular salt; the question is, will the solution which remains after absorption has been going on for some

time still contain 0·1 per cent. of the salt in question, or a lower or a higher percentage? De Saussure was the first to attempt an answer. He employed various substances with which he made aqueous solutions containing about 1 per cent. of the substance, and he found, by quantitative analysis of the unabsorbed residue of the solution, that the water had been absorbed by the plant in much larger proportion than the substance dissolved in it.

These are some of his results :

for every 50 parts of water,	<i>Polygonum Persicaria</i> absorbed	<i>Bidens cannabina</i> absorbed
Chloride of Potassium,	14·7 parts	16·0 parts
„ Sodium,	13·0 „	15·0 „
„ Ammonium,	12·0 „	17·0 „
Sulphate of Copper,	47·0 „	48·0 „
Cane Sugar,	29·0 „	32·0 „

instead of 50 parts of the substance dissolved.

From these results de Saussure concluded that the roots of plants absorb substances in solution in smaller proportion than the water in which they are dissolved, a conclusion which is known as de Saussure's law. Wolf and others, in repeating de Saussure's experiments, used much more dilute solutions, and found that under these conditions the amount of substance absorbed was larger in proportion than that of water.

Wolf obtained, for instance, the following results with *Phaseolus multiflorus* :

	Strength of solution	Amount of water absorbed during expt.	Amount of salt absorbed during expt.
Nitrate of potassium,	0·250 per cent.	46 c.c.	0·080 gm.
„	0·100 „	62 „	0·068 „
„	0·075 „	59 „	0·064 „
„	0·050 „	36 „	0·041 „
„	0·025 „	78 „	0·024 „

hence the strength of the solutions actually absorbed in these cases is

0·174 per cent.,	giving a difference of	- 0·076 per cent.
0·109	„	+ 0·009 „
0·108	„	+ 0·033 „
0·114	„	+ 0·064 „
0·030	„	+ 0·005 „

From these figures it appears that nitrate of potassium is absorbed according to de Saussure's law at a concentration of 0.25 per cent., but that at a concentration of 0.1 per cent. and below it is absorbed in larger proportion than the water in which it is dissolved. This is even more strikingly shewn by nitrate of ammonia.

	Strength of solution	Amount of water absorbed during expt.	Amount of salt absorbed during expt.
Nitrate of ammonia,	0.2456 per cent.	70 c.c.	0.236 gm.
"	0.0982 "	85 "	0.094 "
"	0.0491 "	48 "	0.045 "
"	0.0245 "	56 "	0.022 "

In this case the strength per cent. of the solutions actually absorbed is

0.3371, giving a difference of +0.0915
0.1106 " +0.0124
0.0937 " +0.0446
0.0392 " +0.0147

The absorption of this salt does not take place in accordance with de Saussure's law even at a concentration of 0.2456 per cent.

With the Maize, Wolf obtained the following results which closely resemble those obtained with Phaseolus.

	Strength of solution	Amount of salt absorbed	Time required to absorb 50 c.c.
Nitrate of potassium,	0.100 p. c.	0.138 gm. per 100 of water	12 days
"	0.075 "	0.106 "	10 "
"	0.050 "	0.096 "	8 "
"	0.025 "	0.047 "	7½ "
Nitrate of ammonia,	0.0735 "	0.118 "	12½ "
"	0.0491 "	0.080 "	12 "
"	0.0245 "	0.042 "	10 "

The strength of the solution actually absorbed in each case is indicated by the figures in the second column.

In the above experiments with Phaseolus the *time* of absorption was uniform; it may therefore be well to add, for the purpose of direct comparison with the Maize, some experiments with Phaseolus in which the *quantity of solution* absorbed was as nearly as possible uniform.

Strength of solution	Amount of water absorbed	Amount of salt absorbed	Strength of solution absorbed	Difference
Nitrate of potassium,				
0.100 per cent.	49 c.c.	0.053 gm.	0.108 per cent.	+0.008
0.075 "	50 "	0.048 "	0.096 "	+0.021
0.050 "	50 "	0.041 "	0.082 "	+0.032
0.025 "	51 "	0.022 "	0.043 "	+0.018

Strength of solution	Amount of water absorbed	Amount of salt absorbed	Strength of solution absorbed	Difference
Nitrate of ammonia,				
0·0735 per cent.	50 c.c.	0·059 grm.	0·118 per cent.	+ 0·0445
0·0491 „	49 „	0·044 „	0·089 „	+ 0·0399
0·0245 „	50 „	0·021 „	0·042 „	+ 0·0175

It appears, therefore, that de Saussure's law is merely an account of a special case. The law of absorption is rather this:—for the watery solution of any given salt capable of being absorbed there is a certain degree of concentration at which the proportion of the amount of the salt absorbed to that of the water absorbed is the same as that of the solution; if the solution be more concentrated the proportion of water absorbed will be greater, if the solution be more dilute the proportion of salt absorbed will be greater. It must not, however, be overlooked that although the *proportion* of a salt absorbed is greater when the solution is dilute, the *absolute quantity* of it absorbed in a given time is greater when the solution is more concentrated.

The foregoing figures suffice to shew that plants absorb different substances in different proportions, but, should further proof be needed, it will be found in the tables given below to illustrate the discussion of the question as to whether or not different plants absorb the various salts to the same extent, that is, as to whether or not each plant is endowed with what we may term a specific absorbent capacity.

The fact that different salts are absorbed in different proportions is well illustrated by analyses of water-plants. Thus, von Gorup-Besanez analysed *Traça natans* and the water in which it was growing:

Percentage of	Total Ash	K ₂ O	Na ₂ O	CaO	MgO	Fe ₂ O ₃	SO ₃	SiO ₂	Cl
Water	0·008	9·08	9·22	42·44	18·09	1·12	17·03	1·90	1·18
Plant taken in May	25·55	6·89	1·41	14·91	7·56	29·62	2·73	28·66	0·65
Plant taken in June	13·69	6·06	2·71	17·65	5·15	23·40	2·53	27·34	0·46

In answer to this question it may be at once stated that it has been found that different plants growing in the same soil or water and under the same conditions contain very different quantities of the substances which they must have absorbed from the soil or the water. This has been ascertained by a great number of analyses of the *ash* of plants, that is, of the mineral residue which is left after the plant has been incinerated. Since there is no evidence to prove that a plant loses any of the mineral substances which it absorbs, excepting of course when it throws off parts of itself, such as leaves, bark, and seeds, it is obvious that a knowledge of the composition of the ash must afford valuable information as to the specific absorbent capacity of the plant. Besides this mode of investigation there is the method of *water-culture* (see Fig. 21), to which allusion was made above, which consists in growing plants with their roots immersed in water holding known quantities of salts in solution. By analysis of the plant, or of that portion of the solution which remains unabsorbed at the close of the experiment, the amount of the various salts absorbed can be determined.

A familiar and striking illustration of the difference in the composition of the ash of different plants grown under the same conditions is afforded by a comparison of the amount of silica present in the ash of equal dry weights of gramineous and leguminous plants: thus, according to Wolff,

100 parts of	Meadow-hay	contain	27.01	of silica
„	Wheat-straw	„	67.50	„
„	Red clover	„	2.57	„
„	Lucerne	„	6.07	„
„	Pea-straw	„	6.83	„

It may be further illustrated by citing Trinchinetti's observation that *Mercurialis annua* and *Chenopodium viride* took up more nitre than common salt from a solution containing these two substances, whereas *Satureia hortensis* and *Solanum Lycopersicum* took up more common salt than nitre, and again by analyses of water plants.

Gödechens analysed four species of *Fucus* gathered at the mouth of the Clyde, with the following results :

<i>Fucus</i>	<i>digitatus</i>	<i>vesiculosus</i>	<i>nodosus</i>	<i>serratus</i>
Total ash, per cent.	20·40	16·39	16·19	15·63
100 parts of ash consisted of				
Potash	22·40	15·23	10·07	4·51
Soda	8·29	11·16	15·80	21·15
Lime	11·86	9·78	12·80	16·36
Magnesia	7·44	7·16	10·93	11·66
Ferric oxide	0·62	0·33	0·29	0·34
Sodium chloride	28·39	25·10	20·16	18·76
Sodium iodide	3·62	0·37	0·54	1·33
Sulphuric acid	13·26	28·16	26·69	21·06
Phosphoric acid	2·56	1·36	1·52	4·40
Silica	1·56	1·35	1·20	0·43

From the wide differences in the composition of the ash which, as we see, have been found in different plants, we may infer that each kind of plant is endowed with a specific absorbent capacity. It is upon this, in fact, that the "rotation of crops" in farming depends. Further, since the quantity of a substance absorbed depends, as was stated at the outset, upon its being chemically altered in the metabolism of the plant, we find that the specific absorbent capacity of a plant is an expression of its specific metabolic properties. For example, if we contrast the amount of silica in the ash of a gramineous with that in the ash of a leguminous plant, we cannot but conclude that the former is able to withdraw relatively large quantities of absorbed silica from the sphere of osmotic activity and deposit them in its tissues, whereas the latter can only do so to a comparatively very slight extent. But this is a point which would be more appropriately discussed in connexion with the metabolism of the plant, and we will accordingly defer it to a subsequent lecture.

Gödechen's analyses teach further that the absorbent capacities of nearly allied species are very different, and from the following analyses of potatoes made by Herapath it appears that this is true even of varieties of the same species.

Herapath analysed five varieties which are indicated by the letters in the table.

	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>	<i>E</i>
Ash per cent. in dry tubers	4·81	3·63	4·35	3·46	3·97
Carbonic acid	21·059	16·666	21·400	18·162	13·333
Sulphuric acid	2·774	4·945	3·244	5·997	6·780
Phosphoric acid	5·716	8·920	3·774	6·669	11·428
Potash	53·467	54·166	55·610	55·734	53·029
Calcium carbonate	0·844	2·049	3·018	1·954	2·286
Magnesium carbonate	3·530	0·273	1·257	2·565	0·570
Calcium phosphate	3·363	0·683	3·835	5·374	2·856
Magnesium phosphate	9·247	12·298	7·550	3·545	7·623
Traces of other substances including silica	0·000	0·000	0·312	0·000	2·095

Further, although we may assume that quite similar individuals of the same species growing in the same soil and under the same external conditions would yield an ash of approximately the same composition, yet the fact that the individuals vary in the vigour of their development leads to considerable differences in the composition of the ash. This is shewn by the accompanying table of analyses of plants of *Brassica oleracea* made by Pierre.

1000 grms. of plant contained	Very weakly plants	Weakly plants	Very vigorous plants
Total dry substance	120·2 gm.	105·0 gm.	74·0 gm.
Total ash	80·40 "	114·85 "	143·46 "
Phosphoric acid	9·078 "	12·024 "	12·233 "
Potash and soda	21·800 "	29·955 "	25·555 "
Lime	29·850 "	37·590 "	28·840 "
Magnesia	1·429 "	1·807 "	1·305 "
Silica	3·300 "	4·490 "	17·660 "
Ferric oxide	0·398 "	0·954 "	1·000 "

Finally, the absorbent capacity of the plant varies at different periods of its life. We learn from von Gorup-Besanez's analyses of *Trapa* given above, that that plant contains a larger proportion of ash at an early than at a later period of its vegetation, a result which has been obtained also in the case of other plants. We may cite Arendt's observations on the Oat-plant in illustration.

Arendt analysed Oat-plants at different times during their growth; taking the quantity of silica absorbed as a standard of comparison and fixing it at 10, he found the other constituents had been absorbed in the following proportions :

	Period I. May 4—June 7	Period II. June 8—29	Period III June 30—July 9	Period IV. July 10—20	Period V. July 21—30
Silica	10'00	10'00	10'00	10'00	10'00
Sulphuric acid	1'66	2'32	0'00	2'33	2'53
Phosphoric acid	5'14	3'65	4'49	2'80	8'00
Lime	7'04	5'38	3'22	3'13	1'32
Magnesia	2'40	2'05	1'12	1'86	6'20
Potash	26'65	18'85	9'44	4'49	0'00

But the amount of a substance absorbed is not determined solely by the specific absorbent capacity of the plant, for we found in discussing de Saussure's law that the larger the proportion of any given substance in the solution supplied to the roots, the larger was the amount absorbed. The composition of the soil or of the solution in which the roots of a plant are growing must have an important effect upon the composition of the ash. This has been abundantly proved by a large number of analyses, of which we may cite the following.

Herapath analysed light Oats grown upon sandy soil, and heavy Oats grown on the same soil after manuring with river-mud (warping).

	<i>Light Oats</i>	<i>Heavy Oats</i>
Potash	9'8	13'1 per cent.
Soda	4'6	7'2 "
Lime	6'8	4'2 "
Phosphorus pentoxide	9'7	17'6 "
Silica	56'5	45'6 "

Wolff analysed the ash of various plants grown in poor soil with the addition of certain salts ; the example taken is the Buckwheat.

Ash contained in 100 parts	Soil without any addition	With Sodium chloride	With Potassium nitrate	With Potassium carbonate	With Magnesium sulphate	With Calcium carbonate
Potash	31·7	21·6	39·6	40·5	28·2	23·9
Potassium chloride	7·4	26·9	0·8	3·1	6·9	9·7
Sodium chloride	4·6	3·0	3·2	3·8	3·4	1·7
Lime	15·7	14·0	12·8	11·6	14·1	18·6
Magnesia	1·7	1·9	3·3	1·4	4·7	4·2
Sulphur trioxide	4·7	2·8	2·7	4·3	7·1	3·5
Phosphorus pentoxide	10·3	9·5	6·5	8·9	10·9	10·0
Carbon dioxide	20·4	16·1	27·1	22·2	20·0	23·2
Silica	3·6	4·2	4·2	4·2	4·8	5·2

From Wolff's figures we learn further that the influence of the composition of the soil upon the absorption by the roots is not necessarily a direct one. In some cases we see that it is ; thus, the addition of potassium-salts, magnesium-salts, and calcium-salts to the soil increased the amount of potash, magnesia and lime, respectively, in the ash : but in others it is not, for the addition of sodium chloride to the soil did not lead to an increase in the sodium of the ash. But the indirect influence, which, as we have seen, depends upon double decompositions going on in the soil, or at the surface of the root-hairs, is often very important ; thus, in the case before us, the addition of sodium chloride to the soil brought about the absorption of a considerable quantity of potassium.

The composition of the ash of a plant depends therefore upon two factors, (1) the specific absorbent capacity of the plant, (2) the composition of the soil in which it is growing. It has been attempted to account for the specific absorbent capacity of plants by attributing to the roots a selective power. Such an assumption is as erroneous as it is unnecessary. We have learned that the absorption of a substance depends in the first instance upon the physical relation which exists between its molecules and the cell-wall and primordial utricle of the absorbing cell. If it is presented to the cell in such a form that it can pass through these, its

absorption will take place quite independently of its use or its hurtfulness to the plant. We have also learned that the amount of any substance absorbed depends upon its relation to the metabolism of the plant. We can imagine that a substance might pass readily into the absorbent cells and be distributed from cell to cell throughout the plant, without entering at all into the metabolic processes; sodium, as we see from Wolff's analyses, affords a case in point. The result of the absorption of such a substance would be that the cell-sap of the cells would soon reach such a point of saturation as regards this substance that diffusion-equilibrium would be set up, and then no more of it would be absorbed. The case of a salt which does enter into the metabolic processes is very different: it undergoes decomposition, and some constituent of it is frequently thrown down in the insoluble form. The effect of this is that a constant withdrawal of the salt from the sphere of osmotic action is taking place, and thus a demand for it is set up which is met by the absorption of fresh quantities of it by the roots from the soil. It is thus quite possible to give a satisfactory explanation of the facts observed without making any unwarrantable assumptions.

We will conclude this lecture with an examination of the existing evidence as to the absorption of water and of substances in solution by organs other than roots. In those Thallophytes which possess no root-hairs, absorption is effected by the cell or cells which constitute the thallus. Submerged Cormophytes doubtless absorb, to some extent at any rate, by their general surface, and in *Salvinia* the peculiarly modified aquatic leaves are the only absorbent organs which the plant possesses. In these cases the leaves are especially adapted for the purpose, notably in this respect, that the walls of their epidermal cells are not cuticularised. This is true also of the glands of the leaves of the so-called carnivorous plants which absorb organic substances in solution. It has been thought, though, by many, that the ordinary foliage-leaves of land-plants are capable of absorbing water, and that to such an extent as to constitute an important source of supply. This is a point which has excited considerable interest, and it

has therefore received much attention from physiologists. Hales, Bonnet, Duchartre, Heiden, and others, investigated it without, however, arriving at any very definite results. Among the more recent and more satisfactory researches may be mentioned those of Detmer and of Boussingault. Detmer found that if leaves be immersed in water they distinctly increase in weight in so short a time as a quarter of an hour, and Boussingault obtained similar results by means of experiments of much the same kind. It appears then that leaves can absorb water, but it is by no means proved that they do so under ordinary circumstances. The objection to these experimental results is, as Eder has pointed out, that long-continued immersion in water produces changes in the walls of the epidermal cells of such a nature that they become permeable to water. Leaves are not exposed to this under ordinary circumstances; as a rule their epidermis cannot be moistened by water, so that the rain or dew which falls upon them forms drops which either roll off by their own weight or are shaken off by the wind. The differences in internal organisation as well as in external form which exist between submerged and subaërial leaves go far to prove that since the former are known to absorb water, the latter are not adapted for this purpose. This view is further supported by the fact that these differences do not only exist between the leaves of a submerged plant on the one hand and of a subaërial plant on the other, but that they are very evident also between the submerged and subaërial leaves of plants which, like *Salvinia*, are only partially immersed. It is true that plants which are flaccid very soon become turgid and assume a fresh appearance when rain falls, but it must be admitted that the most important causes of this are the absorption of water by the roots and the diminution of the transpiration of the plant in consequence of the increased moisture of the air. In comparison with these a possible direct absorption of water by the leaves may be neglected.

With regard to the absorption of watery vapour by leaves, it appears, from the observations of Detmer and of Boussingault, that it may take place to a slight extent when the

leaves are very flaccid and dry, the air being at the same time very moist, but that it does not take place when the leaves are in their ordinary condition. The freshening effect which is produced when plants which are beginning to wither are introduced into a moist atmosphere is to be attributed to the consequent diminution of loss of water by transpiration.

Inasmuch as the leaves of land-plants can absorb water under certain special conditions, it is natural to infer that they can also absorb substances in solution. This has been proved experimentally by Boussingault and by Mayer. The former found that if a drop of a solution of calcium sulphate be placed on a leaf, both the water and the salt will disappear in the course of a few hours, and sooner on the lower than on the upper surface; the latter obtained similar results with a solution of ammonium carbonate.

It appears, then, that, under certain conditions, the foliage-leaves of land-plants will absorb water and substances in solution. It must, however, be borne in mind that any part of a plant if immersed in water will absorb a larger or smaller quantity of it. It is a common experience that cut flowers or branches when placed with their cut surfaces in water will absorb for a time sufficient water to prevent withering. The evidence before us is insufficient to prove that the absorption of water is an important normal function of leaves. Their true absorbent function will form the subject of the next lecture.

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LECTURE V.

ABSORPTION (*continued*).

II. *Absorption of Gases.*

AN interchange of gases is constantly taking place between every living cell and the medium in which it exists: in the case of terrestrial plants, between the plant and the air, in the case of aquatic plants, between the plant and the water. When the plant is a simple one, each cell of it is in direct relation with the medium; when it is of complex structure, there is, in terrestrial plants, some means by which the more internal cells are brought into relation with it. The members which are especially adapted for this purpose in the higher plants are the leaves; so we may say that just as their roots are the special organs for the absorption of water and substances in solution, so their leaves are the special organs for the absorption of gases, although this is effected to some extent by other members also.

Let us briefly consider the structure of the leaf. The blade or lamina, the part with which we are especially concerned at present, consists, speaking generally, of a parenchymatous tissue, termed *mesophyll*, between the cells of which there are intercellular spaces more especially towards the lower surface. This tissue is traversed by numerous fibrovascular bundles, forming the so-called *veins* of the leaf, and it is covered on both surfaces by a layer of cells which is the *epidermis*. The parenchymatous cells have thin

cellulose walls, and, in addition to protoplasm and cell-sap, they contain numerous chlorophyll-corpuscles: a full account

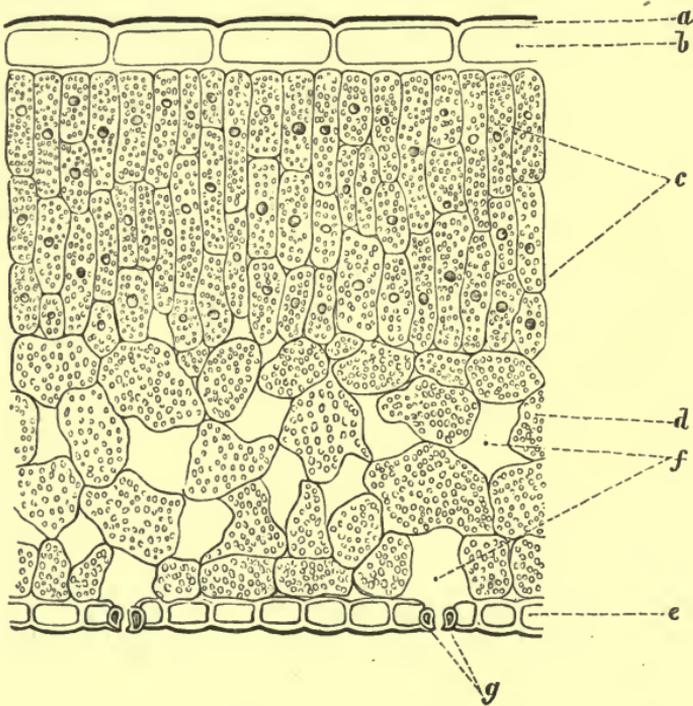


FIG. 13. Transverse section of the lamina of a leaf: *a*, the cuticle; *b*, the epidermis of the upper surface; *c*, the palisade-parenchyma; *d*, the spongy parenchyma; *c* and *d* together constitute the mesophyll; *e*, epidermis of lower surface; *f*, intercellular spaces; *g*, guard-cells of a stoma. The cells of the mesophyll contain chlorophyll-corpuscles.

of the structure of these bodies will be given hereafter. The epidermal cells usually contain no chlorophyll-corpuscles, and their external walls are much thickened and cuticularised: moreover they are packed closely together, so that they form a membrane, the continuity of which is interrupted here and there by intercellular spaces, called *stomata*, each of which is bounded by usually two specially modified epidermal cells, the *guard-cells*. The stomata open internally into the intercellular spaces of the mesophyll, and thus the air can have free access to the interior of the leaf, and from this to the rest of the plant. That the stomata do thus communicate with the intercellular spaces can be proved

not only by microscopical observation, but also by direct experiment. A simple means of doing this is to place the blade of a leaf in the mouth and to immerse the cut surface of the leaf-stalk in water: if now air be forced into the blade by the mouth, a stream of bubbles will escape from the end of the petiole which is in the water.

Stomata are by no means confined to leaves, although they are most abundant on them. They are present, at some time at any rate, in the epidermis of all subaerial organs excepting, in certain cases, some of the floral leaves: they are never to be found on roots, nor on submerged plants, and they are confined to the Cormophyta. In the case of the stems and branches of perennial plants, in which the epidermis is thrown off and is replaced by cork, the stomata are of course lost, but a means of communication between the internal tissues and the external air is provided by certain structures which are termed *lenticels*. These consist

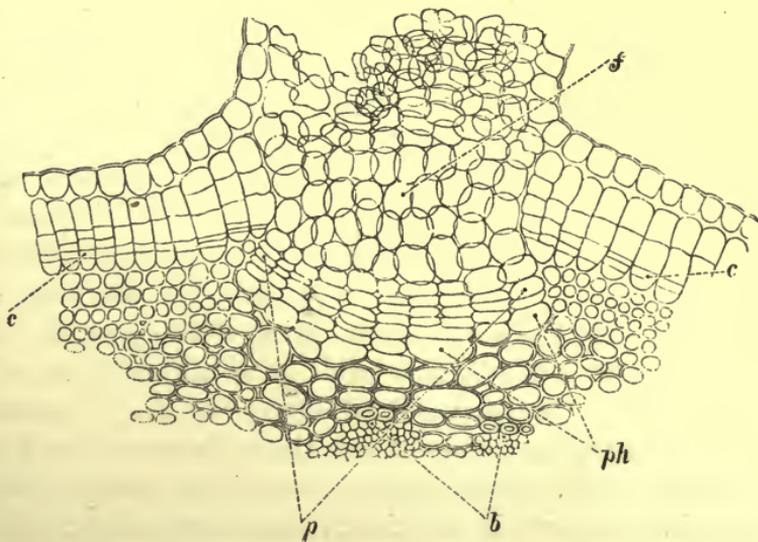


FIG. 14 (after Stahl). Section of a Lenticel of *Sambucus nigra*: *f*, lenticel-tissue; *c*, cork-cambium; *p*, cambium layer of the lenticel; *ph*, phelloderm; *b*, bast-bundles.

of cells belonging to the cork-layer; but whereas the cells of the cork are closely packed, the cells of the lenticels have

intercellular spaces through which gases can pass. That this is the case is proved by the fact that a very slight pressure suffices to force air through them. The lenticels are not, however, permanently open. If an attempt be made in the winter to force air through them, it will be found that none will pass, and microscopical examination will shew that they are closed by a compact layer of cork-cells. It appears that in the autumn, the cork-cambium beneath the lenticel produces, instead of loose lenticel-tissue, corky layers which interrupt the communication between the air and the interior of the plant. In the spring these corky layers are ruptured by the pressure exercised upon them by the lenticel-tissue which is now being formed in consequence of the renewed activity of the cork-cambium, and thus the communication is restored.

Unger made the interesting discovery that the lenticels of stems are developed at points which correspond in position to the stomata of the epidermis. Lenticels also occur very generally on roots.

It is often thought that the stomata are of primary importance in relation to the absorption and exhalation of gases by leaves. Boussingault has found, however, that the upper surface of the leaves of various plants with which he experimented (Cherry-Laurel, Poplar, Chestnut, Peach) absorbed carbon dioxide more actively than the lower surface, although the upper surface had scarcely any stomata whereas they were very numerous on the lower. The stomata have evidently no effect upon the absorption of this gas: it would be interesting to know if this holds good also with regard to the absorption of oxygen. Barthélemy regards the stomata as affording rather a means of exit than of entrance to gases; he concludes that, under normal conditions, a slight rise of pressure in the plant is sufficient to cause an escape through the stomata of the gases in the intercellular spaces. The part played by the stomata in the interchange of gases is not, however, their primary function; their chief physiological significance is in relation to the exhalation of watery vapour (transpiration). We will therefore defer a detailed account of their mode of action until that process is under discussion.

The absorption of gases is effected then, principally at least, by the superficial cells of the leaves. Now as to the mode of absorption. We may consider here, once for all, the mode in which gases are absorbed by the cells of plants, for it is the same in all cases. Gases, like solid substances, can only be absorbed in solution. They may be brought to the surface of the cell-wall already dissolved in water, as in the case of submerged plants, or they may be dissolved from the atmosphere by the sap which saturates the cell-wall, as in the case of land-plants. In either case they reach the interior of the cell in solution. When a gas has been taken up at the surface it diffuses throughout the cell-sap, and thus fresh quantities can be taken up from without until the limit of solubility is reached, when absorption ceases. If, however, the metabolism of the cell changes the chemical condition of a gas, if it causes its decomposition or causes it to enter into new combinations as it is absorbed, then its absorption will be continuous. On comparing these statements with what was said as to the absorption of substances by the roots, we find that the conditions of absorption are essentially the same in the two cases.

There exists another important similarity between the absorption of gases and the absorption of substances in solution, namely this, that just as the root can only absorb a solution below a certain degree of concentration, so the leaf can only absorb a gas below a certain degree of pressure. For instance, the pressure of the carbon dioxide in the air is very slight; it was first observed by Percival that an increase in the quantity of carbon dioxide in the air is favourable to the growth of the plant; de Saussure found that a considerable increase is prejudicial, and Godlewski, by his more detailed investigations, shewed that the optimum proportion is from 8—10 per cent., that is that carbon dioxide is most readily absorbed by the plant when its pressure is about 200 times greater than in ordinary air. Boussingault found that when leaves are exposed to sunlight in an atmosphere of pure carbon dioxide at the ordinary pressure they cannot decompose it, but if the carbon dioxide

is at a low pressure (in his experiment 0.17 mm.) they can do so. Results of a similar nature have been obtained by Bert with reference to the oxygen of the air: they may be briefly stated thus, that increase or diminution of the atmospheric pressure is prejudicial to plant-life, but this prejudicial effect is not produced when the experiment is so arranged that the oxygen present exerts a pressure approximately equal to that which it exerts in ordinary air. These facts fully illustrate the relation of the pressure of a gas to its absorption.

We may now enquire what are the gases which are absorbed by the leaves of plants, without, however, entering upon a discussion of their relative importance to the well-being of the plant; that subject will be treated of in subsequent lectures.

The air, the medium by which the leaves of land-plants are surrounded, is a mixture of gases having the following average quantitative composition.

Oxygen.....	20.61	per cent. by volume.
Nitrogen	77.95	” ”
Carbon dioxide	0.04	” ”
Aqueous vapour	1.40	” ”
Ammonia }	traces.	
Nitric acid }		

Since all these gases are soluble in water, it may fairly be concluded that they can be absorbed by the cells of the leaves, and this is in fact the case. Let us imagine for instance a living cell, the cell-sap of which contains no gases in solution, exposed to air for a short time. In this case, the proportion of each gas absorbed will depend upon its solubility in the cell-sap. Now the solubilities of the gases of which air is composed bear the following relations to each other:

1 vol. of water, at 15° C. dissolves	
Oxygen.....	0.030
Nitrogen	0.015
Carbon dioxide	1.002

hence, since the amount of a gas dissolved from a mixture is proportionate to the relative volume of it in the mixture multiplied into its coefficient of solubility, the proportions of these gases dissolved by the cell-sap of the cell under consideration will be, at a temperature of 15° C. and 760 mm. pressure,

Oxygen.....	0·6183
Nitrogen	1·1692
Carbon dioxide	0·0400

and these may be assumed to be the proportions in which these gases are at first absorbed by the cell.

But it has been abundantly proved that whereas when the cells of a plant are saturated with nitrogen no further absorption of this gas takes place, the absorption of oxygen and carbon dioxide is continuous provided that the conditions are favourable. The total quantity of these gases absorbed in a given time is far greater than that of nitrogen ; in fact the amount of nitrogen absorbed by a plant is nil, inasmuch as the cell-sap is saturated with it from the first. From this we may conclude that oxygen and carbon dioxide undergo chemical change after their absorption, that they enter into the metabolic processes of the living cells, whereas nitrogen does not.

Absorption of Oxygen.

That plants absorb oxygen is a fact which has long been known. Scheele and Priestly both found that, under certain conditions which they did not investigate, plants deteriorate the quality of air ; but Ingenhousz was the first to clearly define the relation of the plant to the atmosphere. With a more developed chemical science at his disposal, de Saussure was able to establish definitely the importance of oxygen for the life of plants, and his results have been confirmed by all subsequent observers.

There are, however, lowly organised plants which can live, for a considerable time at least, without being supplied

with free oxygen; such as the Fungi which produce alcoholic fermentation (*e.g.* Yeast) and putrefaction (*e.g.* Bacteria); but these Fungi readily absorb free oxygen when they can obtain it.

We will now illustrate the absorption of oxygen by different plants and parts of plants, by reference to experiments.

The most marked case of the absorption of oxygen by plants is afforded by Fungi. Pasteur and others have found that Fungi can absorb the whole of the oxygen present in a closed space.

Marcet obtained the following results with *Boletus versicolor*: four specimens weighing 9 grammes remained for 12 hours in a receiver containing 120 c.c. of air.

Composition of the air,	before the experiment,	after the experiment:
Nitrogen	94·8 c.c.	94·7 c.c.
Oxygen	25·2 „	0·6 „
Carbon dioxide	—	28·7 „
	120·0 c.c.	124·0 c.c.

It appears that the property of absorbing the whole of the oxygen present is possessed by all plants. For instance, Wolkoff and Mayer found this to be the case in their experiments on seedlings (*Polygonum Fagopyrum*, *Tropæolum majus*).

Various observers (de Saussure, Oudemans and Rauwenhoff, Fleury) have found that germinating seeds absorb considerable quantities of oxygen, and exhale carbon dioxide.

De Saussure determined that one gramme of seed absorbed oxygen and exhaled carbon dioxide as follows:

Hemp, 43 hours at 22° C.
 absorbed 19·70 c.c. of oxygen,
 exhaled 13·26 c.c. of carbon dioxide.

Colza, 42 hours at 21·5° C.
 absorbed 31·40 c.c. of oxygen,
 „ 0·73 c.c. of nitrogen,
 exhaled 24·39 c.c. of carbon dioxide.

Madia, 72 hours at 13° C.
 absorbed 15·83 c.c. of oxygen,
 exhaled 11·94 c.c. of carbon dioxide.

Oudemans and Rauwenhoff found that the amount of oxygen absorbed varied in the case of the seeds of different species of plants, and that it diminished gradually during the process of germination.

Lory shewed that phanerogamic plants which contain but little chlorophyll, such as various species of Orobanche, and *Neottia Nidus-avis*, absorb oxygen under all circumstances :

A flowering plant of *Orobanche Teucrii* absorbed in thirty-six hours 4·2 c.c. of oxygen for every gramme of its weight : a plant without flowers absorbed 2·68 c.c. of oxygen for every gramme.

but according to Drude the exhalation of oxygen by *Neottia* is greater than the absorption when the plant is exposed to intense light.

De Saussure ascertained that flowers absorb oxygen :

Thus,

flowers of <i>Cheiranthus incanus</i>	absorbed	11·0 vols. of oxygen	in 24 hours,
double flowers of "	"	7·7	" "
flowers of <i>Tropæolum majus</i>	"	8·5	" "
" <i>Datura arborea</i>	"	9·0	" "
" <i>Passiflora serratifolia</i>	"	18·5	" "
" <i>Daucus Carota</i>	"	8·8	" "

the volume of the flower being taken as unity.

he found further that the essential organs of the flower are those which absorb the largest proportion of oxygen, and that the andrœcium does so more actively than the gynœceum.

Cucurbita Melo-Pepo.

The volume of the organ being taken as unity, the organs of the flowers absorbed the following quantities of oxygen :

				absorbed in 10 hours
Staminate flower	7·6 vols. O.
Pistillate "	3·5 "
Anthers "	11·7 "
Stigmas "	4·7 "

Spike of Typha latifolia.

				absorbed in 24 hours	
Pistillate and staminate flowers mixed	9.8	vols. O.
Staminate flowers	15.0	„
Pistillate	„	6.2	„

Zea Mais.

				absorbed in 24 hours	
Spike of staminate flowers	9.6	vols. O.
Spike of pistillate flowers	5.2	„

From his observations it appears that the absorption of oxygen is most active when the flower is fully open.

As to the absorption of oxygen by roots, it appears, from the researches of de Saussure and of Dehérain and Vesque, that if the roots are not supplied with this gas, the plant will soon begin to shew signs of unhealthiness, and will ultimately die. It must not be concluded from this, however, that the root absorbs oxygen and supplies it to the rest of the plant: this effect is to be attributed simply to the fact that, in the absence of oxygen, the roots become incapable of performing their proper absorbent functions. With regard to the quantitative estimation of the oxygen absorbed, de Saussure found that a root, detached from the rest of the plant and placed in a closed receiver containing air, will absorb a quantity of oxygen which never exceeds its own volume: if, however, the root be still in connexion with the stem and leaves of the plant and these be outside the receiver, the root will absorb many times its volume of oxygen. It appears from this that the carbon dioxide formed in the isolated root cannot escape from it after equilibrium is set up between the gases of the root and those of the receiver.

The following figures are taken from Dehérain and Vesque's paper: in their experiments the roots were still in connexion with the stem and leaves which were outside the receiver.

Composition of the air in the receiver after the root
had been in it for 24 hours.

Total quantity of gas in the receiver, 135.2 c.c.

Oxygen, 22.6.

Carbon dioxide, 2.0.

Nitrogen, 110.6.

An equal quantity of normal air contains 28.34 c.c. of oxygen, and a trace of carbon dioxide.

With regard to the absorption of oxygen by plants and parts of plants which contain chlorophyll abundantly, Ingenhousz pointed out that they convert a considerable portion of the air surrounding them into carbon dioxide when they are not exposed to light. De Saussure found that leaves of the Oak, the Acacia, the Spanish Chestnut, and other plants, if left during the night in a receiver containing air over mercury, absorbed oxygen. Boussingault has also found that leaves absorb oxygen in darkness.

Subjoined are some of the quantitative results which de Saussure obtained: in each case the experiment lasted 24 hours, and took place in the dark: the quantities of oxygen absorbed are expressed in terms of the volume of the leaf taken as unity.

Holly	(September)	0·86 vol. O.
Box	"	1·46 "
Cherry Laurel	(May—young leaves)	3·20 "
"	(September)	1·36 "
Beech	(August)	8·00 "
Oak	(May)	5·50 "
Poplar	(May)	6·20 "
"	(September)	4·36 "

From these figures it appears further that young leaves absorb more actively than older ones.

Since it was known that, as we shall see hereafter, leaves and other parts of plants which contain chlorophyll absorb carbon dioxide and give off oxygen when they are exposed to sunlight, it was concluded that an absorption of oxygen takes place only in darkness. It was thought that during the day green plants absorbed carbon dioxide and gave off oxygen, whereas at night they absorbed oxygen and gave off carbon dioxide. The researches of Garreau shewed, however, that this view was not correct. He came to the conclusion that, in leaves exposed to the light, two distinct processes are in operation, in the one oxygen is absorbed and carbon dioxide is exhaled, in the other carbon dioxide is absorbed and oxygen is exhaled. When the light is intense, when the leaves are exposed to bright sunlight for instance, the relative activity of the latter of these processes is so much greater than

that of the former that it appears as if the former only were in operation.

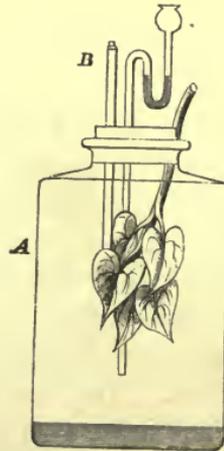
The following may be cited as examples of the results which he obtained ; the figures in the third column denote the amount in c.c. of diminution of the air in the tube (Fig. 15) effected by 100 grammes of the plant.

	Temperature	Time	Diminution in c.c.	Light
<i>Morus dasyphylla</i>	17° C.	9 a.m.—6 p.m.	35	Fine day—shade
<i>Morus dasyphylla</i>	17°	9 " —6 "	64	Badly lighted room
<i>Phaseolus multiflorus</i>	15°	10 " —6 "	40	Dull day
<i>Dahlia variabilis</i>	16°	11 " —6 "	14	Fine day—shade
<i>Acer eriocarpon</i>	17°	12 " —6 "	45	Diffuse daylight
<i>Cerasus Lauro-cerasus</i>	18°	10 " —6 "	20	In a greenhouse

FIG. 15.



FIG. 16.



Figs. 15 and 16 illustrate Garreau's experiments :

FIG. 15. ABC is a glass tube of 1000—2000 c.cm. capacity ; its lower end is immersed in a vessel D containing water ; at B there is a watch-glass contain-

ing solution of potash. The carbon dioxide exhaled by the branch introduced through the cork *A* is absorbed by the potash. The water rises in the lower part of the tube, indicating a diminution in volume of the air; this diminution is due to the absorption of oxygen by the branch.

FIG. 16. *A* is a glass vessel containing a solution of baryta at its lower part; a branch is fixed in the cork, and the baryta solution is introduced through the tubes *B*. As carbon dioxide is exhaled a precipitate of barium carbonate is produced.

In view of the large quantity of oxygen which, as we have seen, is absorbed by plants, more especially by Fungi, we must conclude that this gas is used up in their metabolic processes, and with these we may also connect the exhalation of carbon dioxide. The absorption of oxygen and the exhalation of carbon dioxide constitute what is known as the *Respiration* of plants. The significance of this in the economy of the plant will be discussed hereafter.

Absorption of Carbon Dioxide.

De la Hire (1690) and, after him, Bonnet (1754) found that green plants or parts of plants when immersed in water and exposed to sunlight gave off bubbles of gas; and Bonnet further observed that no bubbles were given off when the water had been previously boiled. Priestley (1772) pointed out that "fixed air" is absorbed by green plants when exposed to sunlight, and shewed that the air evolved by leaves under these circumstances is "dephlogisticated." Sénéquier (1783) proved that the amount of "pure air" evolved by green plants in water is greater when a considerable amount of "fixed air" is held in solution, and he thus established a connexion between the absorption of "fixed air" and the exhalation of "pure air" by green plants when exposed to sunlight. De Saussure (1804) confirmed Sénéquier's results, and made some quantitative determinations of the amount of carbon dioxide absorbed and of oxygen given off.

He obtained, for instance, the following results: the stems and leaves of seven Periwinkle plants (*Vinca*) were introduced into a glass receiver which contained, in addition to the plants, air of the following composition:

Nitrogen	4199 c.c.
Oxygen	1116 „
Carbon dioxide	431 „
Total amount			5746

The apparatus was exposed daily to the sunlight, and in the seventh day the plants were withdrawn and the gas in the receiver analysed ; its composition was found to be,

Nitrogen	4338 c.c.
Oxygen	1408 „
Carbon dioxide	0 „
			<hr/>
Total amount			5746

Boussingault (1844) gave the direct proof that the leaves take up the carbon dioxide which is present in such small proportion in the air. He passed air through a large glass receiver in which a branch of a Vine, bearing about twenty leaves, was hermetically fixed, and he found that, when the apparatus was exposed to light, the proportion of carbon dioxide in the air which had passed through the receiver was much smaller than that in the external air : in one case the proportion found in the air which had passed through was 0.0002, whereas the proportion in the external air was 0.00045, and in another case the proportions were 0.0001 and 0.0004.

This sort of experiment has been repeated with various plants by Vogel and Wittwer, by Rauwenhoff, and by Corenwinder, the results being in all cases of much the same kind.

It is clear, therefore, that the leaves or, more generally speaking, the parts of plants which contain chlorophyll, absorb carbon dioxide from the air, under the influence of sunlight.

There is no experimental evidence which would tend to shew that this property is under any circumstances possessed by plants or parts of plants which do not contain chlorophyll. And yet it was thought for a considerable time that a portion at least of the carbon dioxide which a plant requires, is absorbed by the roots from the soil. Thus Liebig distinctly asserted that roots absorb carbon dioxide, and Unger argued that the increase of carbon in a plant within a given time

is greater than could be accounted for by the absorption of carbon dioxide from the air, and that therefore some other source of supply of carbon—probably the carbon dioxide absorbed by the roots—must be assumed. Recent investigations have, however, shewn that this theory is quite untenable. Böhm has found that a plant cannot live long when its leaves are enclosed in a receiver containing air from which all carbon dioxide has been removed, even although its roots are in soil rich in humus and therefore also in carbon dioxide; and Moll has come to the conclusion that the carbon dioxide, which may be present in one part of a plant does not contribute to the formation of starch in the chlorophyll-corpuscles of another part. We are therefore justified in holding the opinion that the carbon dioxide which a plant requires is absorbed from the air by those of its organs which contain chlorophyll.

Figures illustrating Moll's experiments.

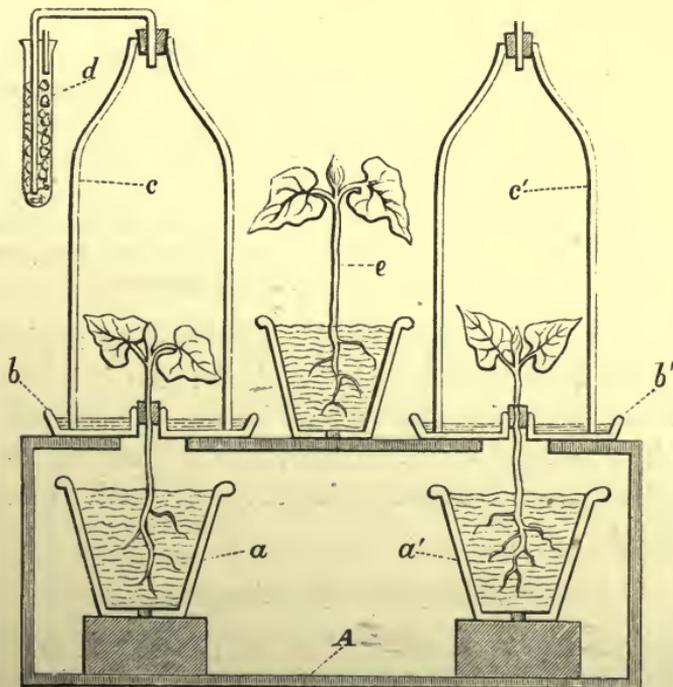


FIG. 17. The glass jar covering the left-hand plant stands in a dish (b) containing solution of potash, and its contents communicate with the air by means of

the tube *d* which contains pumice-stone saturated with solution of potash : the plant passes through a tubulature in the dish *b*.

The left-hand plant is the control-experiment ; the dish *b'* contains only water, and the air has free access to the interior of the jar.

The air in *c* can contain no carbon dioxide, whereas it is present in the air contained in *c'*. Moll found that the chlorophyll-corpuscles in the leaves of the plant in *c* contained no starch grains, after exposure to light, whereas those of the plant in *c'* contained them abundantly.

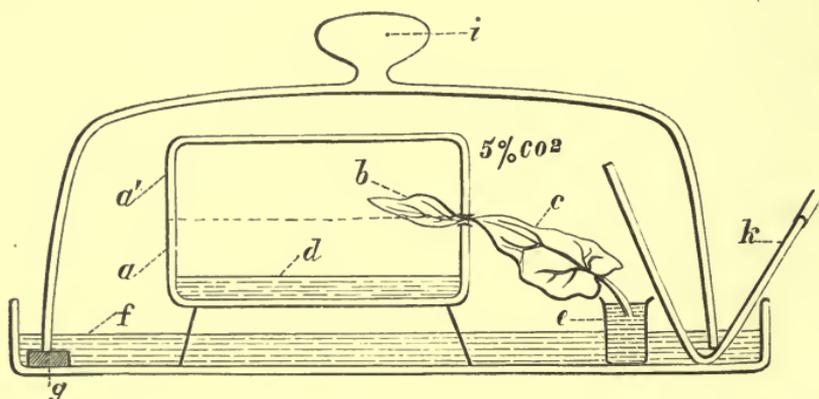


FIG. 18. The glass bell-jar *i* stands in a vessel containing water ; in this is placed a leaf *bc* ; carbon dioxide to the extent of 5 per cent. is introduced into the air of the bell-jar by means of the tube *k* : the apical end of the leaf *b* is introduced into another glass vessel containing a quantity of solution of potash *d*.

Thus one part of the leaf *c* is in an atmosphere which contains a large quantity of carbon dioxide, the other part *b* is in an atmosphere which contains none. Moll found that when the whole apparatus was exposed to light, starch was formed in the chlorophyll-corpuscles of *c*, but none in those of *b*.

The amount of carbon dioxide absorbed by a plant is so considerable that there can be no doubt that it is chemically transformed, after its absorption, in the metabolism of the plant. The nature of the changes which it undergoes will be discussed when we are considering the constructive metabolism of the plant.

Absorption of Nitrogen.

The question as to whether or not plants can take up any appreciable quantity of free nitrogen from the air has long engaged the attention of chemists and physiologists. Priestley and Ingenhousz concluded from their experiments that plants

were capable of doing this ; S en ebier, Woodhouse and de Saussure on the other hand found that no such absorption took place. Boussingault, and after him Lawes, Gilbert, and Pugh, arrived at the same conclusion as de Saussure but by a different method : instead of determining the composition of the air in a closed receiver, containing the plant, at the beginning and at the end of an experiment, they determined the amount of nitrogen in a seed and then allowed a similar seed to germinate under such conditions that no nitrogen except the free nitrogen of the air could have access to it. They ascertained that the amount of the nitrogen in the seedling was not greater than that in the seed, and they therefore concluded that the young plant had not taken up this gas from the air. Their investigations will be discussed more fully hereafter in discussing the nature of the food of plants.

It must, however, be borne in mind that the cell-sap of plants does doubtless hold dissolved in it a certain amount of free nitrogen, since, as we have seen, this gas is soluble to some extent in water. The limit of solubility is soon reached when a plant is growing in the air, and so, if for the purposes of experiment, the plant is then placed in a receiver containing a limited quantity of air, there will be, as de Saussure found, no diminution of the free nitrogen present. There is a very great difference between the relative amounts of oxygen, carbon dioxide, and nitrogen, which are absorbed in the gaseous form by plants. We have seen that under certain circumstances the whole of the oxygen in a limited atmosphere may be absorbed by plants, and this is true also of the carbon dioxide, whereas no nitrogen is absorbed, for the cell-sap of all plants exposed to the air is saturated with this gas. We concluded, on account of the large quantities of oxygen and carbon dioxide which are absorbed, that these gases enter into the metabolism of the plant ; we must therefore conclude that, since the amount of free nitrogen absorbed by a plant is so small that it can be accounted for by the mere solubility of the gas, this gas does not enter into the metabolism of the plant.

Absorption of Ammonia.

The air, as we have seen, occasionally contains minute quantities of ammonia and nitric acid. Of these gases, the former is given off during the combustion and decomposition of nitrogenous organic substances, the latter is formed probably by the direct combination of the nitrogen and oxygen of the air which is effected by lightning-flashes. These gases do not, however, exist isolated in the atmosphere: the ammonia will combine with the nitric acid, and, in the absence of this acid, it will combine with the carbonic acid of the air.

The quantities of these substances present at any time in the air are very small, and, inasmuch as they are very soluble in water, and will therefore be washed out of the air by rain, it is obvious that this source of combined nitrogen cannot be of any great importance to the plant. Still the question as to whether or not plants can absorb ammonia in the gaseous form from the air is an interesting one, and one which has received the attention of many observers. The researches of Ville prove that ammonia can be absorbed from the air by the leaves, but that this absorption is very small under ordinary circumstances is shewn by an experiment of Boussingault. A Dwarf Runner was planted in a soil containing no nitrogen and left to grow in the open air, protected however, from the rain, for nearly four months; it was then estimated that the plant had gained 0.0031 grm. of nitrogen during the experiment. Sachs found that a plant absorbed ammonium carbonate (probably carbamate) when it was present in the air, and this result has been since confirmed by Mayer and by Schlösing.

The following are some of Mayer's results. In his experiments, Cabbage-plants of approximately the same weight were grown under various conditions, and the proportion of nitrogen present in each was determined at the close of the experiment: one of the plants was analysed at the beginning of the experiment, to afford a means of comparison.

	Dry weight	N.	Percentage of N.
Plant at commencement of expt.	0.364 grm.	0.0100	2.7
„ grown in open air—end of expt.	0.713 „	0.0128	1.8
„ „ receiver without NH ₃	{ 0.715 „	0.0138	1.9
	{ 0.779 „	0.0129	1.7
„ „ „ with NH ₃	{ 1.090 „	0.0240	2.2
	{ 1.562 „	0.0380	2.4

Occasionally other gases, such as sulphur dioxide, sulphuretted hydrogen, and hydrochloric acid, are present in the air in the neighbourhood of chemical works. The plants of the district very soon become unhealthy and die, so there is reason to believe that these gases are absorbed by the leaves.

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LECTURE VI.

THE MOVEMENT OF WATER IN PLANTS.

WE have now to consider the distribution throughout the plant of the water which, as we saw in the last lecture, is absorbed by the roots.

There is no doubt that the distribution of water takes place, to some extent at least, in the same manner and by virtue of the same forces as its absorption, that is, it passes by osmosis from one cell to another just as it passed originally from without into the superficial cells of the plant. Further, inasmuch as the movement is the expression of a tendency towards fluid equilibrium in the plant, that is, that the proportion of water in each cell should be the same throughout, the direction of this movement is not necessarily constant: it proceeds from those parts which are relatively rich in water towards those which are relatively poor, and naturally if water is given off at any point of the free surface of the plant, a current will be set up in the tissues towards that point.

These statements apply not only to water, but also to the gases and the substances which the water holds in solution. These travel, as we have seen (p. 44), by osmosis from cell to cell, the direction of their movement being determined simply by the relative quantities of them in different parts of the plant. The final cause of the movement is the removal of the various substances from the sphere of osmotic activity, in consequence of the chemical or physical changes which they undergo in the living cells of different parts of the plant.

These changes are more especially active for different substances in different parts of the plant, and consequently the rapidity of transmission of certain substances in any particular direction will be greater than that of others. Thus, the inorganic substances absorbed by the roots pass into the cells of the leaves where they are concerned in the processes of constructive metabolism which are in operation in those organs, and the products of these processes pass from the leaves, either to those parts of the plant in which growth is actively proceeding and plastic material is required, or to those parts, such as seeds, tubers, etc., in which stores of organic substances are being laid up.

This is the only way in which the distribution of water is effected in cellular plants, in plants, that is, which do not possess fibrovascular bundles. It is only one of the ways in vascular plants, and we will now endeavour to ascertain what the other ways are.

It is a matter of common observation, which Ray seems to have first carefully noted, that when the stems of vascular plants are cut in the spring, a flow of watery fluid frequently takes place from the cut surface of that portion of the stem which is connected with the root. This fact was investigated with great thoroughness by Hales, and he concluded that there is "a considerable energy in the root to push up sap in the bleeding-season." The correctness of Hales' conclusion was confirmed by the experiments of Dutrochet, in the course of which he ascertained that a flow of sap only takes place from the cut surface of a stem when it is organically connected with the roots, and from that of a root when it is in connexion with the soil by means of root-hairs. The *Root-pressure*, as this force is termed, is therefore the expression of the absorbent activity of the root-hairs.

This subject was studied at a later period by Hofmeister. He found that "bleeding" is not peculiar to woody plants, as his predecessors had supposed, but that it occurs in herbaceous plants also; and further, that, although it can be most readily observed in the spring, it may be artificially induced at any season.

The composition of the fluid obtained from a Birch in the spring was found by Schröder to be the following :

1 litre contained

Ash	0.52	grms.
Sugar (Levulose)	12.00	"
Proteid	0.02	"
Malic acid	0.51	"

Schröder confirmed Knight's observation that the proportion of sugar is less the higher the part of the tree from which the fluid is taken, and he found that this was generally true of the other substances also.

But the root-pressure does not only manifest itself by causing a flow of sap from the cut surfaces of plants; it also causes, in many plants, the exudation of drops of sap at the free surface. Thus drops may commonly be seen on the sur-

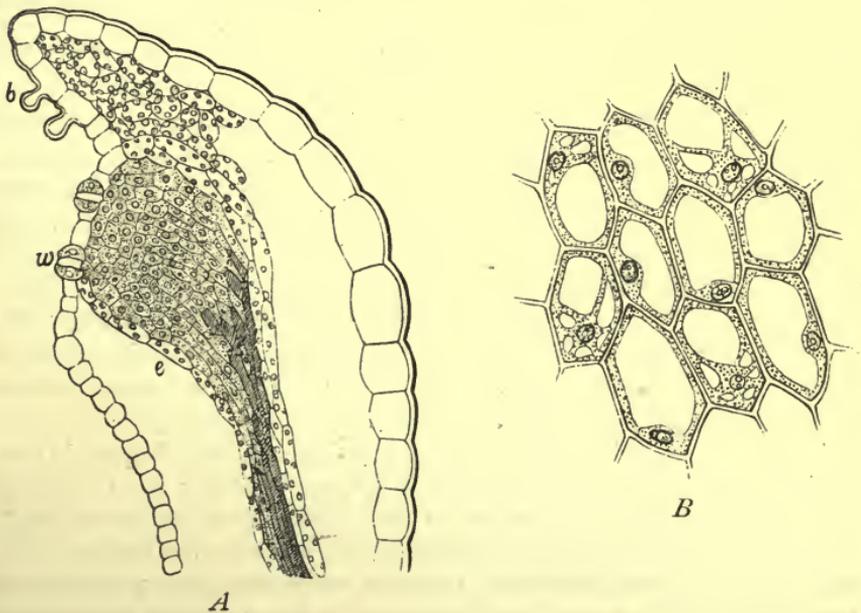


FIG. 19 (after Gardiner): *A*, section of leaf of *Saxifraga crustata*, shewing the water-gland, *e*, which is continuous at its base with a fibro-vascular bundle; *w*, water-pore; *b*, hairs to which the deposit of calcium carbonate becomes attached on the evaporation of the exuded drops of water.

B, cells of the gland more highly magnified.

face of certain Fungi (*Pilobolus crystallinus*, *Penicillium glaucum*, *Merulius lacrimans*) which have been doubtless exuded as a consequence of the hydrostatic pressure existing in the

plant, set up by the active absorption going on in the organs (rhizoids) which here perform the functions of roots. Again, if care be taken to prevent evaporation, it will be found that drops are formed on the margins and at the apices of the leaves, especially the younger ones, of many plants, such as Grasses, Aroids, Alchemillas, Saxifrages, etc. That the formation of these drops depends upon the forcing of water into the cavities of the vessels by the root-pressure is shewn by the fact that if the stem be cut off and placed in water, no more drops will appear on the leaves. If, in this experiment, the cut stems be allowed to remain for some days in water, they will in many cases produce adventitious roots: when this takes place the formation of drops on the leaves at once recommences. Again, Moll has shewn that if the root-pressure be replaced, in the case of a cut-off branch, by the pressure of a column of mercury, an exudation of drops will take place.

Some idea of the quantity of water which thus exudes in the form of drops is afforded by the following observations. Williamson obtained half-a-pint of fluid in one night from a leaf of *Caladium distillatorium*. Unger obtained from *Richardia Ethiopica*, in one case, 26·5 grms. from six leaves in eleven days, and in another, 36 grms. from four leaves in ten days: from a leaf of *Colocasia antiquorum* (var. *Fontanesii*) Duchartre obtained in one night (August) 12 grms., in the following night 13·1, and later (commencement of September) 14·35 grms.; in other instances he obtained as much as 22·6 grms. On several occasions Duchartre observed the formation of 120 drops in one minute.

Those leaves which exhibit this exudation of drops frequently have specially modified apertures, termed *water-pores* (see Fig. 19, A), through which the drops come to the surface, and these pores are placed singly or several together over the termination of a fibrovascular bundle, which may or may not be glandular. In other cases the drops pass through the ordinary stomata, and in others again the water exudes, not through any special openings, but simply through the walls of the epidermal cells.

It can be readily observed that the liquid which is poured out by a bleeding stem escapes from the orifices of the vessels of the wood, and it is also in these channels that it is conveyed to the leaves on which drops are formed. We must now endeavour to become acquainted with the mode in which the fluid absorbed by the root-hairs obtains access to the vessels,

and in order to do this, we will first of all briefly consider the structure of the root.

The structure of the root is tolerably uniform throughout the vascular plants. It consists, generally speaking, of a

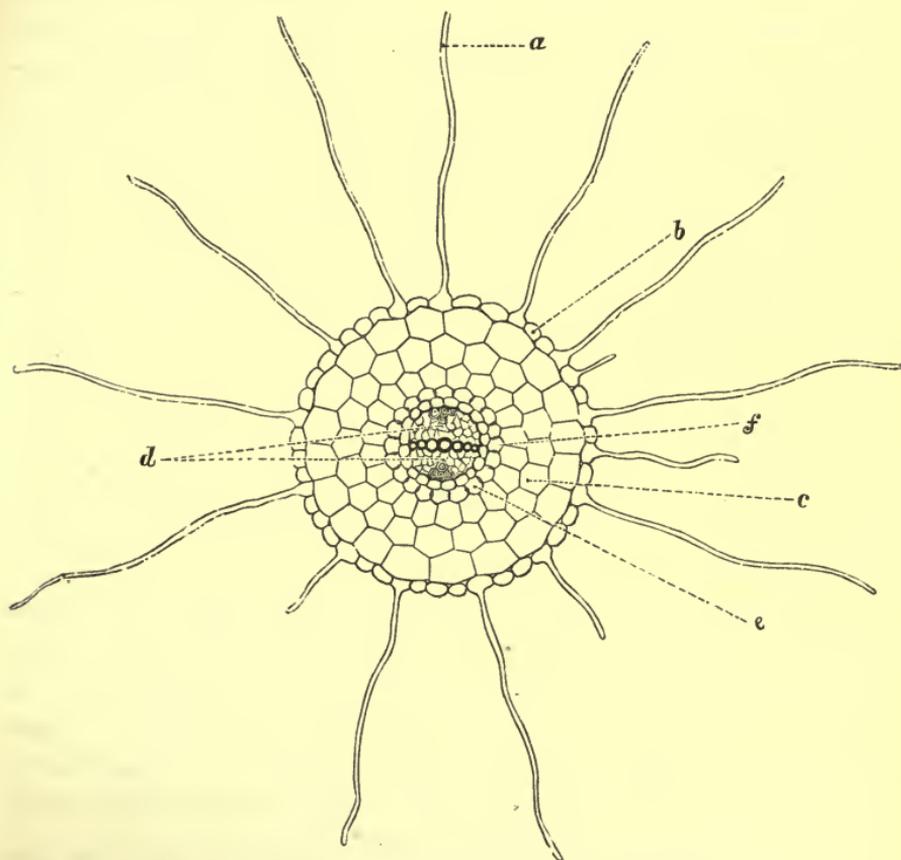


FIG. 20. Transverse section of the root of *Lepidium sativum* (the Cress): *a*, the unicellular root-hairs; *b*, the epidermis; *c*, the cortical parenchyma; *d*, the axial fibrovascular cylinder; *e*, the bundle-sheath (endodermis); *f*, the central wood-vessels.

central fibrovascular cylinder which may or may not enclose a certain amount of pith: this cylinder is surrounded by several layers of parenchymatous cells, and the most external of these layers is in contact with the epidermis, of which certain cells are modified into root-hairs (Fig. 20). Water and substances in solution are absorbed, as we have already seen, osmotically by the root-hairs, and they are transferred in this

way through the layers of parenchymatous cells. It is obvious, however, that water cannot pass by osmosis from one of the cells of the innermost parenchymatous layer into an adjoining vessel, for the conditions of osmosis are not fulfilled, inasmuch as the vessel at first contains no liquid. If water is to pass from a parenchymatous cell into the vessel it can only do so by filtration. For this, a certain pressure is necessary, and this is set up by the absorbent activity of the root-hairs and of the parenchymatous cells; the system of cells absorbs large quantities of water, more indeed than the cells can contain, so that at length the resistance of the cell-walls is overcome at what is presumably the weakest point, and water filters into the cavities of the vessels of the wood. There it collects, and it may in certain cases fill the whole vascular system, and then, since absorption is still going on at the roots, sufficient pressure is set up to cause that exudation of drops on the leaves with which we have already become acquainted: if, however, the stem be cut across, the liquid in the vessels will escape, and the phenomenon of "bleeding" will take place.

Since, as we have seen, the amount of liquid in the vessels necessarily depends upon the absorbent activity of the roots, the amount of liquid which escapes from the cut surface of a root-stock in a given time may be taken as a measure of that activity, and the force with which it escapes may be taken as a measure of the osmotic forces which are in operation in the root.

The following figures will give some idea of the rate of flow from the cut surfaces, and of the pressure under which it escapes. Hofmeister obtained the following quantities of liquid:

<i>Urtica urens</i>	gave in 99 hours, 3025 cub. mm.		
<i>Phaseolus multiflorus</i>	"	49	" 3630 "
<i>Helianthus annuus</i>	"	133	" 5830 "

He also made the following determinations of the pressure by means of a mercurial manometer; the numbers given are maxima.

<i>Pisum sativum</i>	12 mm.
<i>Phaseolus nanus</i>	58 "
<i>Phaseolus multiflorus</i>	179 "
<i>Urtica urens</i>	354 "
<i>Vitis vinifera</i>	804 "

For *Vitis*, Hales determined a pressure of $32\frac{1}{2}$ inches of mercury, or 825.5 mm.

It must not be assumed, however, that either the pressure or the rate of flow is uniform. It was observed by Hales that when the column of mercury in the manometer has reached a certain height, it begins to oscillate. We have seen that the height of the column of mercury is a measure of the root-pressure, and therefore its variations must be due to variations of the root-pressure. Hofmeister, in further investigating this matter, made the interesting discovery that these variations have a regular daily periodicity. The column rises in the morning and during the forenoon; then it usually sinks somewhat, rises again towards evening, and falls during the night: frequently the slight fall in the afternoon does not take place. According to the more recent researches of Baranetzky and of Detmer, it appears that the maximum is generally attained in the afternoon, though the exact hour varies with different species of plants: in any case there is usually an interval of about twelve hours between the maximum and the minimum flow. The daily period is constant for plants of the same species, provided, however, that they are of the same age, and that the conditions of their growth have been the same for some time before the experiment; in fact, quite young plants do not exhibit a periodicity at all.

What, now, are the causes of this periodicity? Since we have already learned in a previous lecture that the temperature of the soil has an important influence upon the absorbent activity of the roots, it seems reasonable to suppose that the daily variations of temperature in the soil induce a similar periodicity in the absorbent activity of the roots. This explanation is, however, shewn to be incorrect by the fact that the absorbent activity of roots is perceptibly affected only by very considerable variations of temperature of the soil, variations which are much greater than those which take place in nature; and by direct experiments in which, whilst the temperature of the soil was falling, the rate of flow was found to be increasing. This periodicity is therefore not the immediate result of variations in external conditions; it is

inherent in the absorbent cells themselves. It has doubtless been induced in plants by the daily variations of external conditions, perhaps more especially of illumination, which are involved in the alternation of day and night; but it has become so much a part of the nature of plants that it is exhibited even when the conditions which originally induced it are not present, and it is transmitted from generation to generation. We shall find hereafter that many of the phenomena of plant-life are periodic, and their periodicity has doubtless been induced in like manner.

But the vessels of the wood of plants do not always contain watery fluid. Hales observed that whereas a Vine will bleed freely if its stem be cut in the month of April, no bleeding will take place if it be cut in July. And yet, since in July the foliage of the plant is fully developed, and it is losing considerable quantities of water by transpiration, it is evident, as Hales did not fail to point out, that a current of water must be passing through the stem from the roots to the leaves. This current we will term the *transpiration-current*. What, then, are the channels by which this current travels, if it is not by the cavities of the vessels? An answer to this question is suggested by the structure of those vascular plants—submerged water-plants—which lose no water by transpiration, and in which, therefore, the current in question does not exist. An examination of a transverse section of the stem of one of these plants shews that the wood is but feebly developed, and that the walls of its constituent cells are but slightly lignified if at all. Inasmuch, then, as the wood of these plants, which do not transpire, differs so much in structure from that of those which do transpire, it must be inferred that the wood is of some importance in connexion with this function. The correctness of this inference can be proved experimentally. If a ring of cortical tissue, extending inwards as far as the cambium, be removed from the stem of a dicotyledonous plant, it will be found that the leaves, which are borne on branches arising from the stem above the level at which the ring has been removed, will not exhibit any signs of withering, and Knight found that this was also the case

when both cortical parenchyma and pith were removed. It is evident that, in spite of the removal of these tissues, the leaves still continue to receive from the roots a supply of water which is sufficient to compensate their loss by transpiration, and thus to enable them to remain fresh and turgid. This supply of water must necessarily ascend to them through the wood of the stem, since this is the only tissue which still connects them with the roots.

It is, then, the wood by which the water which is required to make up for the loss by transpiration, is conveyed from the roots to the leaves. In annual plants, the whole of the wood conducts water, but in perennial plants it is only the younger wood. This is proved by an experiment made by Knight and Dutrochet. They cut a ring of tissue out of the stem of an Oak to such a depth that the younger wood (alburnum) was removed and the older wood (duramen) was laid bare. The leaves soon began to wither, and the tree subsequently died. When the wood once becomes dry it loses its capacity for imbibition, and can therefore no longer serve for the conduction of water in the plant.

Since we know that the water travels upwards through the young wood, and since it is stated that at the time when the current is most active, the cavities of the cells and vessels contain no water, we must conclude that it travels in the substance of their cell-walls. This conclusion is quite in harmony with what we know of the properties of lignified cell-walls. We learnt, in the second lecture, that such cell-walls readily take up water, without, however, exhibiting any perceptible swelling, so that their maximum saturation or imbibition is very soon attained. They part with water as readily as they take it up, so that a very small force will set up a current. This is well shewn by the following experiment of Sachs. If a portion, two or three feet long, of the stem of a young Fir be taken in the winter, when it is saturated with water, and the two ends be cut smooth with a knife, they will be found to be quite dry when the piece of stem is held vertically. If now the upper cut surface be wetted by means of a brush, the lower cut surface will be seen to become moist

immediately ; on reversing the position of the two ends the phenomenon will be repeated. This cannot be explained by assuming that the water placed on the upper surface simply runs through open vessels to the lower surface, for the escape of water at the lower surface takes place first from the young wood (alburnum) which, in the Fir and other Conifers, contains no vessels, but consists of completely closed wood-cells (tracheïdes). The true explanation is that the slight pressure exercised by the layer of water on the upper surface is at once transmitted to the water which saturates the walls of the wood-cells and which forms a continuous column, and consequently an immediate escape of water takes place at the lower surface.

Although the experimental evidence given above applies only to Dicotyledons and Conifers, yet it is equally true that in Monocotyledons and in Vascular Cryptogams, the stems of which differ considerably in their anatomy from those of Dicotyledons and Conifers, the transpiration-current travels in the lignified cell-walls. In these plants the amount of wood in the fibro-vascular bundles is very small in relation to the bulk of the stem ; it is probably insufficient to serve as a channel for the supply of water to the leaves. It is probable, as Sachs suggests, that the deficiency is made up by the conduction of water through the walls of the lignified sclerenchymatous cells which form so large a portion of the ground-tissue in the stems of these plants.

Another account of the conduction of the transpiration current has been given by Böhm. He states, and in this he is confirmed by Elfving and by Hartig, that the conducting cells of the wood always contain some water, even when transpiration is most active. He considers the mechanism of conduction to be this ; that when water is withdrawn from a conducting cell, the air which it contains becomes rarefied and the tension in the cell is then less than in the neighbouring cells ; as a consequence water is forced by filtration under pressure through the pits in the wall of the cell until equilibrium is restored. Inasmuch as the air in the conducting cells of the leaves is constantly undergoing rarefaction in consequence of transpiration, a current is set up towards the leaves from the stem.

According to Hartig the duramen usually contains water, and it seems

to serve as a reservoir upon which the conducting cells of the alburnum can draw.

We are now in a position to give a connected account of the transpiration-current. The water absorbed by the root-hairs filters under pressure from the innermost parenchymatous cells of the root into the walls of the adjacent wood-cells: at the same time water is being withdrawn by the transpiring leaves from the wood of the stem, and the demand is met by the conduction of water upwards from the root through the lignified cell-walls. It may happen that the quantity of water forced in a given time into the wood of the root is not so great as that which is transpired by the leaves. Under these circumstances the plant becomes flaccid and begins to wither. On the other hand it may happen that the quantity of water forced into the wood of the root in a given time is greater than that which is transpired by the leaves. Under these circumstances the water filters into the cavities of the cells and vessels of the wood of the root and collects there. This latter condition is the one which obtains, for instance, in plants in the spring, and gives rise to the phenomenon of "bleeding," which we have already considered.

In the course of the very numerous experiments which have been made on the filtration of water through wood, it has been found that satisfactory results can only be obtained when, in the first place, the water is quite pure (distilled), and in the second, the cut surface is quite fresh. If the cut surface is allowed to become dry, the filtration is much retarded. It has been found, further, that in long-continued filtration-experiments, the rate of filtration gradually diminishes: if, however, a thin layer be removed from the surface of the piece of wood which has been in contact with the water, and the experiment be then resumed, the rate of filtration is again considerable. This gradually increasing resistance to filtration is due, as von Höhnelt has shewn, to the fact that the cut surface becomes covered with a layer of mucilaginous substance, derived partly from the cells which have been necessarily mutilated, and partly from Bacteria which grow and multiply in it. This is also the reason why cut branches wither even when their ends are placed in water.

The most trustworthy observations which we have as to the rate at which the transpiration-current travels in the wood are those of Sachs. His method consisted in supplying the

roots of plants with a solution of a salt of lithium, and determining, by means of the spectroscope, the length of stem in which lithium could be detected after the lapse of a given time. The following are some of the results which he obtained, the plants being under such conditions as to promote their transpiration as much as possible.

Plants with roots in water			Rate of rise per hour
<i>Salix fragilis</i>	85'0 cm.
<i>Zea Mais</i>	36'0 "
Plants with roots in earth			
<i>Nicotiana Tabacum</i>	118'0 "
<i>Albizzia Lophantha</i>	154'0 "
<i>Musa Sapientum</i>	99'7 "
<i>Helianthus annuus</i>	63'0 "
<i>Vitis vinifera</i>	98'0 "

It must be pointed out that Sachs ascertained by means of experiments with strips of blotting paper, that the lithium salt travels as rapidly as the water in which it is dissolved; but it does not necessarily follow that this is the case in the plant.

It is, then, by means of the fibro-vascular tissue that water is distributed to all parts of the plant, and, provided that the supply absorbed by the root is adequate, with sufficient rapidity to maintain the turgidity even of those parts in which transpiration is active. The distribution of water from the fibro-vascular bundle in a transpiring organ, a leaf for instance, follows a course which is the exact converse of that which takes place in the root. In this case the more external cells, those which bound the intercellular spaces, are those which are first affected by transpiration; they obtain fresh supplies of water by osmosis from the more internal cells, and these, in turn, obtain water from the cells of fibro-vascular bundles with which they are in relation. There is thus a current of water set up passing from within outwards.

We became acquainted at the outset with the remarkable property possessed by the parenchymatous cells of the roots of absorbing water to such an extent as to set up sufficient pressure to cause water to filter out of them. This property is, however, not peculiar to the cells in question, and we may, in concluding this lecture, briefly consider the instances which

have been observed of a similar process in other parts of the plant. The most familiar instance is the excretion of nectar by nectaries. The structure of a nectary is essentially similar to that of a water-gland (see fig 19, p. 91), but its properties are very different. We have seen that the excretion of liquid by a water-gland is entirely dependent upon the root-pressure; when the organ bearing the water-gland is separated from the rest of the plant, the secretion at once ceases. It is not so with a nectary. If a flower containing nectaries, that of *Fritillaria imperialis* for example, be cut off, and the drops of nectar be removed by means of blotting-paper, it will be found after a time that large drops have been excreted. The cells of the nectary, like those of the parenchymatous tissue of the root, have the power of setting up within themselves so great a hydrostatic pressure as to force out by filtration the fluid which they contain. This is true also with regard to the pitchers of *Nepenthes*. But it must not be supposed that this property is confined to special organs; it is probable, as suggested in a previous lecture (p. 45), that it is possessed very generally by the parenchymatous cells of the plant, and that it plays an important part in the distribution of substances which, though soluble in water, do not readily diffuse. Sachs has observed, for instance, that if pieces (6—10 ctm. long) of the young haulms of various Grasses be placed with one cut end in damp sand, and be kept in a moist atmosphere, drops of water will exude at the other end. Similar observations have been made by Pitra. The excretion of liquid in these cases is doubtless due to the fact that the parenchymatous cells become tensely filled with water; a considerable hydrostatic pressure is set up in the cells, and the result is the escape of water by filtration, probably into the vessels. This may be readily observed whenever any turgid succulent tissue is cut across; drops of water are formed at the cut surface, which are derived partly from the cells which have been cut open, but also, probably, from uninjured cells which lose water by filtration in consequence of the alteration of the conditions of tension in the tissue which has been induced by section.

In this and in previous lectures allusion has been frequently made to transpiration, a term which, as we have learned, is applied to the exhalation of watery vapour by plants. In the next lecture we will study this process in detail.

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LECTURE VII.

TRANSPIRATION.

UNDER ordinary circumstances, the exhalation of watery vapour is always going on from the surface of all parts of plants which are exposed to the air. Its activity is not the same in all, for the structure of the cell-walls of the superficial cells is not everywhere the same. The walls of the epidermal cells of terrestrial plants for instance, are more or less cuticularised, and the amount of watery vapour which can pass through them varies with the degree of their cuticularisation: it is however in all cases smaller, as Ad. Brongniart pointed out, than that which passes through the uncuticularised cell-walls of aquatic plants when they are exposed to the air. As a consequence, the latter wither much more rapidly than the former. The property which the cuticle is thus seen to possess of offering a resistance to the passage through it of aqueous vapour is due, according to Garreau, to the resinous and waxy substances which it contains.

The structure of all terrestrial plants, from the Mosses upwards, is such that direct communication is established between the external air and the interior of the plant by means of stomata and lenticels. We have already seen that these openings communicate with intercellular spaces which run between cells with uncuticularised walls, cells, therefore, which can readily exhale aqueous vapour. It is, as a rule, in the leaves that the greatest area of uncuticularised cell-wall

is thus brought into relation with the air, and it is therefore from them, as Hales first pointed out, that the greatest loss of water takes place. Hence we may speak of them as the transpiring organs of the plant. The following account of this function may be assumed, unless it is expressly stated otherwise, to apply to them.

The first point which we will consider is as to the amount of water which a plant may lose by transpiration in a given time. This has been determined in various ways: by weighing the plant at stated intervals, as Hales did, or by collecting the transpired water, as was done by Mariotte and by Guettard, or again by observing the amount of water absorbed by the plant, a method which is due to Woodward. Of these, the first two are the more reliable, the third being open to the objection that the activity of absorption of either the root of a plant or of the cut surface of a branch is not necessarily a measure of its transpiration.

The following are some of Hales's results, obtained by the method of weighing:

(a) Sunflower (*Helianthus annuus*).

Maximum loss in 12 hours (day)	30 oz.
Mean " "	20 oz. = 34 cub. in.
Loss during a night	3 oz.
Area of leaf surface	5616 sq. in.
Mean transpiration per sq. in. (day of 12 hrs.)			$\frac{1}{185}$ cub. in.

(b) Cabbage.

Maximum loss in 12 hours (day)	25 oz.
Mean " "	19 oz. = 32.7 cub. in.
Area of leaf surface	2736 sq. in.
Mean transpiration per sq. in. (day of 12 hrs.)			$\frac{1}{80}$ cub. in.

These figures suffice to shew that the amount of aqueous vapour which is exhaled by the leaves of a plant is very considerable; but it is less than that which would evaporate in the same time from an equal surface of water, a fact which was first ascertained by Hales and has since been more accurately determined by Unger and by Sachs.

The following is from Sachs :

A branch of White Poplar, weighing 125·2 grms., with a leaf-surface of 2700 sq. centim., lost 480 c.c. of water in 110 hours ; hence from every square centimetre there evaporated a column of water of 1·8 mm. in height ; from each square centimetre of the surface of the water in an adjacent vessel there evaporated, in the same time, a column of water 5 mm. in height. In an experiment with *Helianthus annuus* it was found that the loss from each square centimetre of leaf-surface was 2·23 mm., and from each square centimetre of water-surface, 5·3 mm. Sachs points out that this proportion is probably too large, for the external surface of a leaf by no means represents the whole surface from which transpiration is taking place ; the intercellular spaces must be taken into account. He assumes, therefore (and this is probably below the mark), that the transpiring surface of the leaves in these experiments may be taken to be ten times greater than their external surface. The proportion between the amount of water evaporated from the leaves and from the vessel will therefore be $\frac{1}{28}$ in the case of the Poplar, and $\frac{1}{23}$ in the case of the Sunflower.

The explanation of this fact is doubtless this, that the living cells offer a considerable resistance to the evaporation of the water which saturates them. This is not the case with a dead membrane ; on the contrary, the experiments of Sachs shew that water evaporates more readily from a membrane than from a free surface, and it has been frequently observed that parts of plants which have been killed dry up very rapidly.

It appears that, *ceteris paribus*, the transpiration is proportional to the surface of a leaf, though, as might be expected, the activity of transpiration is very different in the leaves of different structure : thin herbaceous leaves, for instance, transpire much more freely than do those which are fleshy or coriaceous. Further, it was pointed out by Guettard, and his observations have been confirmed by those of Bonnet, Unger, and Garreau, that transpiration takes place more actively from the lower than from the upper surface of the same leaf, a fact which must be attributed to the greater number of stomata on the under surface.

This may be illustrated by some of Garreau's results :

	Area of transpiring surface	Relative number of stomata	Relative quantity of water transpired
<i>Atropa Belladonna</i>	40	upper surf., 10	48
		lower „ 55	60
<i>Nicotiana rustica</i>	40	upper „ 15	57
		lower „ 20	80
<i>Canna æthiopica</i>	40	upper „ 0	7
		lower „ 25	51
<i>Dahlia</i> (terminal leaflet)	40	upper „ 22	50
		lower „ 33	100
<i>Tilia europæa</i>	20	upper „ 0	20
		lower „ 60	49
<i>Hedera Helix</i>	20	upper „ 0	0
		lower „ 90	4
<i>Syringa vulgaris</i>	20	upper „ 100	30
		lower „ 150	60

The mode in which Garreau conducted the experiments of which these are the results has been recently criticised by von Höhnel. Garreau determined the amount of water given off by the increase of weight of some chloride of calcium which was placed in a receiver together with the leaf. Von Höhnel points out that the chloride of calcium in the lower half of the receiver is under more favourable conditions than that in the upper half for absorbing the moisture exhaled by the leaf. In an experiment made in this manner with *Coleus Blumei*, he found the relative transpiration of the two surfaces to be 1 : 8. In a second experiment, he reversed the position of the leaf so that the true lower (dorsal) surface transpired into the upper half of the receiver : he now found the relative amount of moisture absorbed by the chloride in the upper to be to that absorbed by the lower as 1 : 4'6. It appears therefore that the differences determined by Garreau are too great.

From the foregoing table it appears that although the surface with the greater number of stomata transpires the more freely, yet there is no sort of proportion between the number of the stomata and the activity of the transpiration. Von Höhnel has, however, repeated Garreau's experiments

with an improved form of apparatus by means of which a more complete and a more equal absorption of the water transpired by the two surfaces of the leaf is ensured, and he inclines to the opinion that a proportion of this kind may really exist.

It has long been an accepted view that the activity of the transpiration of a leaf varies with its age, but it is to von Höhnel that we are indebted for a definite account of this relation. He finds that the youngest leaves are those which transpire most freely; the activity of transpiration gradually diminishes as the leaf grows, but it subsequently rises, so that a second, but lower, maximum is attained when the leaf is fully developed; it then steadily diminishes. The explanation which he gives of these facts is that in the very young leaf the cuticle is but feebly developed and offers but little resistance to the passage through it of aqueous vapour; further, there are no stomata: the loss of water at this stage is entirely due to what he terms "cuticular transpiration." With the growth of the leaf, the cuticle becomes thicker and the stomata begin to be formed, the former process, however, taking place more rapidly than the latter, so that the transpiration is on the whole diminished. As the stomata are developed, the transpiration increases again until the secondary maximum is reached: this secondary maximum is the expression of the "stomatal transpiration" of the leaf.

We may now proceed to consider the mode in which the stomata affect transpiration. It has long been known that the guard-cells are capable of opening and closing the apertures of the stomata. Sir Joseph Banks, who was one of the first to notice this fact, was of opinion that the stomata are closed in dry and open in wet weather, and that they thus regulate the transpiration of the plant. Moldenhawer found, however, that the stomata are closed on rainy days and dewy nights and are open when the sun is shining upon the leaves, and his observations have been confirmed by those of Amici, von Mohl, and Unger. The mechanism of the movements of the guard-cells was thoroughly investigated by von Mohl. He shewed that the opening of the stomata depends in the

first instance upon the turgidity of the guard-cells. When they are absorbing water, the only way in which they can yield to the hydrostatic pressure set up within them is, inasmuch as they are firmly connected at their ends, by becoming curved, and this necessarily produces a space between them, corresponding to that part of their adjacent surfaces along which they are not coherent. When the guard-cells are not turgid they are straight, their adjacent walls are in contact, and the opening of the stoma is obliterated. He concludes that the influence of light upon the guard-cells is of such a nature as to increase their power of absorbing water, probably by causing the formation within them of osmotically active substances: in connexion with this it should be mentioned that the guard-cells always contain chlorophyll-corpuscles. Possibly, however, the effect is to be attributed rather to an increased resistance to evaporation than to an increased power of absorption. However this may be, we can account, to some extent at least, for the great difference between the diurnal and the nocturnal transpiration of a plant, by the fact that its stomata are open during the day and are closed during the night: their function is not to check but to promote transpiration.

These considerations naturally lead us on to enquire into the relations existing between transpiration and the external conditions of the plant generally. The hygroscopic condition and the temperature of the air may be first considered. A plant in an atmosphere saturated with moisture will not exhale any watery vapour, provided that the temperature of the plant is not higher than that of the air. It may happen that, in consequence of great metabolic activity, the temperature of the plant is raised above that of the air, and then transpiration will take place, although the air is at its point of saturation. Under ordinary circumstances, when the temperature of the plant and that of the air do not perceptibly differ, the activity of transpiration diminishes with increasing moisture of the air; but when the temperature of the air is high and the proportion of moisture in it small, transpiration is promoted. Further, transpiration is affected not only by the

temperature of the air which surrounds the transpiring organs, but also by the temperature of the medium in which the absorbent organs are situated. Sachs observed that when the soil around the roots of a plant is warmed, the transpiration of the plant becomes more active. We have learnt in a previous lecture (p. 52) that a slow rise in the temperature of the soil causes an increased absorption of water by the roots: we may therefore conclude that the more active transpiration which is induced by a rise in the temperature of the soil is connected with the increased absorbent activity of the roots.

From the observations of Burgerstein on *Taxus baccata* it appears that transpiration may take place to a slight extent even at a temperature of -10.7°C .

It has been found by a great number of observers that transpiration is more active in the light than in darkness. This is doubtless to be accounted for, to a certain extent at any rate, by the fact that, as we have seen, the stomata are open in the light and closed in the dark, and further, that exposure to light usually involves a rise of temperature.

Wiesner has endeavoured to shew by a series of experiments, conducted in such a way that the temperature and the degree of saturation of the air were maintained as nearly as possible constant, that light affects transpiration independently of the stomata. Transpiration is very much increased by exposure of the plant to light, and the rays which are especially active appear to be those which correspond to the absorption-bands of the chlorophyll-spectrum (see plate).

The following are some of Wiesner's figures :

	Light (Gas)	Darkness
<i>Hartwegia comosa</i>		
gave off during 1st hour	59 mgr. water	31 mgr.
„ 2nd „	48 „	30 „
„ 3rd „	44 „	29 „
„ 4th „	42 „	29 „

In both cases the loss of water remained constant to the end of the experiment.

The following table gives Wiesner's results for a number of the plants, calculated per hour for 100 sq. centim. of leaf-surface.



Water transpired	In darkness	In diffused daylight	In sunlight
<i>Spartium junceum</i>	64 mgr.	69 mgr.	174 mgr.
<i>Lilium croceum</i>	38 "	59 "	114 "
<i>Malva arborea</i>	23 "	28 "	70 "
<i>Zea Mais</i> (etiolated)	106 "	112 "	290 "
" (green)	97 "	114 "	785 "

In order to meet the objection that the increased transpiration under the influence of light in these experiments is to be attributed to the opening of the stomata, Wiesner states that in the case of the Maize the stomata were nearly closed whilst the plant was exposed to light, and that in *Hartwegia comosa* the stomata were wide open whilst the plant was in darkness. He refers the more evident action of light in the green Maize-plant, as compared with the etiolated one, to the fact that the rays of light absorbed by the chlorophyll of the green plant are converted into heat, a conversion which is not effected to the same extent by the etiolin of the etiolated plant.

In addition to the external influences already noticed, it has been found that transpiration is considerably affected by the nature of the liquids which are absorbed by the roots. Sénéquier seems to have been the first to notice this, and he endeavoured to investigate it by comparing the transpiration of a number of branches with their cut surfaces in different solutions. The investigation was subsequently resumed by Sachs, and still more recently by Burgerstein. Sachs found that a Tobacco-plant growing in coarse sand transpired less actively than one growing in clay. In a series of water-cultures, he found that when the roots of the plants (*Cucurbita*) were in acidified water the transpiration was much greater, whereas when they were in alkaline water the transpiration was considerably less, than when they were in distilled water. He also watered plants growing in pots (Gourds, Beans, Tobacco) with 1 per cent. solutions of potassium nitrate, ammonium sulphate, and other salts, and found that the presence of the salt diminished the transpiration. Burgerstein's results agree in the main with those of Sachs', as the following figures will shew; but he finds that some salts tend to increase the transpiration.

1. *Acid water.*

(a) With nitric acid :

A Maize-plant with its roots in lost in 53 hours, p. ct. of its weight	}	<i>Distilled water</i>	<i>Acid</i> (0·15 p. ct.)	<i>Acid</i> (0·3 p. ct.)
		96·01	105·87	127·10

(b) With carbonic acid :

A Scarlet Runner with its roots in lost in 95½ hours, p. ct. of its weight,	<i>Distilled water</i>	<i>Acid water</i>
	138·22	165·45

2. *Alkaline water.*

(a) With caustic potash :

A Maize-plant with its roots in lost in 118 hours, p. ct. of its weight	}	<i>Distilled water</i>	<i>Alk.</i> (0·02 p. ct.)	<i>Alk.</i> (0·1 p. ct.)
		110·28	94·30	72·88

(b) With ammonia :

A Maize-plant with its roots in lost in 43 hours, p. ct. of its weight,	<i>Distilled water</i>	<i>Alkaline</i> (0·2 p. ct.)
	83·25	64·08

The following figures give a general idea of the results obtained with regard to salts. The plant used was the Maize, and the quantities, as in the preceding table, represent percentages of the living weight of the plant.

Roots in	<i>Distilled water</i>	<i>Mixed salt soln.</i>	KNO ₃	NH ₄ NO ₃
		0·1 p. ct.	0·1 p. ct.	0·1 p. ct.
Loss due to transpiration in 103 hours	264·17	247·40	283·20	334·20

The general conclusion to which he comes is that transpiration increases with the concentration of the solution of the salt up to a certain point, a point which is reached earlier in the case of alkaline salts and later in the case of acid salts than it is in the case of neutral salts. Beyond this point transpiration diminishes until it becomes equal to that which exists when the roots of the plant are in distilled water, and the transpiration further diminishes with greater concentration. A dilute solution of a mixture of salts causes diminution of transpiration, whilst a solution of the same strength of a single salt increases it.

Vesque has recently re-investigated this subject, and he comes to the conclusion that the phenomenon in question is one of absorption. He finds that when the plants have been

deprived for some time of a supply of salts and are then placed in a saline solution, they absorb it more rapidly than they do distilled water ; and conversely, when they have been supplied with salts, they absorb distilled water more rapidly than a saline solution. The increased or diminished absorption of water brought about in this way naturally affects the amount of water transpired.

The activity of transpiration is further affected by mechanical disturbances. It is a matter of common observation that leaves soon become flaccid when they are agitated by a strong wind. The increased loss of water which the flaccidity indicates may be attributed to some extent to the constant renewal of the air in contact with the surface of the leaves, but this is not the only effect of the wind. Baranetzky has found that disturbances of short duration suffice to induce flaccidity, and the leaves rapidly return to their normal condition when left at rest. If the shaking be repeated at short intervals, the loss of water gradually diminishes with each repetition, until finally no further effect is produced.

Baranetzky considers that the increase of transpiration is a consequence of the rapid expulsion of saturated air through the stomata at the time of shaking, and that the subsequent diminution is due to the flaccid condition of the guard-cells of the stomata which are partially closed. These conditions doubtless contribute to produce the effects, but they do not appear to afford a complete explanation. It is difficult to imagine that the loss of water during the time of shaking is so great as to induce flaccidity of all the mesophyll-cells of the leaf. It seems more reasonable to suppose that the shaking acts as a mechanical stimulus on the protoplasm of these cells in such a way as to facilitate the escape of water from them, and that the water thus set free is in part rapidly transpired and in part reabsorbed by the cells when the leaf is again at rest. From this point of view the flaccidity is the result, not of increased transpiration, but of the shaking, and the increased transpiration is due to the momentary presence of free water outside the primordial utricles of the mesophyll-cells, a condition which is very favourable to the process.

The following figures refer to Baranetzky's experiments with a leafy stem of *Inula Helenium* cut off and placed in water :

Time	Condition	Transpiration in grammes	Temperature of air	Saturation of air per cent.
7.40 a.m. to 8.10 a.m.	at rest	0'50	22'10 ⁰ C.	76
8.10 " 8.40 "	at rest	0'52	22'20 "	76
8.40 " 9.10 "	{after being shaken }	0'68	22'37 "	76
9.10 " 9.40 "	at rest	0'47	22'52 "	76
9.40 " 10.10 "	at rest	0'55	22'67 "	77
10.10 " 10.40 "	at rest	0'54	22'92 "	76
10.40 " 11.10 "	{after being shaken }	0'59	23'15 "	76
11.10 " 11.40 "	at rest	0'45	23'32 "	75
11.40 " 12.10 "	at rest	0'52	23'42 "	76

The following table refers to experiments made with a branch of *Æsculus Hippocastanum*.

Time	Condition	Transpiration in grammes	Temperature of air	Saturation of air per cent.
11.0 a.m. to 11.30 "	at rest	0'82	21'90	70
11.30 "				
11.30 " 11.40 " to 12.0 "	{shaken—loss during shaking }	0'50	21'90	70
	at rest	0'72	22'10	70
Loss after 1st shaking		0'12	22'10	70
" 2nd "		0'06	22'10	70
" 3rd "		0'00	22'10	70

We have now considered in detail the influence of external conditions upon the process of transpiration, and we may proceed to enquire if there is an independent periodicity of transpiration as there is of root-pressure. It is probable *à priori* that such is the case, for as we have already seen, the root-pressure exhibits a periodicity, and, as we shall see hereafter, the tension of the tissues exhibits it also: but, when it is borne in mind how many are the external influences which affect this process and how readily it responds to their action, it will be seen that the difficulties in the way

of definitely observing the periodicity are very great. Unger was the first to assert its existence, he found a maximum between 12 and 2 p.m., and a minimum at night, but inasmuch as his experiments were made with plants in the open air, his results cannot be regarded as at all conclusive.

Sachs also made experiments with a view of settling this point, but he failed to obtain any results which he could regard as satisfactory. Baranetzky kept plants in darkness for 24 hours with the other external conditions as constant as possible: he found that during the hours of the night the loss of water was much greater than during the hours of the day, but he could not detect any periodical variation. He came to the conclusion that there is no independent periodicity of transpiration.

The following table illustrates Baranetzky's experiments made on a plant of *Cucurbita* in a pot.

Time	Transpiration in grammes	Temperature of the air
7 p.m. to 7 a.m.	11·18	22·07
7 a.m. to 9 a.m.	1·60	21·90
9 a.m. to 11 a.m.	1·50	22·00
11 a.m. to 1 p.m.	1·40	22·10
1 p.m. to 3 p.m.	1·25	22·10
3 p.m. to 5 p.m.	1·15	22·05
5 p.m. to 7 p.m.	1·70	22·00
Total transpiration during night	11·18	
„ „ day	8·60	

We have now to consider the physiological significance of transpiration in the economy. As might be anticipated, its significance is great and its effects far-reaching. Hales recognised this when he said, "the motion of the sap is thereby much accelerated, which in the heartless vegetable would otherwise be very slow; it having probably only a progressive and not a circulating motion, as in animals." Thus, it affects the absorption of water by the root, and in so doing it probably promotes the absorption of salts in solution; further, there is

some ground for the belief that it plays an important part in the distribution of these salts throughout the plant; and again, we know from the observations of Hales and von Höhnel that the gases in the vessels of an actively transpiring plant are at a lower pressure than the air, a condition which materially affects the movements of gases and of water in plants. These points we will now discuss in detail, but before doing so we must not omit to notice one very important influence which transpiration exerts, the full consideration of which will come in a subsequent lecture. Inasmuch as loss of water by a plant affects the turgidity of its cells, and since turgidity is a necessary condition of growth, it is clear that the transpiration of a plant and its growth must stand in some more or less direct relation to each other.

We have already learned that transpiration promotes absorption of water by the roots, although these two functions are not proportional. It often happens that the loss of water by transpiration is so great that it cannot be met by the absorbent activity of the roots: in fact it appears to be the rule that, under ordinary conditions, the amount of water absorbed by the roots in a given time is less than that which is transpired by the leaves. Thus Sachs and de Vries found that the root-stock of a Sunflower exuded at its cut surface much less water (2.1 c.c.) than was transpired by the upper leaf-bearing part of the stem (9.5 c.c.) in the same time. Transpiration must therefore draw upon the reserves of water which the plant contains. When these are becoming exhausted, the leaves, and if the plant is a herbaceous one the stem also, begin to droop, for the parenchymatous cells have lost their turgidity and have become flaccid: they may be restored to their normal condition by arresting the transpiration, or, in the case of a cut-off branch, by forcing water under pressure into the cut surface. If the transpiration of a plant be prevented, the absorption of water by the roots gradually diminishes, and finally ceases when the plant has taken up as much water as it can contain.

It is therefore clear that transpiration has a direct influence upon the absorption of water. This naturally suggests the

enquiry as to whether or not the absorbent activity of the roots, or in other words, the amount of water in a plant, affects its transpiration. It appears that this is not the case. Von Höhnel has shewn the transpiration of the leaves is not affected by variations in the quantity of water which they contain. Still it cannot be doubted that if the cells of the leaves have lost a large proportion of their water in consequence of active transpiration and of inadequate supply, the water remaining in their walls and in their protoplasm is retained with considerable force, and that consequently a great resistance will be offered to its evaporation.

Now as to the effect of transpiration upon the absorption of dissolved salts by the roots. It was pointed out, when we were considering the function of absorption, that only very dilute solutions of salts can be taken up by the roots; as a consequence it is necessary that relatively large quantities of water should be absorbed in order that the plant may be supplied with the salts which are of importance in its nutrition. The active absorption which is hereby involved is promoted by transpiration, and it is by transpiration also that the excess of water is got rid of. This is the course of reasoning by which many authors (most recently Wiesner) have come to attribute to the function of transpiration an important physiological significance with regard to the nutrition of plants. The only direct evidence bearing upon the subject is afforded by Schlösing's observation that a Tobacco-plant grown under a bell-jar yielded a smaller proportion of ash than a similar plant grown under ordinary conditions, the proportion of silica in the ash being especially small. This evidence cannot, however, be regarded as conclusive, inasmuch as the conditions were such as to affect many of the functions of the plant: and further, we know that many plants thrive best in an atmosphere which is nearly if not quite saturated with moisture. Still, there is reason to believe that transpiration is of some importance in ensuring an adequate absorption of salts by most plants.

With regard to the distribution by the transpiration-current of substances absorbed by the roots, there is a considerable

mass of evidence to shew that this actually takes place. Thus the very numerous experiments which have been made upon the effect of removing a ring of cortex from stems and branches, although the results are somewhat discordant, tend to shew that the parts above the wound receive sufficient supplies of the salts absorbed by the root, and these supplies must necessarily be conveyed to them by the fibro-vascular tissue. Again, the fact that when coloured solutions are supplied to the root they stain the fibro-vascular tissue, support this conclusion, and it receives further confirmation from Sachs' lithium-experiments, to which allusion was made in the last lecture.

We have finally to discuss the effect of transpiration in producing a negative pressure of the gases in the vessels of the plant, and the influence of this condition upon the movements of fluids in the plant.

The first indication of the fact that, in a transpiring plant, the gases in the vessels are at a lower pressure than that of the atmosphere is to be found in the experiments made by Hales "whereby to find out the force with which trees imbibe moisture." He found that, in a tube connected with a cut-off branch, "the mercury rose highest when the sun was very clear and warm; and towards evening it would subside 3 or 4 inches, and rise again the next day as it grew warm." Further indications of the same kind are given in the experiments of Meyen, Sachs and others, but it was von Höhnel who gave the definitive proof. He found that if the stem of a transpiring plant be cut through under mercury, the mercury will at once rise to a height of several centimetres in the vessels, the greatest height being reached in the youngest vessels. This sudden rise of the mercury can only be accounted for by ascribing it to the difference between the atmospheric pressure and that of the gases in the vessels. It also teaches the important fact that the cavities of the vessels of the wood of a plant are not in direct communication with the external air, but that they form a completely closed system.

An explanation of how this difference of pressure is brought about will perhaps be best given by reference to one particular

case. In a previous lecture we learned that in certain plants, such as *Alchemilla vulgaris* for example, drops of water are to be found in the early morning on the leaves, and that these drops have been exuded by the action of the root-pressure. During the night the roots have been absorbing water actively, so actively in fact that the tissues have become gorged, the vessels more or less filled, and drops of water have been forced out at the margins of the leaves. When the sun shines upon the plant during the day, it transpires actively and the leaves soon begin to draw upon the water which is contained in the cavities of the vessels. As the water is withdrawn from these, a partial vacuum is produced: the gases which are already present in them, and those which pass into them by diffusion, expand, and are at a very much lower pressure than that of the atmosphere. If now the stem of the plant is cut through under mercury, the mercury must necessarily rise into the cavities of the vessels until the gases which they contain are at a pressure approximately equal to that of the atmosphere. Exactly this process goes on also in trees, but on an extended scale. In the spring the vessels of trees are just in the condition in which those of *Alchemilla* are in the early morning: they contain water and bubbles of gases. When transpiration commences after the leaves have unfolded, the water is gradually withdrawn from the vessels, and, as the summer advances, the gases in the vessels become more and more rarefied, as do those in the vessels of *Alchemilla* during the day. It is not until the fall of the leaves that the cavities of the vessels begin to contain water, and that the gases are reduced to their normal volume.

The effect of the existence of this diminished, or negative, pressure in the vessels finds its expression in various ways. In the first place, it must facilitate the filtration of water from the innermost parenchymatous cells of the root into the wood. That this is the case is shewn by the experiments of Vesque, to which reference was made in a previous lecture (p. 52). He found that a sudden rise in the temperature of the air checked the absorption of water by the roots. The interpretation of this fact is that the sudden rise of temperature causes an expan-

sion of the gases in the wood-vessels of the plant, and that consequently an increased resistance is offered to the filtration of water into the wood of the root. Further, this negative pressure must also promote the circulation of gases in the plant. Von Höhnel found that, as might be expected, gases readily diffuse from the surrounding tissues into the vessels when the pressure is low, the gases given off by any one part of the plant being thus brought into a closed system of channels which directly communicates with other parts; and that conversely when there is a considerable root-pressure, the gases in the vessels are forced out of them and pass by diffusion into the neighbouring cells. In the vessels themselves currents are set up which are due partly to the difference of the composition of the mixture of gases in various parts of the system, and partly to differences of temperature.

The principal channels, however, in which gases circulate in the tissues of plants are the intercellular spaces. That these form a continuous system throughout the plant communicating with the external air through the stomata and the lenticels is shewn, not only by microscopical observation, but also by experiments of the kind mentioned in the fifth lecture (p. 71) in which air is forced through leaves, branches, etc. In these, as in the vessels, there are diffusion-currents, and currents due to variations of temperature and probably also to the swaying movements of the leaves and branches.

In submerged plants, which do not transpire and which have rudimentary fibro-vascular bundles, the intercellular spaces are the only channels in which gases circulate. They are usually very large and are termed *air-chambers*. It frequently happens that gases (more particularly oxygen) collect in these chambers until the pressure becomes so great that the surrounding tissues are ruptured, and the gases escape in the form of bubbles.

The mixture of gases contained in the tissues of plants has been analysed in several cases, and, inasmuch as the relative proportions of the gases must vary considerably in correspondence with the varying metabolic processes, the results of the analyses differ widely. The gases found to be present are oxygen, nitrogen, and carbon dioxide. The

general results are that when the proportion of oxygen present is large, that of carbon dioxide is small, and *vicé versa*, the proportion of carbon dioxide being smallest in the winter. In most cases the proportion of nitrogen present was approximately that in which it occurs in atmospheric air, though in some instances it appeared that it was the only gas present; but these observations require confirmation.

We have now concluded the consideration of the absorption and distribution of the various substances which are absorbed by plants, and we will proceed, in the next lecture, to study their relation to the metabolic processes.

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LECTURE VIII.

THE FOOD OF PLANTS.

IF a plant be dried at a high temperature, the analysis of the residue will afford, as pointed out in a previous lecture (p. 60), an adequate account of the substances absorbed by the plant during its life. The first step in the analysis would be to incinerate the residue, and it would be found at the close of this process that it had lost considerably in weight, a proof that a portion of the dry solid of the plant had been burnt up and given off in the form of gas. If this gas were collected and analysed it would be found to consist principally of carbon dioxide, watery vapour, and nitrogen, the inference being that the combustible portion of the plant contained the elements Carbon, Hydrogen, and Nitrogen. The incombustible portion, the *ash*, would be found to be of a mineral nature, containing a number of elements of which the principal would be Sulphur, Phosphorus, Potassium, Calcium, Magnesium, Iron, Sodium, Chlorine, and Silicon.

Of these elements, the Carbon, Hydrogen, Nitrogen, Sulphur, and Phosphorus, are derived more especially from the organised parts of the plant, such as the protoplasm and the cell-wall, and from carbonaceous substances, such as sugar, fats, acids, etc., which had been formed by the metabolic activity of the protoplasm. These elements, together with Oxygen, the presence of which cannot be directly ascertained by analysis, are in consequence frequently, but somewhat

inaccurately, termed the *organic* constituents of plants, the other elements being the *inorganic* constituents.

In illustration of the ultimate chemical composition of various parts of plants the following analyses, taken from Johnson, may be given.

Dry solid contains per cent.	Wheat Grain	Wheat Straw	Potato Tubers	Peas Grain	Clover Hay
Carbon	46.1	48.4	44.0	46.5	47.4
Hydrogen	5.8	5.3	5.8	6.2	5.0
Oxygen	43.4	38.9	44.7	40.0	37.8
Nitrogen	2.3	0.4	1.5	4.2	2.1
Ash, including Sulphur and Phosphorus	2.4	7.0	4.0	3.1	7.7
	100.0	100.0	100.0	100.0	100.0

An enumeration of the constituent elements of a plant is, then, an enumeration of the substances which it absorbed during its life. But some only of these substances can be regarded as constituents of its *food*, if by "food" we mean those substances absorbed by the plant which go to build up its organic substances, which supply it with energy, or which exert some beneficial influence upon its metabolic processes; for a plant, like an animal, takes up not only such substances as these, but others as well which are of no nutritive value, or are even injurious. That this is the case has been already shewn in the fourth lecture (p. 65) in treating of the absorption by the roots. Any substance present in the soil is taken up by the roots, provided that the physical conditions of absorption are fulfilled, quite independently of its beneficial or injurious action upon the plant; and this holds good also with reference to the absorption of gases by the leaves.

An important illustration of this point is afforded by Phillip's recent observations upon the absorption of metallic oxides by the roots of plants. He has found that healthy plants, grown under favourable conditions, may absorb small quantities of lead, zinc, copper, and arsenic. The lead and the zinc appear to be deposited in the tissues without causing any disturbance of the functions of the plant, but when copper and arsenic are present in rather large quantity in the soil they exert a distinctly poisonous influence.

We will now proceed to enquire which are the chemical elements which serve as food to plants. It was pointed out

in Lecture V. (p. 75) that oxygen is absorbed in considerable quantity by all plants, and that carbon dioxide is absorbed by green plants. It has been found that these gases are essential to the life of the plants in question, and we may therefore conclude that carbon and oxygen are important constituents of their food. Further, water is essential to the nutrition of plants; hence hydrogen must be regarded as a constituent of the food. With regard to the salts absorbed by plants, the determination of their essential or non-essential character has been effected by the method of *water-culture* (fig. 21) to which allusion was made in a previous lecture (p. 60).

The following may be taken as an example of a solution for water-cultures.

Distilled water,	1000 grammes.
Potassium nitrate,	1·0 „
Calcium sulphate,	0·5 „
Magnesium sulphate,	0·5 „
Calcium phosphate	} traces.
Ferrous sulphate	

By varying the salts of the solution in a number of experiments, and observing the effect produced upon the plants by the presence or absence of certain salts, their importance to plants, and that of their constituent elements, may be readily ascertained.

The elements which have been found to be essential to the life of plants are the following; Carbon, Hydrogen, Oxygen, Nitrogen, Sulphur, Phosphorus, Potassium, Calcium, Magnesium, Iron (in the case of green plants), and in certain cases apparently also Chlorine.

Inasmuch as the so-called organic substances which are found in plants, such as fats and other hydrocarbons, starch, cellulose and other carbohydrates, proteids and their allies, consist of C and H, or of C, H, and O, or of C, H, O, and N, or of these together with S, or P, it is clear that these elements are of importance to the plant because they compose the substances of which the structure of the plant is built up. Further they are of importance because the complex

substances which they form are readily decomposed and thus energy is set free; this will be fully considered in treating of the destructive metabolism of the plant.

With regard to the other elements, it appears that they do not enter into the composition of the substances of which the tissues of plants consist; their importance being of this nature, that they promote the metabolism of the plant. It is true that in the analysis of protoplasm or of cell-wall an ash containing some or all of these elements is always obtained, and further that proteids and carbohydrates form chemical compounds with the alkalies and alkaline earths, but there is no evidence to shew that the elements in question occur in the living plant as integral constituents of the chemical molecules of the substances which compose its organised structure.

We will now proceed to consider in detail the forms in which these elements are absorbed by plants, and the part which they respectively play in the economy.

Carbon. The form in which this element is absorbed by plants depends upon the nature of the plant. Plants which contain chlorophyll obtain their carbon by the absorption of carbon dioxide, whereas plants which do not contain chlorophyll obtain their carbon by the absorption of organic substances in which C is directly combined with H.

It must not be concluded, however, that plants containing chlorophyll are incapable of absorbing complex carbon compounds. Thus it has been ascertained by the researches of Darwin and others that the "insectivorous" plants absorb such compounds by their modified leaves, and that these compounds are of importance in their nutrition. Further, it is well known that a number of green plants, such as the Mistletoe, Thesium, Melampyrum, Rhinanthus, Euphrasia and others, live parasitically on other plants: it is possible, however, that these plants do not absorb complex carbon compounds from their hosts, but simply water holding inorganic salts in solution. Finally, it has been proved by direct experiment that green plants take up complex carbonaceous substances, such as Urea (Cameron), Glycocoll, Asparagin, Leucin, Tyrosin (Knop and Wolf), when supplied to their roots. These remarks apply also to H, O, and N, inasmuch as these elements are present in combination with C in the substances mentioned.

In order to ascertain whether or not organic acids (oxalic, tartaric, succinic) can serve to supply green plants with carbon, Stutzer grew a

number of plants in artificial soils containing salts of these acids, and prevented any access of carbon dioxide to the leaves. He found, on the whole, that the plants gained in dry weight, and he concluded that these acids can supply carbon to the plant. Schmoeger, however, in repeating the experiments, found that these salts undergo decomposition in the soil, carbon dioxide being evolved, and he attributes the increase of weight observed by Stutzer to the absorption by the leaves of the plants of the carbon dioxide evolved from the salts of the soil during the experiment.

Plants which do not contain chlorophyll, and which must therefore take up their carbon in the form of complex compounds, are either *parasites*, that is they live upon other living organisms, or *saprophytes*, that is they live upon the products of the waste and decay of other living organisms. The plants which do not contain chlorophyll are the Fungi, and a few Phanerogams, *Epipogium Gmelini*, *Cuscuta*, *Monotropa*, *Lathræa*, *Corallorhiza*; of these the Fungi include both parasites and saprophytes, *Epipogium Gmelini* is a saprophyte, *Cuscuta* a parasite, and *Monotropa*, according to Drude, may be either the one or the other. The *Orobanchææ*, which are parasitic, and *Neottia*, which is saprophytic, have not a green colour, but nevertheless small quantities of chlorophyll have been detected in them.

Although the Fungi cannot assimilate carbon in the form of carbon dioxide, yet they can assimilate it in compounds which cannot be assimilated by green plants. This subject has been investigated by Naegeli, and the following is a list of the organic substances, arranged in order according to their nutritive value, which he found to be assimilated by various Fungi (Yeast, Bacteria, Moulds).

1. The different kinds of sugar.
2. Mannite : Glycerin : the carbon-group in Leucin.
3. Tartaric acid : Citric acid : Succinic acid : the carbon-group in Asparagin.
4. Acetic acid : Ethyl-alcohol : Quinic acid.
5. Benzoic acid : Salicylic acid : the carbon-group in Propylamine.
6. The carbon-group in Methylamine : Phenol.

He found that they could not assimilate carbon in the form of cyanogen-compounds, of urea, of formic acid, and of oxalic acid. The acids mentioned above were in combination with ammonia.

The carbon absorbed in any of these forms is used within the plant for the formation of substances which either take part in the building up of the plant, or undergo decomposition,—energy being thereby set free in the plant. The processes by which these combinations and decompositions are effected will be fully considered hereafter.

Hydrogen. This element is absorbed by all plants alike

in combination in the form of water, or in the form of ammonia and its compounds, or, as mentioned above, in complex carbon compounds.

Its use in the economy is very much the same as that of carbon.

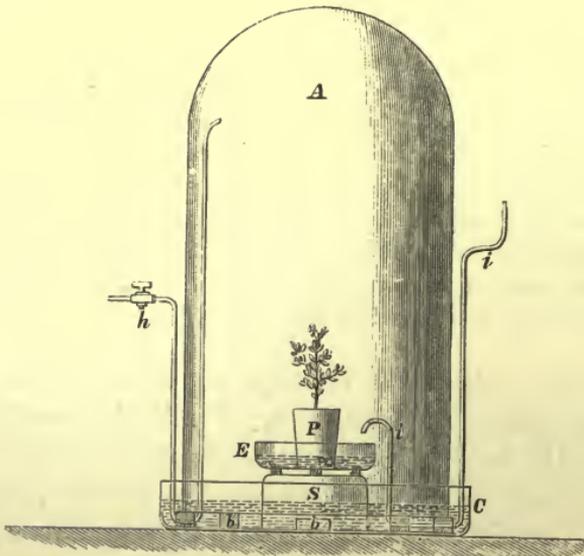
Oxygen. Oxygen is taken up by plants either free, or in combination in the form of water or of salts; the free oxygen absorbed is especially concerned in the processes of destructive metabolism, the combined oxygen in those of constructive metabolism.

It was pointed out in Lecture V. (p. 75), that certain plants are capable of living, for a time at least, without taking up free oxygen; this point will be further considered in connexion with the destructive metabolism of plants.

Nitrogen. It has been conclusively proved by the researches of Lawes, Gilbert, and Pugh, and by those of Bous-singault, that plants are incapable of taking up free nitrogen: they absorb it therefore only in combination (see p. 84).

The annexed figure will give some idea of the method by which Bous-singault arrived at this result: a glass bell-jar *A* stands in a glass

FIG. 20.



dish *C*, which contains water strongly acidified with sulphuric acid, rest-

ing on three small blocks of porcelain *b, b*; within the bell-jar is a glass dish *E*, containing water, which stands upon the glass support *S*; the water in *E* serves to moisten the soil in the flower-pot *P* in which the plant is growing; by means of the tube *i, i* more water can be introduced into *E*, if necessary; carbon dioxide can be introduced, if necessary, by the tube *h*. The soil in *P* is heated to redness before the experiment. The seed is sown in *P* and is then placed under the bell-jar. A similar seed is taken for analysis, and the proportion of nitrogen which it contains is accurately estimated. If now the plant developed from the seed sown in *P* be found, on analysis, to contain no more nitrogen than the seed analysed, it may be concluded that the plant has not absorbed any nitrogen. Since, under the conditions of the experiment, no supply of nitrogen is offered to the plant except the free nitrogen in the air in the bell-jar, it is evident that none of this can have been taken up by the plant.

The analysis of one experiment may be given as an illustration. The seed was that of a Dwarf Runner.

Nitrogen found in the plant	0·0290	grms.
" " soil	0·0033	"
" " flower-pot	0·0017	"
			<hr/>	
			0·0340	"
" " seed	0·0349	"
			<hr/>	
Loss of nitrogen	0·0009	"

The nitrogenous compounds absorbed by plants are, in addition to the organic substances mentioned above (p. 124), ammonia and its salts, and nitrates. From the researches of Boussingault it appears that the higher plants flourish best when supplied with nitrogen in the form of nitrates, whereas the lower plants absorb it more readily in the form of ammonia; in fact Pasteur has shewn that the Yeast-plant cannot assimilate nitrates. It must be pointed out, however, that Boussingault's conclusions are too general. Lehmann has found that many plants flourish better when supplied with ammonia-salts than when supplied with nitrates; this was well marked in the case of the Tobacco-plant. The Beet is another case in point. Schulze and Urich found a large quantity of nitrates in the roots, shewing that the absorbed nitrates had been altered to only a small extent by the plant, and Corenwinder states that he found the amount of nitrates in the roots to be the same as that which he had supplied to the

plant as manure. Further Boussingault himself observed incidentally that a *Helianthus* which had been manured with ammonium carbonate had gained three times as much nitrogen as one which had been supplied with nitrates during an experiment.

Naegeli finds that Fungi can assimilate nitrogen in organic combination in the form of proteids, of methylamine and other amines, in addition to the substances mentioned on p. 124. He concludes that they assimilate nitrogen most readily when it is supplied to them in the form of NH_2 ; less readily as NH ; with difficulty as NO ; and not at all as CN .

It appears that nitric acid may be absorbed in the form of any salt which can diffuse into the plant, the most common bases being soda, potash, lime, magnesia and ammonia; ammonia may be absorbed in combination as chloride, nitrate, sulphate, or phosphate, but the carbonate is injurious, at least in water-cultures, on account of its alkalinity.

Inasmuch as all plants necessarily absorb their nitrogen in the combined form, it will be of interest to enquire into the sources of combined nitrogen. It has been known since the time of Cavendish that a formation of nitric acid attends electric discharges in the atmosphere, and it was thought that this might maintain the supply of combined nitrogen in the soil. But Lawes and Gilbert have found that the quantity thus formed and conveyed to the soil by rain will only account for a fraction of the quantity removed from the soil in the crop (in the absence of nitrogenous manure), so that we are compelled to seek for other sources of supply. These have been suggested by various observers. Thus Schönbein pointed out that a formation of ammonium nitrite takes place when water evaporates at certain temperatures, and that this substance is also formed when various substances, such as phosphorus, fats, etc., are burned in moist air, but this has been shewn to depend upon the oxidation of ammonia. Still it must not be overlooked that a formation of nitrogen-compounds has been found to attend various processes of oxidation; Kolbe and Hofmann observed that when a hydrogen flame was kept burning for a time in a vessel, the water produced always contained nitric acid, and Bunsen observed that when a mixture of air and hydrogen was exploded by the electric spark, the resulting water contained nitric acid. This is also the case when phosphorus is burned under a bell-jar. An important source is probably to be found in the direct combination of nitrogen with organic substances, the combination being dependent upon a slow electrical discharge. Berthelot found, for instance, that when cellulose and dextrine are exposed in air for some hours to the action of a weak electrical current, a substance is obtained which evolves ammonia when heated

with soda-lime. A similar observation has been made by Hermann who found that rotting wood fixes nitrogen, producing a nitrogenous body which he terms "nitrolin." Mulder was of opinion, and in this he is supported by various recent observers, that nitrogen is fixed by a soil rich in humus, a view which is supported by Berthelot's experiments mentioned above. The subject cannot, however, be regarded as fully investigated at present.

A few words may be added here with reference to the loss of combined nitrogen in nature. Living organisms probably effect no change in the total quantity of combined nitrogen; their nitrogenous waste-products are all compounds of nitrogen. It appears that a certain loss of combined nitrogen attends the putrefaction of nitrogenous organic substances and especially their combustion, free nitrogen being evolved.

Another point of interest may be briefly referred to, namely this, that there is going on in the soil a process by which the ammonia supplied to the soil as manure or which is formed there by the decomposition of nitrogenous organic substances is converted into nitrous and this into nitric acid. These processes are termed "nitrification," and are effected by means of organised ferments of the nature of Micrococci (Warrington, Schlösing and Müntz).

With regard to the elements constituting the ash, it may be repeated here (see p. 61) that their absorption by the plant depends essentially upon the activity of its metabolism. This is well shewn in the following table of analyses by Arendt.

He analysed 1000 Oat-plants at various stages of their growth: the figures give the quantity in grammes of each ash-constituent present.

	I. June 18 3 leaves open	II. June 30 Plant heading	III. July 10 Blossoming	IV. July 21 Ripening	V. July 31 Ripe
SO ₃	1'06	2'71	2'68	4'83	5'34
P ₂ O ₅	3'27	5'99	10'32	12'90	14'23
Potash	17'05	31'11	40'20	44'33	43'76
Lime	4'48	8'50	11'60	14'49	14'71
Magnesia	1'53	2'71	3'71	5'42	6'45
Ferric oxide	0'20	0'46	0'61	0'83	0'58
Silica	6'39	15'82	25'45	34'66	36'32
Soda	0'86	1'28	1'47	1'12	0'87
Chlorine	2'28	3'62	5'32	5'96	5'78
Total Ash	37'12	72'20	101'36	124'54	128'04

It must be remembered, however, that although the *absolute* amount of ash increases with the age of the plant, the *proportion* of ash to the dry solid diminishes.

But this table does not only serve to shew that the quantity of ash-constituents absorbed is in intimate relation with the metabolic activity of the plant; it also enables us to form some idea as to the connexion of certain constituents with certain phases of metabolic activity. This will be discussed in the subsequent consideration of ash-constituents in detail. It will suffice for the present to point out that, of the essential ash-constituents, sulphur, phosphorus, and magnesium, are the only elements which continued to increase in quantity in the plant throughout the whole course of the experiment.

Some valuable information is also to be obtained from a consideration of the distribution of the ash in the plant. Speaking generally we may say that the proportion of ash increases from the root upwards to the leaves, a fact which tends to prove that the leaves are the organs in which the metabolism of the plant more especially takes place. The following table of analyses may be given in illustration.

Arendt has obtained the following results by a series of analyses of different parts of the Oat-plant: the figures give the percentage of ash in the dry solid of the plant.

	3 lower joints of stem	2 middle joints	Upper joint	Total stem	3 lower leaves	2 upper leaves	Total leaves	Ears	Entire plant
June 18	4.4	—	—	4.4	9.7	7.7	17.4	—	8.0
„ 30	2.5	2.9	3.5	8.9	9.4	7.0	16.4	3.8	5.2
July 10	3.5	4.7	5.2	13.4	10.2	6.9	17.1	3.6	5.4
„ 21	4.4	5.0	5.5	14.9	10.1	9.7	19.8	2.8	5.2
„ 31	4.6	5.3	6.4	16.3	10.1	10.5	20.6	2.6	5.1
	15.0	17.9	20.6	53.5	39.8	34.1	73.9	12.8	20.9

The constituents of the ash exist in the plant partly in solution and partly in the form of insoluble compounds. Hellriegel determined the following percentage in Clover:

		Young leaves	Mature leaves
Potash	{ dissolved	75·2	37·3
	{ undissolved	24·8	62·7
Lime	{ dissolved	69·5	72·4
	{ undissolved	30·5	27·6
Magnesia	{ dissolved	43·6	78·3
	{ undissolved	56·4	21·7
Silica	{ dissolved	26·8	16·1
	{ undissolved	73·2	83·9
Phosphorus pentoxide	{ dissolved	20·9	19·9
	{ undissolved	79·1	80·1

Sulphur. It was mentioned above that sulphur is a constituent of the proteid substances, and this is practically all that is known as to its use in the economy. It is absorbed in the form of sulphates, those of ammonium, potassium, magnesium, and calcium being the most advantageous. Sulphates occur in solution in the cell-sap of organs in which metabolism is actively proceeding and are doubtless formed in connexion with the decomposition of proteid.

Sulphur occurs in many products of metabolism, such as sulphurised ethers, etc. These will be noticed hereafter.

Phosphorus. Phosphorus is taken up by plants in the form of phosphates. It enters into the composition of some of the substances which constitute the organised parts of plants, namely nuclein and plastin.

According to Hoppe-Seyler, an organic substance containing phosphorus, Lecithin ($C_{44}H_{90}NPO_9$), occurs in actively growing cells of the most various plants. This observation has not, however, been confirmed by Naegeli in his researches upon the chemical composition of Yeast. Lecithin has been found by Loew in the spores and by Reinke in the plasmodium of *Æthelium*.

Hoppe-Seyler has found that phosphorus is present in chlorophyll (see *infra*, p. 155), forming, as he believes, an integral part of the molecule.

Besides being a constituent of some of the substances which enter into the organised structure of plants, phosphorus bears an important relation to certain of their metabolic processes. Phosphates are always to be found in relation with living protoplasm, but the exact significance of this

fact is unknown. It will be observed in the table of ash-constituents given above (p. 129) that the greatest increase of phosphorus in the plant takes place during the period of its most active development. Experiments upon animals have shewn that phosphorus and phosphates promote the metabolism of nitrogenous substances, and possibly this may be also the case in plants. As a matter of fact Boussingault and Lawes and Gilbert have found that phosphates exercise an important beneficial influence upon the assimilation of nitrogen, whether supplied in the form of nitrates or of ammonia salts, by the plant. This is clearly shewn by the following table taken from Boussingault.

The experiments were made with *Helianthus*-plants.

Plant supplied with nitrates and phosphates, 86 days old, contained dry solid 21·22 grms : N = 0·170 gm.

Plant supplied with nitrates, but no phosphates, 72 days old, contained dry solid 1·175 grms : N = 0·016 gm.

Plant supplied with ammonium carbonate, but no phosphates, 74 days old, contained dry solid 1·130 grms : N = 0·042 gm.

Potassium. Potassium is absorbed in a variety of compounds, such as the sulphate, phosphate, chloride, and probably also the silicate. Of these the chloride is, according to Nobbe, the most advantageous form in which it can be supplied to plants.

Like phosphorus, potassium is always found in relation with living protoplasm; in fact it appears from de Saussure's observations that the amount of potash in an organ affords an indication of the metabolic activity of the organ.

This may be illustrated by some analyses, in addition to those given in the above Table (p. 129).

1. 100 parts of Potato-tops contained (Wolff)

at end of August	2·3	of potash
at beginning of October	0·7	„

2. The proportion of potash in 100 parts of dry solid of different organs of the Horse-Chestnut (Wolff) :

Leaves, in the Spring	2·80
„ „ Autumn	1·50
Young wood	„	0·65
Bark, young	„	1·60

FIG. 21.



Water-cultures of Buckwheat, after Nobbe.

- | | | | |
|--------|--|---|------------------------------------|
| No. 1. | Plant grown in normal saline solution. | | |
| „ 2. | „ | „ | without potassium. |
| „ 3. | „ | „ | with soda instead of potash. |
| „ 4. | „ | „ | without calcium. |
| „ 5. | „ | „ | without nitrates or ammonia salts. |

The functions with which potassium appears to be especially connected in plants containing chlorophyll, is that of the formation of organic substance. Thus Nobbe found, in a number of water-cultures, that a plant not supplied with salts of potassium grew but little (Fig. 21, 2, 3), did not increase in weight, and that the amount of starch in the plant was very small, being represented only by a few grains in the chlorophyll-corpuscles of the leaves. On the addition of potassium chloride the starch-grains became more numerous in the chlorophyll-corpuscles, and made their appearance also in the tissues of the stem. It is, however, not known what is the precise significance of potassium in relation to the formation of organic substance.

Liebig was of opinion that potassium played an important part in the distribution of carbohydrates throughout the plant, but this has not been adequately confirmed. It appears rather that the observed facts upon which this view was based, point to the effect upon the plant not of the potassium itself but of the particular form in which it was presented. This point will be again touched upon when we are considering the use of chlorine in the plant.

That potassium bears some important relation to the formation and to the storing-up of carbohydrates is shewn by the fact that the organs in which these processes are taking place, such as leaves, seeds, tubers, etc., are those parts of plants which are richest in this element.

Potassium occurs in considerable quantities in plants in combination with organic acids.

Nægeli has observed that Cæsium or Rubidium can replace potassium in the food of certain Fungi (Moulds, Yeast, Bacteria).

Calcium. The compounds in which calcium is usually supplied to plants are the sulphate, phosphate, nitrate, and carbonate, the last undergoing decomposition in the process. When absorbed in these forms it contributes to the well-being of the plant, whereas when it is absorbed in the form of chloride the effect is unfavourable.

The precise use of calcium to plants is unknown. It cannot be replaced in the food of plants which contain chlo-

rophyll by any other metal, but Naegeli's researches have shewn that it can be to some extent replaced by Strontium, Barium, or Magnesium, in the food of certain Fungi (Moulds). It is especially abundant in the leaves of green plants. The effect of an insufficient supply of calcium is shewn in Fig. 21, 4.

It was pointed out in the second lecture (p. 22) that calcium occurs commonly in the cell-wall, and it is well known that it forms compounds with proteids. It is therefore possible that it contributes to the building up of the tissues in the form of organic compounds.

Calcium very commonly occurs in the cells of plants in the form of crystals of the carbonate or oxalate, and it is possibly one of the important functions of calcium to form insoluble salts with acids which are of no further use in and are even injurious to the plant.

Magnesium, like calcium, may be advantageously absorbed by plants in the form of all its salts except the chloride. Very little is known as to its use. Its distribution appears to be tolerably uniform. It appears, from Naegeli's observations, that it can be replaced in the food of Moulds by calcium. X
out of
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Magnesium occurs in the aleurone-grains of seeds in combination with phosphoric acid and calcium in the form of rounded masses termed *globoids* (see *infra*).

Iron. It appears that iron may be absorbed by plants in the form of the most different compounds.

With regard to its use in the plant it may be mentioned in the first place that iron has been detected in the most different plants and in the various parts of plants, either in the cell-contents or in the cell-wall, but it has been found to be essential only to those plants which contain chlorophyll. If a seedling be cultivated by means of the method of water-culture, with its roots in a solution which contains no iron, the leaves which are formed will be successively paler in colour until at length they are nearly white; in this state the plant is said to be *chlorotic*. If now a small quantity of a salt of iron be added to the solution in which the roots are immersed, or if the white leaves are painted with a dilute solution of iron, they will very shortly become green. Iron plays,

therefore, an important part in the formation of the green colouring-matter, chlorophyll, but, as will be subsequently shewn, it does not enter into its chemical composition. It doubtless affects in some way the processes in the cell which lead to the formation of the chlorophyll and also of the chlorophyll-corpuscles, for Arthur Gris observed that no differentiation of corpuscles had taken place in the cells of chlorotic leaves.

We have now concluded the consideration of those constituents of the ash of plants which have been found to be essential to their nutrition: we will now consider some of those which, though universally present, have been found to be unessential.

Sodium. This element, one of the most widely distributed is, as might be expected, never absent from the ash of plants, and in some cases, especially in maritime plants, it is present in considerable quantity. It was thought that possibly it might serve as a substitute for potassium in the nutrition of the plant, but this has not been found to be the case (see Fig. 21, 3). A glance at the table given above (p. 129) will suffice to shew how small a quantity of this element is absorbed, and from this an inference may be drawn as to its uselessness.

Chlorine. Chlorine also is a very constant constituent of the ash of plants, but it does not appear to be essential to their nutrition. It has been indeed observed that plants of Buckwheat, Barley, and Oats, did not flourish when grown in solutions containing no chlorides, and, as in these plants the chlorophyll-corpuscles became overfilled with starch-grains, it was thought that chlorine was of importance in connexion with the translocation of carbohydrates (Nobbe, Leydhecker, Beyer). On the other hand it has been observed that Maize-plants will grow well in solutions containing no chlorine, and further that the accumulation of starch in the chlorophyll-corpuscles may be induced by various abnormal external conditions (Knop and Dworzak). It seems probable, therefore, that chlorine has no direct influence upon the metabolism of plants, but only an indirect one, the chloride being the com-

pound of potassium which is most advantageous to the plant. Farsky's observations, however, seem to shew that chlorine is itself of importance.

Silicon. Silicon, as already pointed out in the fourth lecture (p. 54), is absorbed in the form of soluble silicates or possibly as soluble silicic acid. It principally occurs in plants in the cell-wall, but Lange appears to have found it as silicic acid dissolved in the cell-sap in *Equisetum hiemale*, and Pfitzer has described certain cells in the pseudobulbs of epiphytic Orchids which contain each a plate of silica.

Inasmuch as silica is always present in the ash, and frequently in very large quantity (see p. 21), it was thought that silicon must be essential to the nutrition of plants. Sachs found, however, that a Maize-plant will grow in a solution containing no silicon, though the ash of such a plant contains but 0.7 per cent. of silica, whereas that of a plant grown under ordinary conditions from 18 to 23 per cent., and his results have been confirmed by many observers. Wolff has, however, found by means of water-cultures, that in the case of Oats, the number of perfect seeds formed is greater when the plant is abundantly supplied with silica.

Still it is possible to imagine that even if silicon does not play any important part in the metabolism of the plant, it may be of use to it in giving firmness and rigidity to its tissues. It was suggested by Humphry Davy, and the view has found many supporters, that the cause of the "laying" of wheat and other cereals might be an insufficient supply of silica. On investigation this has been found not to be the case. The structure of the haulm is not affected by the supply of silica. The real cause of "laying" has been found to be the imperfect development of the tissues due to an inadequate exposure of light, a point which will be considered hereafter.

Inasmuch as all the chemical elements are present in one place or another in the soil, it will not be surprising to find that they have nearly all been detected at different times in the ashes of plants; there is no need therefore to enumerate further the ash-constituents.

In the next lecture we shall consider the changes which

the *plastic* food-materials—those, namely, which are used for the building up of the organised structures of plants—undergo after their absorption, in other words, the processes of constructive metabolism.

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LECTURE IX.

THE METABOLISM OF PLANTS.

IN the first lecture we found that when the Yeast-plant is adequately supplied with food-materials, it is capable of forming from them proteid and cellulose. Inasmuch as the size of the Yeast-plant is limited, the result of this formation of proteid and of cellulose is the production of new cells, each of which consists, like the parent, of a cell-wall and protoplasmic contents: and further, inasmuch as the Yeast-plant is unicellular, each of the newly formed cells is a distinct individual plant. In the case of multicellular plants, the result of constructive metabolism is, as in the Yeast-plant, the formation of new cells, but here the new cells remain in connexion with and form part of the plant, and tend to increase its size and weight. For example, if a seedling be placed under such conditions that it can take up and assimilate food, it will be found that it grows and that its dry weight gradually increases to many times that of the seed from which it was developed, the excess of weight being a measure of its constructive metabolism.

But the whole of the organic substance formed by the plant is not used for the building-up of its tissue. A certain portion of it undergoes decomposition in the processes which we include under the head of destructive metabolism, and certain of the products of decomposition are excreted by the plant. So the increase in weight is not an absolute

one ; it is simply the expression of the fact that the gain of the plant is greater than its loss. Further, another portion of the organic substance is in all cases stored-up in various forms as *reserve-material*, in connexion either with the production of new individuals or with the renewed growth of the plant itself at a subsequent period. For example, reserve-material is deposited in all seeds and spores to serve as food to the plant to be developed from them during the early stages of its growth. Again, the most various parts of perennial plants, stems, rhizomes, bulbs, roots, buds, etc., contain during the winter, in our climate, stores of reserve-material, which are deposited there whilst the plant is actively assimilating in the summer, and which will supply it with the means of recommencing its growth in the spring.

In the last lecture we ascertained what substances constitute the food of plants ; we have now to enquire into the nature of the constructively metabolic processes by which the comparatively simple food-materials are converted into complex organic substances.

1. *The Formation of Non-nitrogenous Organic Substance.*

We will take as our starting-point the fact mentioned in a previous lecture (p. 81), that green plants and parts of plants absorb carbon dioxide when exposed to bright light, and that the absorption of carbon dioxide is accompanied by an evolution of oxygen. We will endeavour to ascertain the nature of the chemical processes of which this interchange of gases is an expression, and to determine the connexion of these processes with the presence of chlorophyll and with the action of light.

We shall find it convenient in discussing this subject, to trace step by step the historical development of our knowledge concerning it. Priestley was the first to observe that green plants absorb carbon dioxide and evolve oxygen under the influence of sunlight, or, as he put it, "dephlogisticate" the air. Then Ingenhousz drew special attention to the influence of sunlight upon this process, proving that it is not the heat of the sun but its light which is of importance.

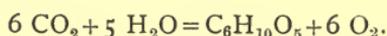
Sénébier proved that the amount of "pure air" (O) evolved by green plants in water is greater when a considerable amount of "fixed air" (CO₂) is held in solution. De Saussure endeavoured to determine the relation existing between the volume of carbon dioxide absorbed and the volume of oxygen evolved, and found that the latter was smaller than the former. He made, moreover, the important observation that the decomposition of carbon dioxide by green plants under the influence of light is accompanied by an increase in their weight.

Our knowledge on this subject at the beginning of the present century may be briefly summed up as follows: green parts of plants decompose carbon dioxide when exposed to sunlight, and exhale a somewhat smaller volume of oxygen, these processes being accompanied by an increase in weight.

Of the various facts which are included in this summary the one which especially concerns us now is the increase in weight. Many years after the publication of de Saussure's observations, von Mohl, in investigating the structure of chlorophyll-corpuscles, noticed the almost universal occurrence of starch-grains in them, and found that the starch-grains are not constituent parts of the corpuscles, but are secondary formations within them. These observations were subsequently confirmed and extended by Naegeli and Cramer, and by Böhm, but no explanation was offered of the connexion between chlorophyll-corpuscle and starch-grain. It was left to Sachs to do this. In endeavouring to determine fully the conditions of the decomposition of carbon dioxide by green plants, he had become impressed with the importance of chlorophyll in the process. The fact that in the absence of chlorophyll no decomposition of carbon dioxide takes place, led him to investigate the structure of the chlorophyll-corpuscles. As the result of careful and extended observation he found that the presence of starch-grains in chlorophyll-corpuscles is dependent upon exposure to light. The formation of starch-grains in chlorophyll-corpuscles was thus shewn to depend upon the same conditions as the decomposition of carbon dioxide, and Sachs was therefore justified

in concluding that these phenomena belong to the same function, that the formation of starch is intimately connected with the decomposition of carbon dioxide. Sachs' conclusion was fully confirmed by Godlewski, who found that if leaves exposed to light are not supplied with carbon dioxide no starch-grains are found in their chlorophyll-corpuscles. The explanation of the increase of weight observed by de Saussure is then this, that the decomposition of carbon dioxide by the green parts of plants is connected with the formation of organic substance, and that starch is the visible product of the constructive processes.

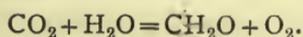
But is the starch which makes its appearance in chlorophyll-corpuscles under the influence of light to be *directly* connected with the decomposition of carbon dioxide which goes on in them? It is generally held that this is the case, a view which is based upon the fact that the volume of oxygen exhaled is approximately equal to the volume of carbon dioxide absorbed, the process being roughly represented by the equation



Let us now submit this view to a critical examination. The fact that the volume of the exhaled oxygen is approximately equal to that of the absorbed carbon dioxide may be accepted as established. It is true that, as mentioned above, de Saussure found the volume of the exhaled oxygen to be considerably less than that of the absorbed carbon dioxide, but it is probable that his method of observation may have been imperfect. Boussingault, who subsequently investigated the subject, obtained very different results. In fifteen out of his forty-one experiments, the volume of oxygen exhaled was perceptibly greater than that of the carbon dioxide absorbed; in thirteen the volumes were approximately equal; in the remainder the volume of oxygen was perceptibly smaller. Taking all the forty-one experiments together, Boussingault found that for every 100 volumes of carbon dioxide absorbed, 98.75 volumes of oxygen had been set free. Further, it has been found by a number of other observers, such as

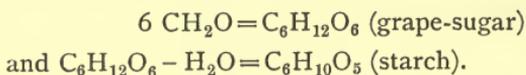
Pfeffer, Godlewski, and Holle, that when a green plant is exposed to sunlight in a closed glass vessel containing air, the volume of the air remains approximately constant. It must be borne in mind, however, that the interchange of gases going on between a green plant and the outside air is not merely the absorption of carbon dioxide and the evolution of oxygen. We have seen in a previous lecture (p. 75) that plants also absorb oxygen from the air and give out carbon dioxide. The change in the constitution of the atmosphere in a closed vessel in which a green plant has been exposed to light, is then the resultant effect of the operation of these two processes. The green parts of the plant have absorbed carbon dioxide and given out oxygen, the parts which are not green have absorbed oxygen and given out carbon dioxide. The fact that the volume of the oxygen exhaled is frequently slightly smaller than that of the carbon dioxide absorbed, is doubtless to be attributed either to the exhalation of a small quantity of carbon dioxide by the parts of the plant which are not green, this exhaled carbon dioxide not having been subsequently decomposed in the green parts, or to the retention of a small quantity of oxygen in the plant in the form of highly oxidised organic compounds.

We accept, then, the fact upon which this view is based, but we have yet to assure ourselves of the correctness of the inference. Does the equality in the volumes of the gases absorbed and exhaled warrant the conclusion that the starch which appears in the chlorophyll-corpuscles is connected with the gaseous interchange in the manner indicated by the equation given above? It is easy to point out that a gaseous interchange of this nature might accompany the formation of a substance altogether different from starch; for instance, methyl or formic aldehyde might be formed according to the equation

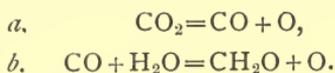


This very suggestion has, however, been brought forward in support of the view that the starch formed in chlorophyll-corpuscles when exposed to light is derived from carbon

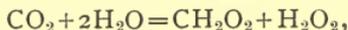
dioxide and water. It is well known that formic aldehyde is a substance which readily undergoes polymerisation, so that a carbohydrate might be easily derived from it thus



Baeyer considers that the carbon dioxide is decomposed into carbon monoxide and oxygen, and that the carbon monoxide combines with hydrogen, derived from water, into formic aldehyde.



Erlenmeyer, whilst accepting this view, considers, on chemical grounds, that the process is effected somewhat differently; that formic acid is first produced together with hydrogen peroxide,



and that then the formic acid and hydrogen peroxide are decomposed formic aldehyde and water being formed and oxygen evolved,



It must be admitted that Just's observation that green plants cannot assimilate carbon monoxide is unfavourable to this hypothesis, but it must be borne in mind that the absorption of carbon monoxide from without and the formation of it in the plant may involve very different chemical conditions.

Such a derivation of carbohydrate from formic aldehyde is not entirely theoretical, for Butlerow has found that by the action of alkalis upon a polymer of formic aldehyde, a saccharine substance (methylenitan) is produced: similarly from trioxymethylene ($\text{C}_3\text{H}_6\text{O}_3$), Renard has obtained a syrupy substance which has the formula $\text{C}_6\text{H}_{12}\text{O}_6$, and which reduces Fehling's solution.

The facts do not, however, suffice to prove that the starch formed in the chlorophyll-corpuscles under the influence of light is actually derived from carbon dioxide and water. All that has been proved is this, that a substance is formed which has the ultimate chemical composition of a carbohydrate.

In order to thoroughly understand the formation of starch in chlorophyll-corpuscles, we must become acquainted with the mode in which carbohydrate is formed elsewhere in

the plant. It was pointed out in a previous lecture (p. 15) that, according to Schmitz and Strasburger and in harmony with the older statements of Pringsheim, the cell-wall is produced by the actual conversion of a layer of protoplasm, and we shall see hereafter that the same is asserted of the layers of the starch-grains found in seeds, tubers, etc. Translating this into chemical language we find it to mean that molecules of protoplasm may undergo dissociation in such a way as to give rise to molecules of carbohydrate among other products. The conclusion to be drawn is, that the starch which is formed in chlorophyll-corpuscles under the influence of light is also the product of such a dissociation of protoplasm. Some valuable support is afforded to this view by the observations of Schimper and others that starch-grains may make their appearance in chlorophyll-corpuscles under circumstances which preclude any formation of them from carbon dioxide and water.

The non-nitrogenous organic substance which is first formed in the chlorophyll-corpuscle from carbon dioxide and water is, then, not starch, but a substance (possibly allied to formic aldehyde) which goes to construct proteid, by combining either with the nitrogen and sulphur absorbed in the form of salts from the soil, or with the nitrogenous residues of previous decompositions of proteid. The starch deposited in the corpuscle is, however, the first *visible* product of the constructive metabolism going on within it, for, unless protoplasm is being formed, no starch can be produced: it may be regarded as a temporary reserve-material.

Inasmuch as we now know that the visible deposits of non-nitrogenous organic substance in the plant, in the form of starch or cellulose, are derived from protoplasm, we can understand how it is that the great differences in dry weight which exist between plants which have and which have not been supplied with assimilable nitrogen during their growth, are brought about. The absence of assimilable nitrogen prevents the formation of proteids in the latter case; as a consequence, cellulose and starch are formed only in small quantity, and the plant remains small, its development being only due to

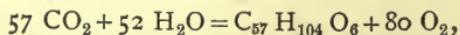
the nitrogenous substances stored in the seed from which it was grown. On the other hand, when the plant is supplied with assimilable nitrogen, the increase in weight which the plant exhibits is much greater than can be accounted for by supposing that just so much carbon, hydrogen, etc., is assimilated as is necessary to form proteid with the absorbed nitrogen; there is evidently an accumulation of non-nitrogenous organic substance as well. ✓

In illustration of these points the results obtained by Boussingault with *Helianthus* seeds and seedlings may be cited.

	Weight of seed.	Nitrogen in seed.	Nitrogen supplied to the soil as nitrates.	Dry weight of plants.	Nitrogen of plants.
1.	0·062	0·0019	0·1536	6·685	0·1126 grammes.
2.	0·068	0·0021	0·0000	0·325	0·0022 „
3.	0·116	0·0033	0·0111	1·168	0·0102 „
4.	0·116	0·0033	0·0222	2·120	0·0148 „

Plants 3 assimilated 0·420 grammes of carbon = 780 c.c. CO₂, the daily assimilation being 8·75 c.c. CO₂; plants 4 assimilated 0·848 grammes of carbon = 1566 c.c. CO₂, the daily assimilation being 17·6 c.c. CO₂.

We may here briefly notice the fact that in many cases substances other than starch have been found in chlorophyll-corpuscles. For instance, Briosi failed to detect starch-grains at any time in the chlorophyll-corpuscles of the Musaceæ, but found oil-drops instead, and Pringsheim made similar observations on *Vaucheria sessilis*. It has been found, in the case of the Musaceæ at least, that the organic substance first formed is not different from that in other plants. Both Holle and Godlewski, who have carefully investigated the subject, point out that if oil be the substance first formed, its production must take place according to some such equation as the following :



and that this would necessarily involve the evolution of a volume of oxygen considerably larger than that of the carbon dioxide absorbed. As the result of experiment they found that such a relation between the volumes of the gases absorbed and exhaled does not exist, but that the relation is in this case also that which obtains in other plants, namely, that the volume of oxygen exhaled is approximately equal to that of the carbon dioxide absorbed. The substance first formed in the chlorophyll-corpuscles of the Musaceæ also is then one which has the ultimate chemical composition of a carbohydrate.

The oil which was detected in the chlorophyll-corpuscles of the plants above-mentioned is doubtless derived from protoplasm. Its presence is

not, however, confined to the chlorophyll-corpuscles, for Holle found that it was also generally diffused throughout the protoplasm of the cells. The formation of the oil is doubtless to be attributed to the action of certain conditions which were unfavourable to the formation of starch from proteid and which led to the decomposition of protoplasm in such a way that oil was one of the products. In fact Godlewski found that when an abundant supply of carbon dioxide and exposure to bright light were ensured, starch-grains were abundantly produced in the chlorophyll-corpuscles of the leaves, especially the younger leaves, of the Musaceæ.

Pringsheim has found that a substance which he terms Hypochlorin can be made to appear in chlorophyll-corpuscles by treating them with dilute acid. No analysis of this substance has as yet been made, but it probably contains either no oxygen, or less than a carbohydrate. He regards this substance as the first visible product of constructive metabolism in the corpuscle, but this requires proof. The substance may be merely a product of the decomposition of chlorophyll by the acid.

The conditions essential to the formation of non-nitrogenous organic substance from carbon dioxide and water by the chlorophyll-corpuscle are briefly these; exposure to light, of some considerable intensity, and a sufficiently high temperature. De Saussure came to the conclusion that the presence of free oxygen is essential to the process, for he found that green plants soon die in an atmosphere of pure carbon dioxide, and that plants which can live for a time in an atmosphere of nitrogen, die when a proportion of carbon dioxide, which would have been beneficial if added to ordinary air, is added to the nitrogen. Boussingault carefully re-investigated the subject, and found that the effect of the presence of any other gas, not in itself hurtful, upon the absorption of carbon dioxide is simply a mechanical one (see p. 73).

The various processes which result in the formation of starch in the chlorophyll-corpuscles are gone through rather rapidly, especially in the more lowly-organised plants. Thus Kraus found that starch-grains made their appearance in the chlorophyll-corpuscles of *Spirogyra* within five minutes after exposure to bright sunlight, within two hours in diffuse daylight; in *Funaria* they made their appearance after two hours' exposure to sunlight, and after six hours' exposure to diffuse daylight.

The great physiological difference between plants which

do and which do not contain chlorophyll is the fact which we are now considering, namely, that plants which contain chlorophyll can, under the influence of light, construct non-nitrogenous organic substance out of carbon dioxide and water. A plant which does not contain chlorophyll cannot do this; it is therefore necessary that it should be supplied from without with food in which carbon is already in organic combination (see p. 124). In connexion with this we may mention the fact that no starch is ever found in the tissues of Fungi, though it is difficult to say why this should be. It is very remarkable that although the protoplasm of these plants undergoes dissociation in such a way as to produce cellulose and other carbohydrates, it does not undergo dissociation so as to produce the carbohydrate starch.

2. *The Formation of Nitrogenous Organic Substance.*

We learned in the last lecture that plants can only avail themselves of nitrogen in the combined form, either as inorganic salts or as certain organic compounds, for the purposes of their constructive metabolism. With regard to the conditions of the formation of nitrogenous organic substance in the plant, we know, from our study of Yeast, that it is independent of the presence of chlorophyll, and it apparently goes on as well in the absence as in the presence of light. In these respects it contrasts in a marked manner with the formation of non-nitrogenous organic substance. All that we shall have to say about it will refer to the probable mode and the probable place of its occurrence, and unfortunately we are compelled, in the absence of definite information on these points, to confine ourselves to probabilities.

We know that green plants form non-nitrogenous organic substance, that plants destitute of chlorophyll, parasites or saprophytes, absorb substances of this nature, and that all plants absorb inorganic compounds of nitrogen, such as nitrates and salts of ammonia, as well as sulphates: here then are the materials for the formation of nitrogenous organic substance. But though we know what are the necessary

materials, we can only guess at the probable process. Emmerling, from a series of analyses of the Bean (*Vicia Faba* var. *major*), comes to the conclusion that the nitrates absorbed by the root are decomposed by the organic acids (especially the oxalic) present in the plant with liberation of nitric acid, and that this nitric acid is then used in the formation of proteid. According to Holzner it is probable that the absorbed sulphates also are decomposed by the organic acids, sulphuric acid being set free. It is doubtless by the combination of the nitric and sulphuric acids formed under these conditions with some form of non-nitrogenous organic substance, Loew and Bokorny suggest formic aldehyde, that nitrogenous organic substance is ultimately produced.

In the detailed discussion of this difficult subject we will principally direct our attention to the highly organised plants, for our knowledge of their chemistry is relatively great. We will begin by ascertaining what organ it is in which the formation of nitrogenous organic substance takes place.

From what has just been said respecting the origin of the starch which is to be found in the chlorophyll-corpuscles, there can be no doubt that proteid is formed in cells which contain this substance; and since it is so abundant in leaves, we may conclude that the leaf is more especially the organ in which the formation of proteid takes place. Moreover this conclusion is supported by other though less direct evidence. Emmerling observed in the Bean that whereas the root contained a quantity of nitric acid (0.0756 per cent.) and the stem also (0.0891 per cent. in the lower part, 0.0238 per cent. in the upper), no trace of it could be detected in the leaves; from this he inferred that it is in the leaves that the nitrates absorbed by the roots and conveyed through the stem are used up in the formation of nitrogenous organic substance. Further, Pott found that the proportion of proteid in the plant increases from the roots towards the leaves, the proportion of proteid in the leaves being about twice as great as that in the roots of many of the plants which he analysed.

With regard to the chemistry of the process, there can be little doubt that proteid is not directly formed, but that nitro-

genous organic substances of less complex composition are formed as intermediate products. From the researches of Biltz, of Kellner, of Emmerling, and of Borodin, it appears that crystallisable nitrogenous organic substances, such as asparagin, leucin, and others (we may, for the sake of brevity, term them *amides*) are frequently to be found in leaves. It is quite possible, as Kellner and Emmerling have suggested, that these substances may be formed synthetically in the leaf. We may imagine the processes to be somewhat as follows. Since all these substances contain nitrogen in the form of ammonia, the first step would be the formation of ammonia or ammonia compounds from the nitric acid absorbed as nitrates by the root; that some process of this kind actually takes place is suggested by Emmerling's observation that no nitrates are usually present in the leaf, by the fact mentioned in a previous lecture (p. 127) that certain plants are unable to assimilate the nitrates which they absorb, and by Hosæus' observation that ammonia salts were to be found in a number of different plants which he analysed, even when they had been supplied with manure which did not contain ammonia. The ammonia thus formed combines with formic aldehyde or one of its polymers to form one or other of these amides, and this combines with some form of non-nitrogenous organic substance and with sulphur to form proteid. This view of the mode of formation of proteid is supported by the fact, mentioned in a previous lecture (p. 124), that even green plants can take up their nitrogen in the form of amides.

But we must not overlook the fact that amides, and probably also ammonia, are produced in the plant by an analytic process, by the decomposition of proteid, and it must be admitted that they may be formed in this way in the leaf. The conditions which determine this process have been made evident by the observations of Borodin. He found that no asparagin could be detected in shoots of certain plants when they were growing under normal conditions, but that the appearance of asparagin in considerable quantity could be induced by cutting off the shoots and keeping them for some time in the dark. The explanation of this fact is doubtless this, that the proteids

in the shoots undergo decomposition, asparagin being one of the products, and that the asparagin accumulated in consequence of the absence of any appropriate non-nitrogenous organic substance with which it could combine to form proteid.

Taking all these facts into consideration, we may conclude that these amides are formed both synthetically and analytically in the leaves. But in whatever way they may be formed, they are used in the construction of proteid: hence their presence or absence depends upon the supply of appropriate non-nitrogenous organic substance; when the supply is adequate, no trace of the amides can be detected, when it is inadequate they begin to accumulate.

The synthesis of amides with non-nitrogenous organic substance to form proteid is not, however, confined to the leaf: probably every living plant-cell is capable of effecting it. It has been found, for instance, by many observers that the tissue of the growing-point, the primary meristem, never contains any starch or sugar or asparagin, although these substances are abundantly present in the rest of the plant. There can be no doubt that proteid is being formed there in connexion with the production of new cells. The only explanation which can be offered is that the asparagin and the sugar with which these cells are supplied are rapidly converted into proteid. We shall have occasion to discuss these facts in detail in a subsequent lecture.

Strasburger and Schmitz have suggested, as already mentioned (p. 27), that the nucleus is in some way connected with the formation of proteid in the cell. This suggestion is based upon the following facts: that a nucleus has been found to be present in the living cells of the vast majority of plants; that it is the last structure to disappear from the cell when its death is approaching; that it is present in cells which never contain starch, and is therefore not directly connected with the production of non-nitrogenous organic substance; that it gives very marked proteid reactions.

3. *The Function of Chlorophyll.*

We have seen that it is only the green parts of plants that are capable of absorbing carbon dioxide and of exhaling oxygen; it is only in these, then, that a formation of organic

substance *de novo* can take place in the plant. We have now to ascertain what is the part played by the green colouring-matter, the chlorophyll, in the process.

Carbon dioxide is absorbed and oxygen is exhaled by some plants and parts of plants which are not green, such, for instance, as the brown Algæ (Fucoideæ), the red Algæ (Florideæ), and the leaves of the Copper Beech. Chlorophyll is, however, present in all these cases, but the green colour is not perceptible on account of the presence of other colouring-matters.

It was pointed out long ago by Draper that the chlorophyll-corpuscles of etiolated plants, of plants, that is, which have grown in darkness, can absorb carbon dioxide and exhale oxygen under the influence of light, an observation which has been recently confirmed by the researches of Engelmann. These corpuscles are not green, but yellow; they contain a colouring-matter known as *etiolin*, which is doubtless closely allied to chlorophyll and is converted into chlorophyll when the etiolin-corpuscles are exposed to light. It appears from the above-mentioned observations that etiolin plays the same part in relation to the decomposition of carbon dioxide as chlorophyll: and Engelmann is of opinion that this is true also of the colouring-matters of the Algæ (phycoxanthin, phycocyanin, phycoerythrin).

In the simpler unicellular plants, *Hæmatococcus* for example, the chlorophyll is distributed throughout the protoplasm of the cell, but in all the higher forms it is confined to specialised portions of the protoplasm, usually somewhat oval in outline and discoid or lenticular in form, the *chlorophyll-corpuscles* with which we have already become so familiar. In certain Algæ, the Conjugatæ, a group to which the Desmids and Spirogyra and its allies belong, these chlorophyll-corpuscles are imbedded in plates of green protoplasm, the *chlorophyll-bodies*, but it is apparently only in the corpuscles themselves that the formation of starch takes place.

We may begin our study of the function of chlorophyll by saying that the absorption of carbon dioxide, the evolution of oxygen, and the formation of new organic substance, are effected entirely and solely by chlorophyll-corpuscles, for we may be permitted to regard the green protoplasm of a unicellular Alga as constituting one large chlorophyll-corpuscle. These processes go on in the chlorophyll-corpuscle quite independently of the uncoloured protoplasm of the cell, for Engel-

mann has shewn, by an extremely ingenious method, that isolated chlorophyll-corpuscles continue for a long time to exhale oxygen.

We will now study the structure of a chlorophyll-corpuscle. If a cell containing chlorophyll-corpuscles be treated with alcohol, it will be seen that the corpuscles soon lose their green colour; the chlorophyll is in fact dissolved out of them by the alcohol. There remains a colourless corpuscle which gives the reactions of proteid substance, and is, doubtless, of a protoplasmic nature. As regards the mode in which the chlorophyll and the protoplasm are connected together, our only information is afforded by the observations of Pringsheim. He has found that if chlorophyll-corpuscles be treated with dilute acids or be exposed to the action of steam, the chloro-

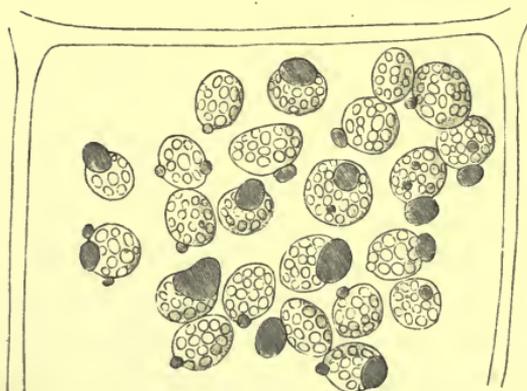


FIG. 22 (after Pringsheim). Cell from a leaf of *Vallisneria spiralis* which had been macerated in dilute hydrochloric acid for six days, and then exposed for some hours to the action of steam. The chlorophyll of the corpuscles has collected into drops at the surface, leaving the corpuscles colourless. The corpuscles are seen to present a spongy or porous structure.

phyll will exude from the corpuscles in viscid drops, leaving the corpuscles colourless. A colourless corpuscle obtained in this way presents a spongy or trabecular structure, the now empty spaces between the trabeculæ having been previously occupied by the chlorophyll (Fig. 22). We learn from this that the chlorophyll is not actually combined with the protoplasm, but that it is retained mechanically within it; and further, that the chlorophyll is in solution, most probably in some kind of oil.

In the consideration of the chemical composition of chlorophyll the first point is as to whether chlorophyll is a distinct substance or a mixture of two or more colouring-matters. Without going into the very extensive literature of the subject, it may just be pointed out that both these views have found supporters. Thus Frémy, Stokes, Sorby, and others, state that it consists of a mixture of one or more blue with one or more yellow colouring-matters, whereas Konrad, Pringsheim, and others, regard it as a definite chemical substance. It is true that an alcoholic extract of leaves contains colouring-matters which are not green, but there is no evidence to prove that these belong directly to the green colouring-matter. They are present in the chlorophyll-corpuscles in addition to the chlorophyll itself, and, as we shall see hereafter, are probably either substances from which chlorophyll is formed or products of its chemical alteration.

Our knowledge of the probable chemical composition of chlorophyll has been considerably extended of late years by the researches of Gautier and of Hoppe-Seyler. Both these observers have succeeded in obtaining crystals of a green substance by evaporating to dryness the alcoholic extract of green leaves, but this substance is probably not pure chlorophyll, for, as the following table of analyses will shew, the crystals contain a considerable percentage of ash. Hoppe-Seyler has, in fact, termed the substance *chlorophyllan* in order to emphasize this point. Analysis of the substance has given the following results:

	Gautier.	Hoppe-Seyler.
C.	73'97	73'34
H.	9'80	9'72
N.	4'15	5'68
O.	10'33	9'54
Ash	1'75	P. 1'38
	<hr/>	Mg. 0'34
	100'00	<hr/>
		100'00

It is of interest to note that iron was not found to be present, although, as we learned in a previous lecture, a supply of iron is essential to the formation of chlorophyll in the plant.

Fig 1.
Alcohol-Chlorophyll.

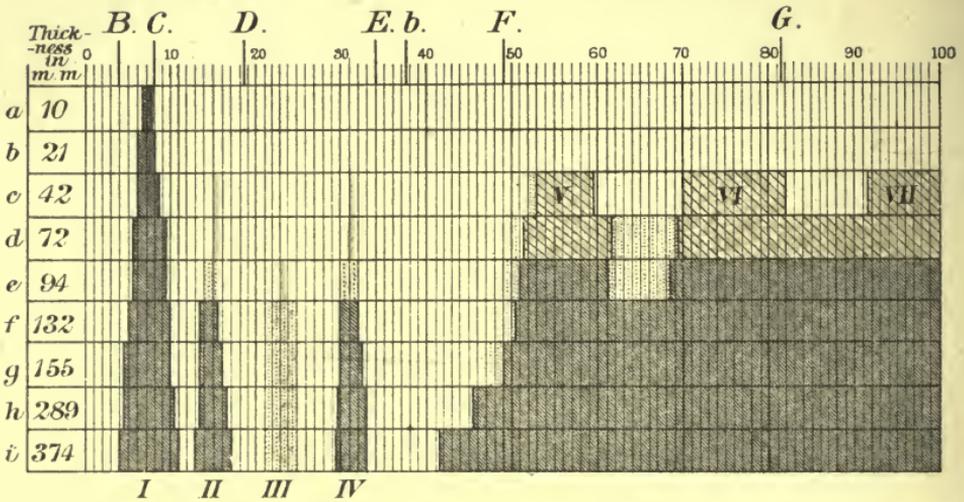
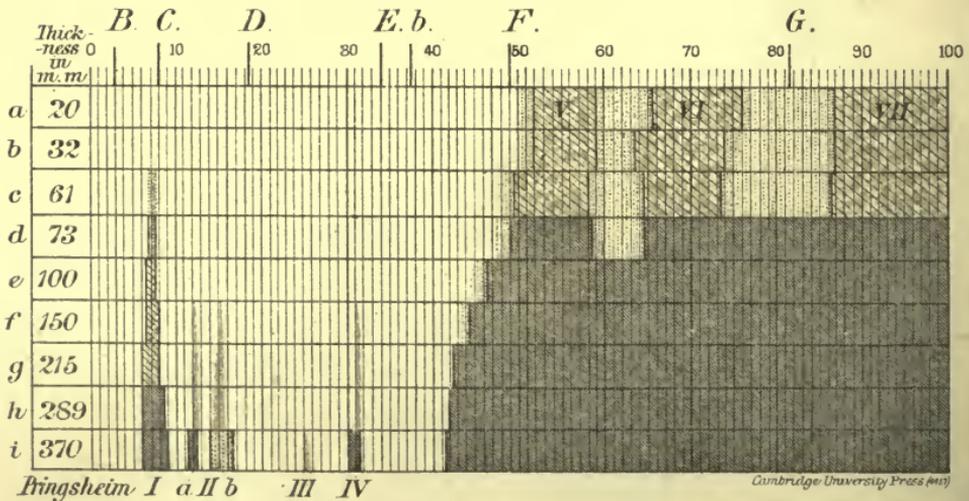


Fig 2.
Alcohol-Etiolin.



Pringsheim I a II b III IV

Cambridge University Press (1917)

From the percentage composition of the crystals Gautier deduces the formula $C_{19}H_{22}N_2O_3$, and draws attention to its resemblance to that of Bilirubin ($C_{16}H_{18}N_2O_3$). Hoppe-Seyler finds that when his chlorophyllan is boiled with alcoholic solution of potash, cholin, glycerin-phosphoric acid, an acid which he terms chlorophyllanic acid, and possibly also some fatty acids are produced. He concludes that chlorophyllan contains phosphorus in its molecule, and is either a lecithin or a lecithin-compound.

Now as to its physical properties. We have seen that it is soluble in alcohol, and it is likewise soluble in ether, benzol, carbon disulphide, and in various oils. A solution of chlorophyll possesses the property of *fluorescence*, so that when it is viewed in reflected light it appears opaque and of a deep lake-red colour; the light transmitted through a thin layer is green. If the light which has passed through a layer of a moderately strong solution be examined with the spectroscope, a characteristic absorption-spectrum will be observed. Beginning at the red end of the spectrum (see Plate, Fig. 1, *f*) a well-marked dark band will be seen between Fraunhofer's lines B and C extending rather beyond C, a second dark band in the orange between C and D, a third very faint band at the junction of the yellow and green, and a fourth more distinct band in the green near the line E; the whole of the blue end of the spectrum beyond the line F is absorbed. The absorption of the whole of the blue end of the spectrum is due to the coalescence of three bands which can be seen separately when very dilute chlorophyll solutions are used (Plate, Fig. 1 *c*), two in the blue between the lines F and G, and one at the end of the violet. The absorption-spectrum of chlorophyll presents then seven absorption-bands.

The figure of the chlorophyll-spectrum in the Plate is due to Pringsheim, who has devised an ingenious method for observing the spectrum. Instead of using solutions of different degrees of concentration he employs different thicknesses of a dilute solution. The numbers at the left-hand side of the figure indicate the thickness in millimetres of the layer examined: thus in *a* the thickness of the layer was 10 millimetres, and so on.

It may be added, with regard to the fluorescence of chlorophyll, that when the light reflected from a solution is examined with the spectroscope, it is found to be all red, the red being most intense in the positions corresponding to the absorption-bands of the chlorophyll-spectrum.

The views which have been held as to the probable relation between the presence of chlorophyll and the formation of non-nitrogenous organic substance in the plant are so numerous, that it will be possible only to mention the more important of them here. The first to be considered, which we may term the chemical theory and of which Sachs is the principal exponent, is that chlorophyll is actually converted into starch, that it is a substance intermediate between carbon dioxide and water on the one hand, and starch on the other. The reasoning upon which this theory is based is very complicated and abstruse, and cannot be regarded as conclusive; besides, it is contradicted by Sachs' observation that etiolated plants turn green when exposed to a light in an atmosphere which contains no carbon dioxide, that is, that chlorophyll is formed under circumstances which render impossible the decomposition of carbon dioxide. Then there is what we may term the physical theory which seeks to connect the function of chlorophyll with its absorption-spectrum. This theory is held from two exactly opposite points of view. Lommel and N. J. C. Müller argue that, according to the principle of the conservation of energy, the rays of light which are absorbed by chlorophyll, that is, more especially the red and the blue, must be converted into some other form of energy, and they conclude that these rays supply the energy necessary for the decomposition of carbon dioxide and water. The correctness of this view is confirmed by Timiriazeff and by Engelmann who find that the decomposition of carbon dioxide by green plants is most active in those parts of the solar spectrum which correspond to the more conspicuous absorption-bands of the chlorophyll-spectrum. It has indeed been found by Draper and by Pfeffer, that the most active decomposition of carbon dioxide takes place when green plants are exposed to yellow light, that is, to rays of the spectrum which are not absorbed by chlorophyll: but this result is not contradictory of those mentioned above; the discordance is due simply to physical conditions which will be discussed hereafter in connexion with the action of light. It appears, then, that the rays absorbed by chlorophyll are those which

are active in the decomposition of carbon dioxide. The other view is that taken by Pringsheim. He urges that the rays absorbed by chlorophyll are not active in the decomposition of carbon dioxide, but that still the absorption must have some physiological significance, and he considers this to be that the rays absorbed are such as would interfere with the synthetic processes; that the chlorophyll acts as a kind of filter to the rays of light which fall upon the plant, allowing those to pass which promote the synthetic processes and absorbing those which would be prejudicial to them. As we shall discuss this view in a subsequent lecture, it will suffice for the present to say that there is no evidence to prove that the rays absorbed by chlorophyll have any effect in diminishing the decomposition of carbon dioxide. It has been further suggested that chlorophyll combines with and fixes carbon dioxide just as the hæmoglobin of the blood combines with and fixes oxygen. But experiments made with various solutions of chlorophyll shew that this is not the case; still, it is possible that what the chlorophyll cannot do when extracted in solution it may be able to do when it is in the living chlorophyll-corpuscle.

Of these various views, the one which is most strongly supported by experimental evidence is that of Lommel, and it is therefore this one that we shall accept. The function of chlorophyll may, then, be briefly stated as follows; that it absorbs certain rays of light, and thus enables the protoplasm with which it is intimately connected to avail itself of the radiant energy of the sun's rays for the construction of organic substance from carbon dioxide and water.

4. *The Action of Light.*

Attention has been repeatedly drawn both in this and in previous lectures to the fact that the absorption of carbon dioxide and the evolution of oxygen, in other words, the formation of organic from inorganic substance, can only be effected by green plants when they are exposed to light. This subject will not be entered upon at present; it will be

more convenient to consider it when we are in a position to discuss the whole question of the relation of the metabolism of plants to external conditions (Lect. XIII).

We may consider, in conclusion, the formation of organic substance by the plant in its more general aspect. We have found that the constructive metabolism of the green plant, like that of all living organisms, has, as its end, the formation of the extremely complex substance which we have termed protoplasm; this is destined to undergo decomposition into simpler substances, some of which are and some are not of use to the plant, the decomposition being accompanied by the setting-free of energy in the plant. We have seen that the materials which a green plant has at its disposal for this purpose are of very simple composition, carbon dioxide, water, and salts containing nitrogen and sulphur. The steps of the process we have traced as closely as our information will allow; the first is probably the formation of comparatively simple substances containing C, H, and O (perhaps formic aldehyde and its polymers); then the formation of more complex substances containing N in addition (asparagin, leucin, etc.); and finally, by further synthesis, of still more complex substances (proteids). We have found that the starch which makes its appearance in the chlorophyll-corpuscles when constructive metabolism is in active operation, is not the first product of the synthetic processes, but only an indirect product: protoplasm is the substance which is formed in the chlorophyll-corpuscles, and it is only in consequence of the decomposition of the protoplasm formed that starch is produced. We will consider the nature of this decomposition in detail in a subsequent lecture.

We may enquire, too, if the constructive metabolism is equally energetic in all green plants. We should be inclined to say *a priori* that this is not the case, a decision which is confirmed by Weber's comparative observations on the leaves of certain plants. He determined the amount of organic substance formed in 10 hours by one square metre of

the leaves of the following plants under as nearly as possible the same conditions. The following are his results :

<i>Tropæolum majus</i>	.	.	4'466 grammes.
<i>Phaseolus multiflorus</i>	.	.	3'215 „
<i>Ricinus communis</i>	.	.	5'292 „
<i>Helianthus annuus</i>	.	.	5'559 „

We are now in a position to compare the constructive capacity of plants which contain chlorophyll, of plants which do not contain chlorophyll, and of animals. The first of the series of synthetic processes which we have traced above, the formation of non-nitrogenous organic substance from carbon dioxide and water, can only be effected by organisms (animals as well as plants, according to the observations of Geddes) which contain chlorophyll, and with this we must correlate the production of starch. The second process, the formation of proteid from organic non-nitrogenous carbon-compounds and inorganic salts containing nitrogen and sulphur, can, apparently, be performed by all plants alike, but it cannot, so far as we know, be performed by animals, excepting, possibly, those which contain chlorophyll. Stating the case in the most general terms, we may say that whereas a plant is nourished when nitrogen is supplied to it in the form of inorganic salts, an animal can only assimilate nitrogen in the form of proteid.

The last of all the processes of constructive metabolism yet remains to be considered, the conversion of dead unorganised proteid into living organised protoplasm. This must take place in every cell so long as it is living, and it must necessarily accompany the formation of new cells. But little can be said as to the nature of this process, for our knowledge of the differences between dead proteid and living protoplasm is very slight. We are indeed acquainted with certain facts; we know, for instance, that the primordial utricle of dead cells readily allows of the passage into it and through it of substances which could not enter or pass through it in life (p. 44); that the interchange of gases between the cell and the atmosphere which goes on so actively during life, and which is the expression of unceasing chemical combination and decomposition, is arrested; that the evolution of energy in the form

of heat, motion, or otherwise, does not take place: but these facts afford us but little insight. We may admit that during life the atoms in the molecule of protoplasm are in active vibratory movement, whereas in death this movement is arrested, but this does not tell us what is the essential difference between dead proteid and living protoplasm. Though it be granted that in the latter there is this active intramolecular movement, and that in the former it is absent, the question still remains why this is the case. The only kind of answer which has been offered is that there is a chemical difference between the molecule of dead proteid and that of living protoplasm. It is generally held that the molecule of living protoplasm is a very large, complex, and unstable one, and that proteid is only one of many products resulting from its decomposition; the conversion of dead proteid into living protoplasm would, according to this view, involve the building-up of the complex protoplasmic molecule from the simpler proteid molecule. But whatever the view which may be accepted as to the nature of the protoplasm-molecule, the difference in the properties of living protoplasm and of dead proteid is probably to be ascribed to a difference of molecular structure. Pflüger conceives it to be this, that in dead proteid the nitrogen is present in the form of ammonia, whereas in living protoplasm it is in the form of cyanogen. Loew and Bokorny, assuming that in the molecule of proteid a number of aldehyde-groups are present, consider that in living protoplasm the atoms in these groups are in active movement, whereas in dead proteid they are not, in consequence of the altered relation of the aldehyde-groups to the amide-groups in the molecule. But these are after all mere hypotheses; we cannot consider that the secret of life has been discovered as yet.

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LECTURE X.

METABOLISM (*continued*).

5. *The Distribution of Organic Substance throughout the Plant.*

IN the last lecture we studied the processes by which the formation of organic substance is effected in the plant, and we found that in highly organised plants the leaves are the organs in which these processes especially take place. We will now proceed to ascertain in what forms and by what means the organic substance thus produced is distributed throughout the plant, either to serve as *plastic material* for the building up of the structure of the plant, or to be deposited as *reserve-material* in some part of it.

Our knowledge on this subject depends principally upon the results of micro-chemical investigation, that is, upon the detection of the various substances in the cells under the microscope by means of appropriate reagents. It is extremely important to bear in mind, in the consideration of the results obtained by this method, that although it may not be possible to detect the presence of any given substance in the cells of an organ, we must not conclude that this substance is therefore not being formed there. The presence of a substance in the cells of an organ depends upon this condition, namely, that the amount of the substance conveyed to or formed in the cells is greater than the amount which is being conveyed away from or consumed in the cells. If these two amounts

are equal, then it will be impossible to detect the substance by micro-chemical methods, although the production of it may be actively proceeding. It is in many cases possible so to alter the conditions under which an organ is placed as to disturb the relation between supply and demand (as we see in Borodin's experiments mentioned in the last lecture) and thus to bring about the accumulation of substances which cannot be detected in it micro-chemically under normal conditions. All that we can detect by micro-chemical methods is then the excess of plastic material in the cell, and this we may regard as temporary reserve-material.

With this preliminary caution in our minds, we will discuss first the distribution of the non-nitrogenous organic substance formed by the leaves. This we have found to be starch, in the vast majority of cases, and we have seen that it is deposited in the chlorophyll-corpuscles in the form of grains. The proof that this starch is conveyed away from the leaves is afforded by the observation of Sachs that if a leaf which contains starch abundantly in its chlorophyll-corpuscles be placed in the dark for some hours the starch-grains will be found to have disappeared, and by those of Godlewski, Pfeffer, and Morgen, that the starch-grains disappear from the chlorophyll-corpuscles of a leaf when it is exposed to light in an atmosphere containing no carbon dioxide. We learn, then, that if chlorophyll-corpuscles be placed under conditions which prevent the continued formation of starch, no trace of starch will usually be detected in them. It is obvious that the starch-grains cannot be bodily conveyed as such from one cell to another inasmuch as the walls of the mesophyll-cells, so far as we know at present, are closed membranes; and even admitting, as was mentioned in a previous lecture (p. 23) that the protoplasm of adjacent cells may possibly be continuous through pores in the cell-wall, still the size of the starch-grains is too great to allow of their passing through these pores. The suggestion naturally occurs that the starch must pass from cell to cell in solution, and that, since it is practically insoluble in water, it must be converted into some substance which is soluble. There are reasons for believing that this

substance is sugar. By the researches of Kossmann and of Baranetzky it has been ascertained that leaves and shoots contain a substance, an unorganised ferment, which possesses the property of converting starch into sugar, and Sachs has found that sugar is very commonly present in the parenchyma surrounding the veins, more especially the midrib, of leaves. It might be expected that sugar would be found to be present in the mesophyll-cells themselves so long as they contain any starch; but this is not the case. De Vries, who has minutely studied the distribution of sugar in various plants, has failed to find it in the mesophyll in the cases which he has investigated. But, according to the principle laid down at the outset, we cannot conclude from this that sugar is not formed: the more probable explanation of the facts is that the sugar is formed and is rapidly conveyed away from the mesophyll to the parenchyma around the veins, where, as we have seen, it can be readily detected.

I have found that if a leaf be removed from the plant and be kept for some hours in a moist atmosphere, in the light or in the dark, sugar can be readily detected in its mesophyll-cells, although no trace could be found at the beginning of the experiment. The accumulation of sugar in the leaf is evidently due to the isolation of the leaf, the sugar formed in it being no longer conveyed away to other parts of the plant.

With regard to the nitrogenous plastic substances formed in the leaves, we have seen that these are amides and proteids. If the proteids are to be conveyed away from the leaves, they must, like the starch, be converted into substances which are diffusible. They may possibly be converted into peptone: as a matter of fact traces of peptone have been detected in leaves and shoots (Kern), and from the researches of Schulze and Barbieri it appears probable that these organs contain a ferment which can convert proteid into peptone. The information on this point is, however, very incomplete. But it is probable in any case that the changes do not stop here. The peptones are substances which, according to the most recent investigations, do not very readily diffuse through membranes. If, then, it is in the form of peptone that nitrogenous organic substance

travels from the leaves we should expect to find peptone in leaves more commonly and in larger quantity than is actually the case. On the other hand we have seen that crystallisable nitrogenous organic substances, amides, have been found in the leaves of various plants and in considerable quantity. We may infer that the proteid which is formed in the leaf is decomposed, and that these amides are some of the products of the decomposition. These substances diffuse readily, and, if we neglect the possibility of the direct conduction of proteid by means of the communicating protoplasm of adjoining cells, it is in the form of these substances that nitrogenous organic substance is distributed throughout the plant.

Without entering at present into detail regarding the chemistry of the changes which the organic substances formed in the leaf undergo as a preliminary to their distribution throughout the plant, we will proceed to ascertain what is the mode of their distribution and what are the tissues in which they travel. Their distribution takes place according to the same principle as that of the substances absorbed from without by the roots: they travel to those parts of the plant in which a chemical alteration of them is going on, either to the growing-points, at which new branches and leaves are being formed and material is required for the formation of protoplasm and cell-wall, or to organs which serve as depositories of reserve-materials such as buds, bulbs, roots, tubers, etc., in which both nitrogenous and non-nitrogenous substances are being stored up for the use of the plant at the commencement of its next period of growth, or seeds or spores, in which similar provision is being made for the nutrition of the young plant to be developed from them during the early stages of its growth. They travel either in the parenchymatous tissues by osmosis from cell to cell; or in continuous vessels the *sieve-tubes* and the *laticiferous cells and vessels*, by diffusion, their movement in these vessels being promoted by the swaying to and fro of the subaërial parts of the plant under the influence of the wind.

It has been observed that the sieve-tubes of many plants (Vine, Lime, Poplar, Walnut) cease to be continuous vessels during the winter in con-

sequence of the filling-up of the pores of the sieve-plate by a formation of callus in the autumn. In the spring the callus is absorbed and the continuity restored (De Bary, Janczewski).

From the researches of Sachs and others it appears that the sugar and the amides travel in the parenchymatous tissues, and Sachs observed that these tissues have an acid reaction. But the conduction of these substances is, generally speaking, not direct: it is frequently interrupted by their conversion into an insoluble or at least an indiffusible form at some intermediate stage in their journey. For instance, there is in the petioles and stems of many of the higher plants a layer (seen in transverse section) of parenchymatous cells near the periphery of the ring of fibrovascular bundles or of each fibrovascular bundle, in which, so long as the plant contains any excess of non-nitrogenous organic substance, starch-grains are to be found. On account of the constant occurrence of starch in its cells, this layer has been termed the *starch-layer*. But a temporary deposit of starch may take place in other cells as well. Thus Briosi has observed the presence of starch-grains in sieve-tubes, they are present also in laticiferous tissue, and they may be found throughout the parenchymatous tissue. Again, drops of oil are frequently to be found, especially in the laticiferous tissue, and even in the chlorophyll-corpuscles themselves; these too may be regarded as transitory reserve-materials. Finally, the sieve-tubes and the laticiferous tissue contain proteids, for the most part unorganised and indiffusible, for, in the sieve-tubes at least, they are soluble in dilute potash solution but not in water; these proteids are probably to be regarded as temporary reserve-materials. Inasmuch as the sieve-tubes and also the laticiferous cells and vessels are continuous throughout the plant, the contained proteids can travel in them as such from one part of the plant to the other; but doubtless their distribution to the tissues involves a conversion into a diffusible form, for it has been found that the latex of certain plants is rich in proteolytic ferment. It is worthy of note that Sachs found the contents of the sieve-tubes to have an alkaline reaction.

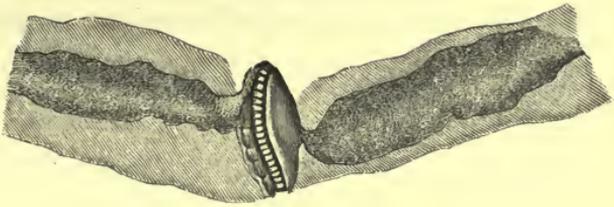


FIG. 23 (after Hanstein). Part of a sieve-tube (from the Hop) shewing a sieve-plate. The central granular portion is the protoplasmic content of the tube; the shaded portion around this is the cell-wall swollen by treatment with potash. The dark lines traversing the sieve-plate represent protoplasmic filaments.

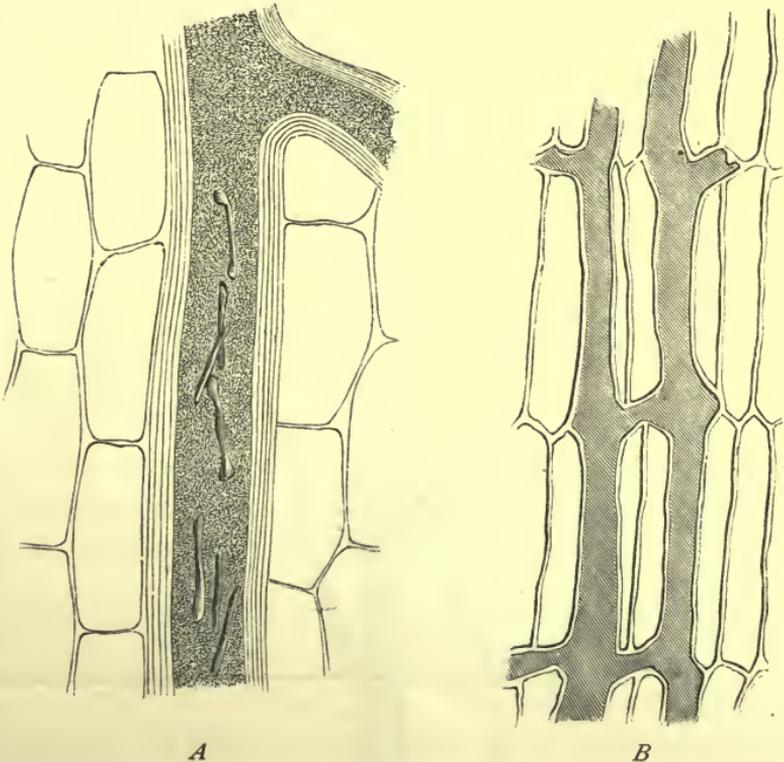


FIG. 24 (after Dippel). *A*, Part of a laticiferous cell from *Euphorbia splendens*; in the latex the peculiar rod-shaped starch-granules are to be seen.

B, Laticiferous vessels from the root of *Cichorium Intybus*.

The fluid contained in the laticiferous tissue is termed *latex*. It is a watery fluid holding proteids, carbohydrates, and mineral matters in solution. It is frequently milky in consequence of the presence of fats

and waste-products, such as resins and caoutchouc, which form an emulsion. It has been observed in some cases that the latex coagulates spontaneously.

Weiss and Wiesner found the following substances in the latex of *Euphorbia platyphyllos*:

Undissolved proteid and starch	2.02 per cent.
Dissolved proteid and carbohydrate	0.51 "
Fat	1.33 "
Sugar and extractives	6.41 "
Gum	2.15 "
Resin	8.12 "
Ash	1.51 "

The statements made above as to the tissues in which organic substances travel from one part of the plant to another

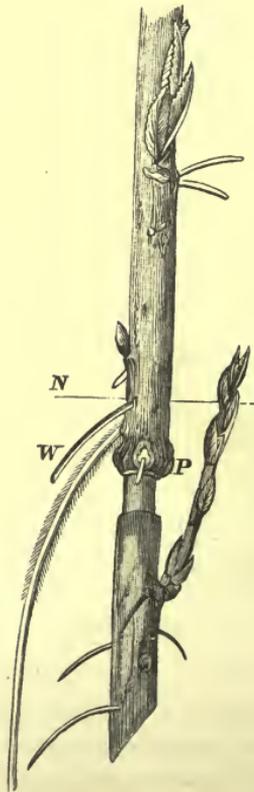


FIG. 25 (after Sachs). A twig which had been kept standing in water after the removal of a ring of cortical tissue. *N*, level of the water: *P*, swelling formed at the upper margin of the annulation: *W* roots.

are well illustrated by experiments in which layers of tissue are removed. Thus Knight observed that when a ring of cortical tissue down to the wood was removed from the stem of a dicotyledonous tree below the leaves, the part of the stem below the incision scarcely grew at all, whereas the part of the stem above the incision grew normally; again Hanstein found that if a ring of cortical tissue be removed from a detached branch of a tree of this kind, and the branch be placed in water, roots are formed abundantly above the incision but scarcely at all below it; if, however, the experiment be tried upon branches of plants which contain scattered fibrovascular bundles in their medulla, the removal of the ring of cortical tissue has no appreciable effect upon the development of the roots: Faivre too has obtained similar results by the same method. The significance of these facts is this, that the removal of the ring of cortical tissue, including the soft-bast, from a branch or stem of a normal dicotyledonous plant almost completely cuts off the supply of organic substance to the parts below the incision; if the branch or stem contains fibrovascular bundles in its medulla, the supply of organic substance is diminished by the operation, but enough is still conveyed to enable the parts below the incision to maintain their growth.

With regard to the laticiferous tissue, it appears, from the researches of Faivre, that it contains organic substances which are derived from the leaves and which are used up in building up the tissues of the growing parts of the plant.

It has been suggested that a formation of proteid takes place in the sieve-tubes; Strasburger is however of opinion that, since no nuclei have been found in them, this is not the case (see p. 151).

In order to obtain a connected idea of the changes which these nitrogenous and non-nitrogenous organic substances undergo in connexion with their distribution throughout the plant, we will trace them to some organ in which they are to be stored up for a time as reserve-materials, and then from this organ when, after a period of quiescence, it resumes active life. For this purpose we will take the seed as our

example, for our knowledge of its chemistry is more complete than is that of any other similar organ.

Non-nitrogenous organic substance is conveyed to the seed in the form of sugar, the nitrogenous in the form of amides, and they are there deposited, the non-nitrogenous substances in the form of starch or of oil, the nitrogenous in the form of masses of proteid (consisting of peptones, globulins and albuminates) known as *aleurone-grains*. It appears, therefore, that a formation of proteid takes place in seeds doubtless from the sugar and the amides which are supplied to them. The greater part of the sugar, however, reappears in the form of starch or oil. It has been found in many cases that asparagin and other amides are present in seeds in small quantity, and occasionally nitrogenous glucosides are present, as, for instance, amygdalin in the Bitter Almond, potassium myronate in the Black Mustard.

We may distinguish different kinds of seeds according to the form and the place in which the reserve-materials are stored up. Thus there are *starchy seeds* which contain much starch and more or less oil, and *oily seeds* which contain oil and no starch: in the former the aleurone-grains are small, in the latter they are large. Further, in some seeds the reserve-materials are deposited in the cells of the seed itself, either outside the embryo-sac (*perisperm*), or within it (*endosperm*), and in some both perisperm and endosperm are present; in others they are deposited in the seed-leaves or *cotyledons* of the embryo which then occupies the whole of the seed. Seeds of the former kind are said to be *albuminous*, those of the latter *exalbuminous*.

We will defer, for the present, the consideration of the structure and of the chemical composition of the starch-grains and aleurone-grains. It need only be stated now that aleurone-grains always contain a mass of mineral matter, the *globoid*, and frequently a crystal of proteid, the *crystalloid*.

These are the principal forms in which the reserve-materials are stored up in seeds. Less frequently they occur, in addition, in other forms; thus in the seeds of the Date and of *Phytelephas* carbohydrate is deposited in the form of thickened cell-walls, that is, as cellulose, constituting, in the latter case, what is known as "vegetable ivory"; again glucosides are occasionally present, substances

which yield glucose as one of the products of their decomposition; these may be either non-nitrogenous (*e.g.* digitalin) or nitrogenous (*e.g.* amygdalin). Starch and oil are also the forms in which the non-nitrogenous reserve-materials are most commonly stored up in other depositories: thus starch is to be found in the winter in the cells of the ground-tissue of perennial roots and rhizomes, of the trunks of trees, also in the septate and unseptate fibres and in the parenchymatous cells of the wood of the stems of Dicotyledons (Sanio) so long as these cells contain protoplasm, in bulbs and corms; oil occurs in some fruits, such as the Olive, and in the spores of many Fungi. In certain cases, however, carbohydrate is stored up in other forms; in the root of the Beet it is present as cane-sugar; in the bulb of the Onion and in many fruits as glucose; in the tuberous roots of the Dahlia as inulin; glycogen has been found by Errera in various Ascomycetous Fungi, especially in their asci, and by Reinke in the plasmodium of *Æthelium*; mannite has been found to be commonly present in Agarics by Müntz, and many of these Fungi contain a form of sugar known as trehalose; mannite has also been found by de Luca in the leaves, flowers, and unripe fruits of the Olive, and in various parts of a great number of plants; the dried juice (manna) obtained from *Fraxinus Ornus* consists principally of mannite. The proteid reserve-materials are not known to be deposited in the form of aleurone-grains in any other organs besides seeds, but crystalloids have been found free in the cells of various plants, for example, in the peripheral cells of the potato-tuber (Bailey), in the nuclei of the epidermal cells of the integument of the ovule of *Lathræa squamaria* (Radlkofer), in the cells of the Florideæ (Cramer, Klein), in the mycelium of the Mucorini (Klein, van Tieghem). Amides have been found stored up in roots and tubers. Schulze and Urich found glutamin in Beet-roots, and Scheibler found asparagin and a substance termed betaïn; it appears that in some years glutamin, in others asparagin is the more abundant. In potatoes Schulze and Barbieri found asparagin, leucin and tyrosin.

Since Schmiedeberg, Drechsel, and others have succeeded in producing proteid crystals artificially, we may infer that their formation in the plant is not due to the organising activity of the protoplasm, but that it is a process of ordinary crystallisation.

When once deposited the reserve-materials undergo no further change, or at most the proteids may slowly undergo some alteration, so long as the organ in which they are deposited remains in an inactive condition. An organ in this state is practically dead for the time being, all its metabolic processes being arrested. It is capable, moreover, of resisting injurious influences, such as extremes of temperature and desiccation, which would prove fatal to it were it actively living. It is obviously in consequence of this property possessed by such organs during what we may term their state of suspended animation, that vegetation is maintained in regions in which the cold of winter is severe and in arid tropical regions. The time of the possible duration of this state without permanent loss of vitality varies very widely; spores, for example, lose their power of resuming the active vital condition, of *germinating*, in a word, in a comparatively short time; oily seeds retain the power of germinating for a much shorter time than starchy seeds; in some instances starchy seeds have been known to retain it for many years. When the external conditions become favourable, when the temperature is sufficiently high and there is a supply of water, these quiescent organs readily germinate, and then the reserve-materials which they contain undergo great chemical changes. Germination is essentially connected with growth; in a seed, with the growth of the embryo; in a bulb or a rhizome, with the growth of a shoot. The chemical changes which the reserve-materials undergo are of such a nature as to convert them into substances which can readily travel to the seat of growth, and which can be used as plastic material by the growing cells. We will study these changes as they occur in a seed.

It has been observed by all who have investigated the subject that, as the embryo grows, the reserve-materials in the seed diminish in quantity. They are evidently conveyed to

the seedling, and are used by it to form new protoplasm and cell-wall. In considering the changes which they undergo we will begin with the non-nitrogenous reserve-materials. The starch (and cellulose, in the Date) is undoubtedly converted into sugar; this is proved by the detection of sugar as well in the seed as in the seedling, and further by the detection in germinating seeds of an unorganised ferment which possesses the property of converting starch into sugar. The first change which the oils undergo is apparently a decomposition into glycerin and fatty acid, which is probably effected by the action of an unorganised ferment (Schützenberger); these substances are then replaced by carbohydrate (Sachs). The glucosides which, as we have seen, are present in some seeds, are decomposed into sugar and other substances also by the action of an unorganised ferment. The absorption of non-nitrogenous reserve-material soon makes itself apparent in the embryo by the formation of a large quantity of temporary starch in its cells, which gradually disappears as its growth proceeds.

With regard to the proteid reserve-materials of the seed, there can be no doubt that they are converted into substances which are diffusible. The visible effect of germination upon the aleurone-grains is, according to Pfeffer, that they swell up and fuse to form a granular viscid mass; the globoids undergo solution, and so do the crystalloids when they are present. It was thought that the proteids which are insoluble in water (globulins and albuminates) were converted into peptone by the action of an unorganised ferment; von Gorup-Besanez believed that he had extracted a ferment of this kind from the seeds of Vetches, but Krauch has shewn that his results are not trustworthy. In the absence of any evidence to prove the conversion of these proteids into peptone, we must conclude that they are directly split up so as to give rise to amides. The peptone of the aleurone-grains undergoes the same change. It might be thought that the peptone, inasmuch as it is somewhat diffusible, is directly conveyed to the seedling, but this is not the case. In endeavouring to determine this point I found, in the case of

Lupins, that whereas peptone was abundant in the cotyledons of seedlings a week old, it was not present in any other part. Seedlings, it is well known, contain considerable quantities of amides, and the presence of these can only be accounted for by regarding them as having been derived from the reserve-proteids of the seed. It is then in the form of amides that nitrogenous organic substance is supplied to the seedling. All the various crystallisable nitrogenous organic substances which have been already mentioned are to be found in germinating seeds, but they are present in various proportions in different seeds. For example, Vetch-seeds contain principally asparagin and leucin, together with small quantities of glutamin and tyrosin (von Gorup-Besanez): Pumpkin-seeds contain principally glutamin and asparagin, with some tyrosin (Schulze and Barbieri).

The effect of the absorption of these substances by the embryo is that the cell-sap of the cells of its ground-tissue become charged with them, for the supply is much more rapid than the consumption in the formation of proteid; consequently the seedling soon comes to contain a larger percentage of them than does the organ in which they are being formed. If the seedling is growing under favourable conditions these substances gradually diminish in quantity and finally disappear, and this is accompanied by an increase in the amount of proteid contained in the seedling.

The nature of these conditions has been clearly made out by Pfeffer. He found that Lupin-seedlings grown in the dark contained a very large quantity of asparagin so long as they continued to live, but that if they were exposed to light the asparagin gradually diminished. But he ascertained further that mere exposure to light is not the cause of this, since the asparagin did not diminish in seedlings exposed to light in an atmosphere which contained no carbon dioxide. The disappearance of the asparagin depended therefore upon conditions which were essential to the formation of non-nitrogenous organic substances by the seedlings. The accumulation of the asparagin depended upon the absence of a supply of appropriate non-nitrogenous substance with which

it could combine to form proteid ; when this supply was provided the asparagin disappeared.

The following tables of analyses will illustrate the foregoing remarks :

1. The production of asparagin at the expense of proteid in the depositories of reserve-materials.

Beyer's analysis of Yellow Lupin seeds and seedlings, 2—3 inches long ; the cotyledons are the depositories, as the seed is exalbuminous.

100 parts dry weight contained	Quiescent seed	Seedling	
		Cotyledons	Other parts
Proteids	61.268	60.450	50.080
Asparagin	—	1.450	29.640

2. The changes undergone by the non-nitrogenous reserve-materials.

These are well illustrated by Peters' comparative analyses of the oily seed and of the seedling of the Pumpkin (*Cucurbita*).

100 parts dry weight contained	Quiescent seed	Seedling		
		1st Period	2nd Period	3rd Period
Oil	49.51	17.22	11.14	4.24
Sugar	traces	5.45	5.41	5.33
Gum	traces	1.73	2.20	2.70
Starch	0.00	4.17	7.61	2.77
Cellulose	3.02	7.87	10.00	12.70
Albuminoids	39.88	39.88	39.67	43.65
Ash	5.10	7.62	8.10	9.33
Extractives	2.49	16.06	15.87	19.29
	100.00	100.00	100.00	100.00

Also by those of Boussingault of the starchy seeds and of the seedlings of the Maize; the seedlings had grown in dark for 20 days.

a. Absolute weights, in grammes :

	Total dry weight	Starch and dextrin	Sugar	Oil	Cellulose	Nitrogenous substances	Ash	Extractives
Seeds (22)	8·636	6·386	0·000	0·463	0·516	0·880	0·156	0·235
Seedlings	4·529	0·777	0·953	0·150	1·316	0·880	0·156	0·297
Differences	-4·107	-5·609	+0·953	-0·313	+0·800	0·000	0·000	+0·062

b. Weights calculated in percentages :

	Seeds	Seedlings
Starch and dextrin	73·9	17·2
Sugar	0·0	21·0
Oil	5·3	3·3
Cellulose	6·0	29·1
Nitrog. subst.	10·3	19·4
Ash	1·8	3·5
Extractives	2·7	6·5
	100·0	100·0

The foregoing statements as to the changes which the reserve-materials of the seed undergo at the time of germination apply to other depositories of reserve-materials as well. As regards the non-nitrogenous material stored up in bulbs, tubers, rhizomes, roots, etc., we have seen that it is deposited in the form of carbohydrates, such as starch, inulin, cane-sugar, and glucose. Of these, starch, inulin, and probably also cane-sugar, are converted into grape-sugar (glucose) on germination, and are supplied in that form to the growing shoot. As to the nitrogenous organic substance stored in these depositories, it is, as we have seen, accumulated in the form of amides for the most part, and can

therefore be directly transferred to the growing shoot : when it is accumulated in the form of proteid, as in the potato for instance, the proteid is doubtless converted into amides, just as in the seed, and these are used by the shoot for its nutrition and growth.

It remains for us to become acquainted with the mode in which the plastic materials are used for the building-up of the structure of the plant. We may take the growing-point as the object of our study. We know that in a growing-point a formation of new cells is taking place, that is, that cell-wall and protoplasm are being produced. This production must be effected at the expense of plastic materials supplied to the growing-point from other parts of the plant. But these plastic materials cannot be detected as such in the tissue of the growing-point, the primary meristem (see p. 151). Schacht, Sachs, and others have found that although starch is usually present in considerable quantity in a growing member, and can be traced into the immediate neighbourhood of the growing-point, yet it cannot be detected in the cells of the growing-point itself. Sachs also failed to detect sugar, and the various observers (Pfeffer, Borodin, Schulze, de Vries) who have studied the distribution of amides in the plant have likewise failed to detect them in the cells of the growing-point. On the other hand, proteids are abundantly present, and these are doubtless formed from the amides and the carbohydrates (together with sulphates and perhaps phosphates) supplied to the cells of the growing-point. These proteids serve as material for the construction of the protoplasm which is required in connexion with the processes of cell-multiplication. The cell-walls are formed, according to Schmitz and Strasburger, from portions of the protoplasm (see p. 26). The processes going on in a growing-point are then these : the cells are being supplied with plastic materials from the cells lying behind them which contain these materials ; from these plastic materials proteid is constructed so that the plastic materials themselves cannot be detected in the meristematic cells ; from the proteid living protoplasm is produced, and from a portion of the protoplasm cell-walls are formed.

We have now obtained a general insight into the mode of distribution of the plastic materials in the plant, as well as some knowledge of the different forms in which they may make their appearance. We will conclude our consideration of this subject with a few general considerations, leaving the discussion of the chemical details for another lecture.

We may gather from the facts before us that the parts of the plant which do not contain chlorophyll are, as it were, parasitic upon those which do. Just as a plant which does not contain chlorophyll must have organic substances supplied to it, so must also those parts of a green plant which do not contain chlorophyll. The cells in which chlorophyll is present can make organic substance, both nitrogenous and non-nitrogenous, from carbon dioxide, water, and salts; those in which it is not present can only decompose and recombine the organic substance supplied to them from those in which it is present. This relation is well marked in the development of shoots from bulbs, tubers, etc.; a shoot is incapable at first of constructing its own plastic materials, and draws its supplies from the depository of reserve-material with which it is connected; it behaves like a parasite. On the other hand, as far as continuity of tissue is concerned, a parasite is as closely connected with its host, as a shoot is with the organ which bears it. The relation of the embryo in this respect is peculiar. In albuminous seeds, the embryo is simply imbedded in the endosperm (or perisperm); there is no continuity of tissue. When the seed germinates and the further development of the embryo commences, the reserve-materials in the endosperm undergo the changes with which we have become acquainted, and the products are absorbed by the embryo through its external surface; in some cases a special absorbent organ is present, as in Grasses (the scutellum), and at a later period in the development of the embryo the cotyledons frequently act as absorbent organs.

Traub's interesting observations on the embryo of Orchids, the suspensors of which grow out of the ovule, in certain species, and attach themselves to the placenta from which they absorb nourishment, seem to suggest that possibly the suspensor may have an absorbent function in all cases.

The question has naturally arisen in reference to albuminous seeds, as to how far the changes in the reserve-materials of the endosperm are to be ascribed to the embryo. In order to answer this question van Tieghem experimented with the embryo of *Mirabilis*, depriving it of its endosperm and supplying it artificially with nutriment; under these conditions the embryo grew and developed, but not so well as under normal conditions. From this we may infer that, in the seed, changes go on in the endosperm, independently of the embryo, by which the reserve-materials stored up in it are prepared for absorption by the embryo. The results of the similar experiments of Blociszewski on Rye-seeds lead to the same conclusion, and it is further supported by van Tieghem's observation that the isolated endosperm of *Ricinus* can grow, under favourable conditions, and that the aleurone-grains become disorganised and the oil replaced by starch. There can be no doubt, however, that the embryo exerts an important influence in bringing about the changes in the reserve-materials of the endosperm, though it is difficult to determine what the exact nature of this influence is. It may be that the embryo excretes a ferment, or it may simply act by removing the products of ferment-action, thus preventing their accumulation and so assisting the processes.

The difference in structure between albuminous and exalbuminous seeds is essentially this, that whereas in the former the reserve-materials of the endosperm are only absorbed by the embryo during germination, in the latter they are absorbed by the embryo during the ripening of the seed, and are deposited in the cotyledons.

We will now discuss the structure and composition of the starch-grains and of the aleurone-grains. The starch-grains present evident structure: though they vary in size and shape in different seeds, yet in all cases they present a stratified appearance, consisting apparently of layers deposited concentrically or excentrically around a certain point, the *hilum* (Fig. 26): in fact, as Strasburger points out, the optical section of a grain resembles the transverse section of a thickened stratified cell-wall. They are formed by the protoplasm; and

although the exact mode of their formation in seeds has not been investigated, it may be assumed that it is the same as in other parts of the plant. Schimper has observed that the formation of starch-grains is commonly effected, in parts of plants not exposed to light, by certain specialised portions of the protoplasm, which are termed *starch-forming corpuscles* or *amyloplasts*. These corpuscles closely resemble the chlorophyll-corpuscles, though of course they contain no chlorophyll; in some cases, in fact, an actual conversion of an amyloplast into a chlorophyll-corpuscle, under the influence of light, has been observed. In both cases, if we accept the view of Strasburger, the starch formed is a product of the decomposition of protoplasm; the difference in function between chlorophyll-corpuscle and amyloplast is then this, that in the former the synthetic processes begin with such simple substances as carbon dioxide, water, and salts, and are effected under the influence of light, whereas in the latter they begin with tolerably complex substances (*e.g.* asparagin and glucose), and in this case the influence of light is not essential. Strasburger has found that in certain cases (macrospores of *Marsilia*, cells of medullary rays of *Pinus sylvestris*) the starch-grains are formed in the general protoplasm of the cell. At their first appearance the starch-grains are minute bodies usually more or less spheroidal in form; as they increase in bulk they begin to present the stratified appearance mentioned above. When the grains are formed in the

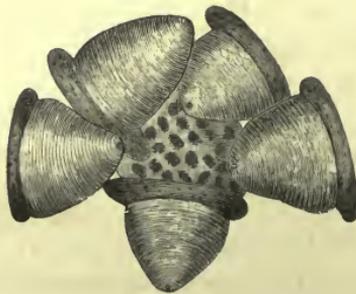


FIG. 26 (after Schimper). Group of amyloplasts, each bearing a starch-grain, collected round the nucleus in a cell of the tuber of *Phajus grandifolius* (*Bletia Tankervilleæ*).

general protoplasm or inside the amyloplasts the spheroidal form is retained and the planes of stratification are concentric around the hilum which is the part of the grain which was first formed : when, however, the grains are formed, as they frequently are, on the outside of an amyloplast, they soon become oval and the layers excentric ; the end of the grain in contact with the amyloplast becomes broad, and the number of layers of stratification is greater there than at any other part ; hence the hilum is gradually removed further and further away from the amyloplast, so that the long axis of the grain coincides with the direction of greatest growth (Fig. 26). We naturally conclude from these facts that the grain grows by the deposition of new layers on its surface, and that the successive layers produce the stratified appearance of the grain.

In addition to the planes of stratification, the starch-grain is marked by lines radiating from the hilum, which are planes of striation. Schimper and Arthur Mayer were led by this to regard a starch-grain as a spherocrystal, consisting of a number of radially-placed prisms. According to their view the formation of a starch-grain is effected in this way, that the amyloplast takes up sugar from the cell-sap and converts it into starch, which is deposited in successive layers consisting of prismatic crystals. Strasburger, however, finds that, as in the case of cell-walls, each layer of the grain is formed from a layer of protoplasm, and he thinks it probable that the striation of the layers, like that of the layers of cell-walls, is connected with the arrangement of the microsomata in the layers of protoplasm from which the layers of starch have been derived.

According to Naegeli, a starch-grain increases in bulk not by apposition but by intussusception, that is by the intercalation of new particles (micellæ) of starch between those which are already present ; he regards the stratification of the starch-grain not as the result of the deposition of successive layers one upon the other, but as being due to the differentiation of the growing starch-grain into layers containing alternately a greater or a smaller proportion of water. The most important of the facts upon which this view is based is that the most external layer of a starch-grain is always a dense layer, whereas the hilum is relatively

watery : from this he argues that the layers cannot be successively deposited for, were that the case, the most external layer would be the youngest and therefore probably the most watery part of the grain. Schimper, however, has pointed out that, under certain circumstances, a starch-grain which has lost its regular outline in consequence of partial solution, may have new layers deposited upon it with a regular outline, and that, the irregular outline of the corroded grain can still be seen within; this fact affords considerable support to the apposition theory. The stratification of starch-grains, he admits, is due, as Naegeli states, to the alternation of more and less watery layers ; he ascribes this distribution of water to tensions in the grain which cause each apposed layer to become differentiated into three, a middle watery layer with a dense layer on each side of it. Strasburger denies the alternation of more and less watery layers. He comes to the conclusion that, in starch-grains as in cell-walls, the layer last formed (*i.e.* the one next the cell-contents) is the most dense one, and that the older layers gradually absorb water : hence the external layer of a starch-grain is the most dense, and the inner layers are successively more and more watery until the maximum proportion of water is reached in the hilum. Each layer is therefore stretched by the

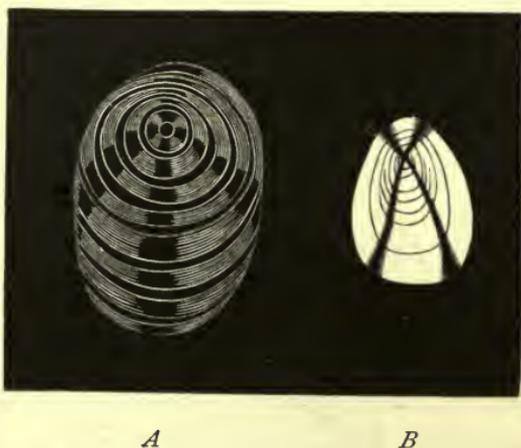


FIG. 27. Starch-grains (Potato) under the polariscope: *A*, (after Dippel) a starch-grain seen with crossed Nicols: *B* (after Weiss) a starch-grain seen with parallel Nicols.

layer within it (positive tension), compressed by the layer external to it (negative tension). The tensions in a starch-grain are thus precisely the opposite of those in a thickened cell-wall (see p. 36), but this statement of them applies quite accurately only to concentric starch-grains : it is true of the older concentric part of excentric grains, and in these grains the external layer is always the most dense, but the excentric incomplete layers are not successively more and more watery from within outwards.

With reference to the optical properties of starch-grains von Mohl pointed out that the interference colours of starch-grains are complementary to those of cell-walls, the former being optically positive and the latter negative. Strasburger refers this difference in optical properties to the differences of the tensions in the two cases, the tensions in starch-grains being of the nature of traction, in cell-walls of compression.

A few words may be added as to the chemistry of starch. A starch-grain consists of two forms of carbohydrate. If a starch-grain be treated with dilute sulphuric or hydrochloric acid, a portion of it will be dissolved, leaving a skeleton which retains the form of the grain, and which consists of a substance termed *starch-cellulose*, closely allied to ordinary cellulose. The dissolved substance is termed *granulose*; it turns blue on treatment with iodine, and it is in fact to the presence of this substance that the characteristic blue colour which starch-grains assume with iodine is due; it appears to be slightly dissolved when starch-grains are rubbed in a mortar with cold water; it is soluble in dilute acids and in concentrated solutions of certain salts such as potassium bromide and iodide, calcium and zinc chloride. When a starch-grain is treated with a solution of an unorganised ferment, the granulose first disappears, and then the cellulose-skeleton is slowly dissolved (Fig. 28).

From the researches of W. Naegeli and of Sachsse it appears that the formula of starch (granulose?) is $6(\text{C}_6\text{H}_{10}\text{O}_5) = \text{C}_{36}\text{H}_{60}\text{O}_{30}$: Pfeiffer, however, concludes from the compounds which it forms with alkalies, that its formula is probably $4(\text{C}_6\text{H}_{10}\text{O}_5) = \text{C}_{24}\text{H}_{40}\text{O}_{20}$.

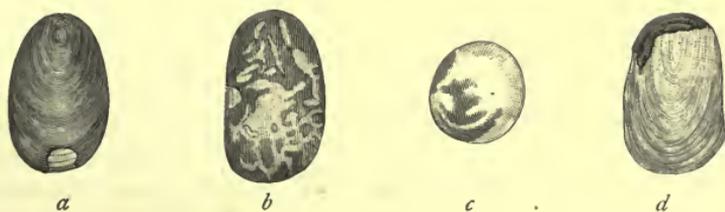


FIG. 28 (after Baranetzky). Starch-grains from a potato in various stages of solution under the action of a diastatic ferment: in *c* and *d* scarcely anything is left but the cellulose-skeleton.

The reserve-proteids of seeds are stored up, as before mentioned, in the form of granules, aleurone-grains. These granules are especially well-developed in oily seeds, being much larger than they are in starchy seeds. When a section of an oily seed is examined, the aleurone-grains are seen occupying the interstices of the protoplasm in some or all of the cells. On the addition of water they swell-up, and, owing to the solution of part of their substance, their structure becomes

apparent. In some cases they contain one or several crystals of calcium oxalate, in most an amorphous mass of mineral matter, the *globoid*, which consists, according to Pfeffer of double phosphate of lime and magnesia. It frequently happens (*e. g.* Castor-oil plant, Brazil-nut) that a crystal of proteid is also present. In order to distinguish this crystal from mineral crystals, from which it differs in its property of swelling-up, it is termed the *crystalloid*.

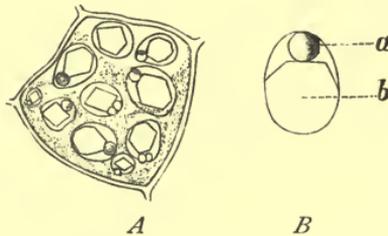


FIG. 29 (after Pfeffer). *A*, an endosperm-cell of *Ricinus* containing aleurone-grains; *B*, a single aleurone-grain; *a* the globoid, *b* the crystalloid.

I have found that aleurone-grains consist chemically (apart from the globoid or the crystal of calcium oxalate) of proteids of three kinds: (1) of proteids soluble in water, not precipitated from solution by boiling, belonging therefore to the group of *peptones*; (2) of proteids insoluble in water, but soluble in 10 per cent. or saturated solutions of common salt (NaCl), belonging to the group of *globulins*; (3) of proteids insoluble in water and in solutions of common salt, but soluble in alkalies; these are probably derived from the globulins, and are to be regarded as *albuminates*. The crystalloids consist either of a globulin or of an albuminate.

Pfeffer gives the following account of the development of aleurone-grains. The formation of them begins when the seed has ceased to receive supplies of plastic material from the plant; for if a seed be removed at the time when the formation of the aleurone-grains is commencing, the formation of them is not interrupted. The inorganic contents, the crystals of calcium oxalate or the globoids of double phosphate of lime and magnesia first make their appearance in the protoplasm of the cell, and, in the seeds which contain them, the proteid crystalloids. As the seed in ripening gradually loses water, proteids aggregate at various points in the cells around a single crystal of calcium oxalate or a group of crystals, or around one or more globoids, as the case may be, and around a crystalloid when it is present, and each such aggregation constitutes an aleurone-grain.

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LECTURE XI.

THE METABOLISM OF PLANTS (*continued*).

THE last two lectures have made us acquainted with the more general facts as to the formation of organic substance and as to the changes which it undergoes in connexion with its distribution in the plant. We will now study the nature of these processes in detail.

6. *The Metabolic Processes.*

Inasmuch as the processes of constructive metabolism have been treated of as fully as our knowledge will allow in a previous lecture (Lect. IX.), we need only repeat here the principal conclusions at which we then arrived. We found that the protoplasm of the plant is capable, under appropriate conditions, of building up more and more complex organic substances from the relatively simple materials of its food, the last of the series of processes being the formation of living protoplasm. Our conception of the nature of this last process will depend upon the view which we take of the nature of protoplasm. If we regard the molecule of protoplasm as a highly complex one containing besides proteid, carbohydrate, fatty, and other radicles, the process in question will be one of remarkable constructive activity: if, on the other hand, we regard protoplasm as simply modified proteid, the process in question will consist essentially in the rearrangement of the radicles in the molecule of proteid (see p. 160).

But it is with the processes of destructive metabolism that we are now especially concerned, the processes by which complex substances are decomposed into others of simpler composition. The principal factor in destructive metabolism is doubtless what Pflüger terms the "self-decomposition" of the living protoplasm. According to this view living protoplasm is constantly undergoing spontaneous decomposition, and one important use of the various complex organic substances present in the organism, such as proteids, fats, and carbohydrates, is that they serve as plastic material for the reconstruction of living protoplasm. The metabolism of the protoplasm thus consists in unceasing construction and decomposition, the constructive and the destructive processes being intimately connected. Of the products of decomposition some can be again used in the constructive processes, whereas others are of no nutritive value.

This view of Pflüger's, though, from the nature of the case somewhat hypothetical, is supported by some direct observations. In treating of the formation of starch-grains (pp. 145, 180) it was pointed out that the starch is a product of the dissociation of molecules of what we must regard as living protoplasm, and the same holds good of the cellulose produced in the formation of cell-walls (p. 15). Again, Sachs has observed that in the autumn the cells of deciduous leaves become entirely emptied of their protoplasmic contents; protoplasm, nucleus, chlorophyll-corpuscles, all disappear: they are decomposed into soluble and diffusible substances which are conveyed away to the persistent parts of the plant.

But the destructive metabolism of an organism is not by any means confined to the decomposition of protoplasm: the various complex organic substances in the cells may undergo chemical change quite independently of their entering into the metabolism of the protoplasm. We have already learned that various substances are decomposed by means of certain bodies which have been termed *unorganised ferments* in order to distinguish them from the so-called *organised ferments* such as Yeast and Bacteria. These unorganised

ferments are formed by the protoplasm and appear to resemble proteids in their ultimate chemical composition, but we do not know what is the nature of the peculiarity of their chemical structure upon which their characteristic properties depend.

The following are the analyses of certain of these ferments :

	Emulsin (Schmidt).	Papaïn (Wurtz and Bouchut).	Diastase (Zulkowsky).
C	48·76	42·20	47·57
H	7·13	6·60	6·49
N	14·16	12·22	5·14
S	1·25		} 37·64
O	28·70	(and S?) 26·08	
Ash		12·90	3·16
	<hr/>	<hr/>	<hr/>
	100·00	100·00	100·00

Loew has come to the conclusion, by the analysis of ferments, that they are proteids allied to the peptones.

The unorganised ferments may be classified, according to our present knowledge in the following four groups, the classification depending upon the nature of their action :

(1) Ferments which convert starch into sugar; the first of these to be discovered was called *diastase* and was found in malt; we may speak of these ferments generally as *diastatic* ferments. They are very widely distributed in plants; they have been found in germinating seeds (Persoz and Payen, von Gorup-Besanez), in leaves, shoots, etc. (Kossmann, Krauch); Wortmann has recently found reason to believe that Bacteria convert starch into sugar by means of a diastatic ferment which they excrete; in fact it seems probable from the researches of Baranetzky that a ferment of this kind is present in all living plant-cells.

(2) Ferments which decompose glucosides with production of sugar: the best-known members of this group are *emulsin* or *synaptase* found in the Bitter Almond; *myrosin* in the seed of the Black Mustard; *erythrozym* in the root of the Madder.

It is doubtful whether or not these ferments are also capable of converting starch into sugar. According to Schmidt, emulsin does not possess this property, its action

being confined to the decomposition of aromatic glucosides; Kossmann indeed states that the diastatic ferments which he obtained acted also on glucosides, but it is probable that his extract contained more than one kind of ferment.

(3) Ferments which convert cane-sugar into glucose: a ferment of this kind, termed *invertin*, has been extracted from Yeast; it is probable that a similar ferment is present in succulent fruits, for they commonly contain a mixture of cane-sugar and glucose.

(4) Ferments which convert proteids into peptones; these, which are only active in the presence of free acid, are termed *peptic* ferments; such a ferment has been found in the latex of *Carica Papaya* and in that of *Ficus Carica* (Wurtz and Bouchut), and in the liquid excretion of carnivorous plants (von Gorup-Besanez and Will).

Von Gorup-Besanez believed that he had succeeded in extracting a peptic ferment from germinating seeds (Vetch, Hemp, Flax, and Barley). Krauch has pointed out that this result is not trustworthy, inasmuch as the glycerin-extract of Vetch-seeds, prepared according to von Gorup-Besanez' method, contains peptone to begin with (see last lecture, p. 173).

These are the only ferments which have been actually extracted, but it is probable that others may also be present in plants. Thus, from the researches of Müntz and of von Rechenberg, it appears that the quantity of free fatty acids in oily seeds increases very much during germination, doubtless in consequence of the decomposition of fats into glycerin and the respective fatty acids. It is well known that in animals this decomposition is effected by a ferment contained in the pancreatic secretion, and it may be fairly inferred that it is effected by this means in plants also. In fact Schützenberger states that when an oily seed is rubbed-up with water, an emulsion is obtained in which glycerin and free fatty acids soon make their appearance. Again, there is, in the pancreatic secretion of animals, a ferment (trypsin) which decomposes proteids with the formation of crystallisable nitrogenous organic substances such as leucin and tyrosin. We have learned that these amides are of common occurrence in plants, and it is possible that they may be

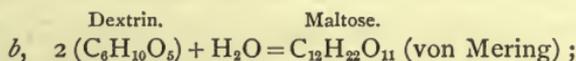
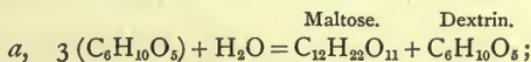
formed by means of a proteolytic ferment. There is, however, no positive evidence forthcoming in support of this view. Finally there is probably, in certain plants at least, a ferment which acts upon cellulose, converting it into sugar. For instance, we have seen that carbohydrate is stored up in the Date-seed in the form of cellulose, and that this cellulose is used up during germination in supplying the embryo with plastic material; it is difficult to imagine that the solution of the cellulose is brought about otherwise than by ferment-action. The penetration of the absorbent organs of parasites into the tissues of their hosts is probably effected by the same means.

We have now to enquire into the nature of the chemical processes of which the decompositions enumerated above are the result. The mode of action of unorganised ferments is that they induce chemical change in the substance upon which they act without themselves entering into or being affected by the process. The change which they effect is probably, in the first instance, one of hydration, that is, the addition of one or more molecules of water to the molecule of the substance acted upon; this appears to diminish the stability of the substance so that its molecules readily dissociate to form two or more other substances.

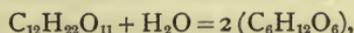
The following examples will serve to illustrate ferment-action :

I, the conversion of starch into sugar by diastase ;

the relation of the quantity of the products to each other and to the starch has been found to vary with the temperature ; the equations here given represent what takes place at ordinary temperatures (below 60°C). The conversion takes place in two stages ;

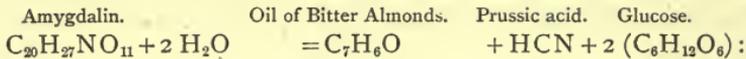


if the action be long continued the maltose is converted into dextrose according to O'Sullivan,

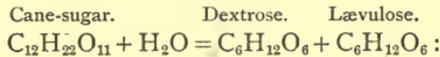


but Brown and Heron have failed to confirm this statement.

2, the decomposition of glucosides ;

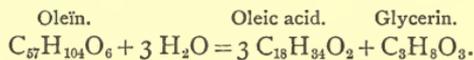


3, the conversion of cane-sugar into glucose ;



it was long thought that the product was a substance termed "inverted cane-sugar"; Dubrunfaut, however, pointed out that it is a mixture of dextrose and lævulose ; it rotates the plane of polarization to the left on account of the more powerful optical properties of the lævulose.

4, the decomposition of fats (glycerides) ;



No equation can be given of the conversion of insoluble proteid into peptone for the formula of proteid is not known.

For the same reason no equation can be given of the production of amides from proteid by ferment-action. It appears that in pancreatic digestion the first step is the formation of peptone, and that the peptone then undergoes decomposition ; leucin and tyrosin are the principal products, and aspartic acid, bodies belonging to the xanthin group an aromatic acid, and certain little-known substances, are also formed.

The action of the ferments of plants is considerably affected by external conditions. For instance, it was pointed out above that the action of a diastatic ferment on starch is not the same at different temperatures, and it has been found that there are limits of temperature above and below which the action does not take place at all. This is doubtless true of the action of all ferments. Again, Baranetzky has observed that the diastatic ferments are only active when the liquid in which they are dissolved has a distinct, but not too strong, acid reaction, a condition which is also essential in the case of the peptic ferments. Further, it appears that the presence of free oxygen is of importance in the case of the diastatic ferments : thus Wortmann observed that Bacteria do not convert starch into sugar in the absence of free oxygen, and Baranetzky found that a solution of freshly prepared extract (of leaves of *Melianthus major*, also of potato-tubers) was inactive, whereas after standing for a few days its action upon starch was rapid. But it is probable that these conditions affect rather the formation

than the action of the ferment. With the foregoing observations those of Brown and Heron and of Atkinson are doubtless to be connected. Brown and Heron' observed that the diastatic action of malt-extract is much increased after the addition of Yeast, and Atkinson has made similar observations on rice when attacked by a certain Mould (apparently a *Eurotium*). It appears from all these facts that the formation of the ferment depends upon the decomposition of some mother-substance, a *zymogen*, probably a proteid. This decomposition is promoted in an organ by the presence of an acid, and by the presence of oxygen; when the *zymogen* has been extracted from the organ (as in the case of malt-extract), or when the organ has been killed (rice), it may be effected by another organism altogether.

The ferments may be obtained by the following methods. Baranetzky extracted the seeds or other parts of plants with water for about half an hour; if much fat or chlorophyll were present the material was first extracted with a mixture of ether and alcohol, then pressed and left to dry; the watery extract was filtered and then precipitated with strong alcohol; when the precipitate had collected the alcohol was decanted, and the precipitate was washed with weaker alcohol (about 85 per cent.) to remove all traces of sugar; the precipitate was collected on a filter and treated with water; the clear filtrate contained the ferment in solution. Another method is to extract the material with glycerin, after having treated it for 48 hours with strong alcohol; the glycerin-extract is then to be strained and allowed to drop into a tall cylinder containing a mixture of 8 parts of alcohol to 1 of ether; a precipitate is formed which is to be kept for some days in alcohol, and then treated with glycerine which dissolves the greater part of it; the glycerin-solution is then precipitated as above by alcohol, the precipitate being the nearly pure ferment which was readily soluble in both glycerin and water. It was by this method that von Gorup-Besanez attempted to extract ferment from seeds (see p. 173), but it is doubtful if he extracted anything but peptone.

But there are certain chemical changes which we are unable to account for in either of the above-mentioned ways: these are the *fermentations*, which we usually associate with the life of lowly Fungi, such as Yeast and Bacteria. It is difficult to believe that the sugar which is decomposed by Yeast into carbon dioxide and alcohol, that the alcohol which is converted into acetic acid by the *Mycoderma Aceti*, that the

proteids which undergo putrefaction in the presence of Bacteria, are assimilated by these organisms, that they are built-up into living protoplasm, and that the characteristic products of the decomposition of these substances are set free in consequence of the self-decomposition of the protoplasm-molecules of the organisms, for the weight of the organisms formed is but a small fraction of the weight of the substances decomposed in these processes. Taking the alcoholic fermentation for example, Pasteur has shewn that for a weight a of Yeast-cells formed, a weight of $100a$ or more of sugar may be decomposed, and, if similar determinations were made with respect to the other fermentations, the result would probably be the same. Nor is it more easy to believe that these organisms contain substances of the nature of unorganised ferments which effect the chemical changes peculiar to them; that Yeast, for instance, contains an unorganised ferment which is capable of decomposing sugar into carbon dioxide and alcohol, or that Bacteria contain some sort of trypsin by means of which they decompose proteids. As a matter of fact all attempts to extract such substances from Yeast and Bacteria have met with no success, and, when we bear in mind that these fermentations only go on in the presence of *living* organisms, the existence of such substances is rendered extremely improbable. It is urged, however, by those who hold that the fermentations are effected by unorganised ferments produced by the organised ferments, that these unorganised ferments may be extremely unstable and that their formation may only go on so long as the organised ferment is living. But this suggestion by no means accords with our present knowledge of unorganised ferments, for they have been found to be remarkably stable; we must therefore regard this interpretation of the phenomena of fermentation as highly hypothetical.

But if we reject these two explanations of the nature of fermentation, what other more satisfactory explanation can be offered? It seems to be a fair and unstrained inference from the facts before us, that living protoplasm, besides undergoing decomposition itself, can induce decomposition

in certain substances which are brought within the sphere of its influence, though we can give no satisfactory account of the mode in which such decomposition is effected, any more than we can of the mode in which unorganised ferments act, or of the mode in which the decomposition of protoplasm itself is brought about. We may, for the sake of precision, term this the *fermentative action* of protoplasm, and though we usually associate fermentative action with the so-called organised ferments, such as Yeast and Bacteria, it is by no means peculiar to them, for, as will be shewn hereafter, it is manifestly exhibited by all living plant-cells when placed under appropriate conditions.

The characteristic accompaniment of the destructive metabolism of plants, as of all living organisms, is, under normal conditions, that interchange of gases between the plant and the surrounding atmosphere which has already been mentioned (Lect. V., p. 81) as *Respiration*, and which consists in the absorption of oxygen and the evolution of carbon dioxide, an interchange which is precisely the converse of that which accompanies the constructive metabolism of green plants. Carbon dioxide is not, however, the only respiratory excrement, for de Saussure, and, more recently, Laskowsky have shewn that watery vapour is also exhaled in the respiration of plants. Respiration involves, therefore, a loss of weight to the plant, inasmuch as the absorbed oxygen is given off in the excreted carbon dioxide and water.

The following illustration of the loss in weight which is involved by respiration is taken from Boussingault.

Forty-six grains of wheat were sown on May 5: the seedlings were reaped on June 25, having been in darkness all the time.

At the commencement of the expt. the grains consisted of . . .	Total Dry Weight.	C.	H.	O.	N.	Ash.
. . .	1'665	0'758	0'095	0'718	0'057	0'038 grms.
At the end of the expt. the seedlings con- sisted of	0'712	0'293	0'043	0'282	0'057	0'038 grms.
Loss during experiment	0'953	0'465	0'052	0'436	0'000	0'000 grms.

It is comparatively easy to detect the evolution of carbon dioxide by plants which are not green, and even of those which are green when they are not exposed to light. When a green plant is exposed to light the gaseous interchange which is the expression of its constructive metabolism is so much more considerable than that which accompanies its destructive metabolism, that (as pointed out in Lecture V., p. 79) the former obscures the latter. Still, as the researches of Garreau shew, the respiration of green plants can be detected even in the presence of light. In order to avoid the disturbing influence of the action of light experiments upon respiration are usually conducted in the dark. It may be assumed that all the experiments which will be cited below as illustrations were performed in the dark, unless the contrary is expressly stated.

The respiration of young organs is, in general, more considerable than that of old ones, for it is in young organs (germinating seeds, leaf-buds, etc.) that the metabolic processes of which respiration is an expression are being most actively carried on. In the case of flowers, in which respiration is especially energetic (as compared with leaves, for example), de Saussure states that they respire more actively when fully expanded than when in the bud; this increased respiratory activity is doubtless connected with the process of fertilisation or with the preparation for it.

We will begin our study of respiration by endeavouring to ascertain in how far the exhalation of carbon dioxide and of watery vapour is related to the absorption of oxygen.

In considering the constructive metabolism of a green plant under the influence of light we found that the volumes of carbon dioxide absorbed and of oxygen exhaled are approximately equal, and we could account for this equality on ascertaining the nature of the chemical processes in operation in the chlorophyll-corpuscles. But there is no such constant relation between the volumes of carbon dioxide exhaled and of oxygen absorbed in respiration, and the processes of destructive metabolism are so complex that we cannot account for the relation, whatever it may be, between the volumes of

these gases in any particular case. We may, in fact, say that the evolution of carbon dioxide is not directly connected with the absorption of oxygen, for it has been found that, in the absence of free oxygen, Yeast can decompose sugar with evolution of carbon dioxide, that Bacteria can do the same with proteids, and that fruits, and seeds, and opening flowers continue to exhale carbon dioxide for a time: and again, it has been found by de Saussure, by Mayer, and by Dehérain, that plants may absorb oxygen without exhaling any perceptible quantity of carbon dioxide.

The organs which have been found to be capable of absorbing oxygen without an accompanying evolution of carbon dioxide are succulent leaves, such as those of Agave (Dehérain), of Saxifragaceæ and Crassulaceæ (Mayer), and stems, such as those of Cacti, and fruits (de Saussure). The following table refers to an experiment of de Saussure's with Opuntia. A segment of the stem was placed in a closed receiver containing air, and was left all night; on the following morning the volume of the air was found to be diminished by 79 c.c.

The air contained at the commencement of the experiment	198 c.c.	O			
" "	conclusion	" "	" "	" "	" "
				119	" O
				Amount of O absorbed	79 "

Hence the amount of O absorbed exactly corresponded to the diminution in volume which the air in the receiver had undergone. No CO₂ could be detected in the receiver. These results will be considered subsequently.

It has been found, however, in most instances that, at ordinary temperatures, the volume of carbon dioxide exhaled is approximately equal to the volume of oxygen absorbed.

In illustration we may cite the following experiments:

1. With Fungi (Marcet).

Three Lycoperdons, weighing 72 grains, were left in a closed receiver containing 100 c.c. of air for six days.

Composition of the air.	At the commencement.	At the end of the experiment.
N	79'0 c.c.	79'0 c.c.
O	21'0 "	18'0 "
CO ₂	00'0 "	3'0 "
	100 0 "	100'0 "

2. With germinating seeds (de Saussure).

24 grains of Wheat were left for 21 hours in a closed receiver containing air.

Composition of the air.	At the commencement.	At the end of the experiment.
N	148·84 c.c.	148·32 c.c.
O	39·86 "	37·44 "
CO ₂	0·00 "	2·47 "
	<hr/> 188·70 "	<hr/> 188·23 "

3. With leaves in air (Boussingault).

Duration of expt.	Plant.	O absorbed.	CO ₂ evolved.
31 hours	Oleander	18·3	19·60 c.c. (several leaves)
24 "	do.	8·40	8·10 " (one leaf)
" "	do.	2·80	2·60 " "
11 "	do.	2·00	1·80 " "
4 "	do. ^a	1·31	1·57 " "

It would be easy to add to this list out of the very large number of experiments of this kind which have been made, but further illustration is unnecessary.

There is evidence to shew that variations of temperature affect the relation between the volumes of the gases absorbed and exhaled. As regards the absorption of oxygen, it has been observed by von Wolkoff and Mayer, that this takes place to a slight extent at a very low temperature, and that it increases as the temperature is raised up to a certain degree; any further rise of temperature is accompanied by a diminished absorption of oxygen.

Tropæolum majus.

5 seedlings absorbed	0·60 c.c. O per hour at a temp. of 22·4° C.
" "	0·77 " " " 27·0° "
" "	0·76 " " " 30·5° "
" "	0·77 " " " 30·0° "
" "	1·04 " " " 35·0° "
" "	0·91 " " " 38·2° "

Wheat.

4 seedlings absorbed	0·10 c.c. O per hour at a temp. of 15·6° C.
" "	0·038 " " " 4·4° "
" "	0·067 " " " 9·8° "
" "	0·088 " " " 15·4° "
" "	0·022 " " " 0·3° "
" "	0·016 " " " 0·1° "

With regard to the evolution of carbon dioxide, it has been found that it is smaller at low temperatures than the absorption of oxygen, and more considerable at higher temperatures.

Pedersen determined the amount of CO₂ evolved by Barley-seedlings :

at 4.5° C.	they evolved per hour	9.5 mgr. CO ₂ .
„ 8.1°	„ „	10.8 „
„ 15.3°	„ „	16.5 „
„ 18.0°	„ „	24.3 „

Similar determinations were made by Rischawi with Wheat-seedlings :

at 5° C.	they evolved per hour	3.30 mgr. CO ₂ .
„ 10°	„ „	5.28 „
„ 15°	„ „	9.90 „
„ 20°	„ „	12.54 „
„ 25°	„ „	17.82 „
„ 30°	„ „	22.04 „
„ 35°	„ „	28.38 „
„ 40°	„ „	37.60 „

Dehérain and Moissan experimented with leaves :

100 grmes. of leaves of *Sinapis alba*

	evolved in 10 hours	0.240 grme CO ₂ at a temp. 14° C.
„ „ „ „	0.720	„ „ 31° „
„ „ „ „	0.636	„ „ 40° „
„ „ <i>Pinus Pinaster</i> „	0.031	„ „ 0° „
„ „ „ „	0.058	„ „ 8° „
„ „ „ „	0.095	„ „ 15° „
„ „ „ „	0.703	„ „ 30° „
„ „ „ „	1.333	„ „ 40° „

It appears that in the experiment with leaves of *Sinapis alba* at 40° C., the optimum temperature had been surpassed.

We may further illustrate this point by some of Moissan's results.

Weight and nature of organ.	Vol. of O absorbed in 10 hrs.	Vol. of CO ₂ evolved in 10 hrs.	Temperature.
10 grmes petals of Yellow Tulip	11.72 c.c.	7.41 c.c.	13° C.
„ „ „	11.56 „	9.95 „	22° „
„ „ <i>Iris germanica</i> „	9.92 „	7.24 „	14° „
„ „ „	13.48 „	10.34 „	19° „
„ „ „	6.53 „	5.44 „	13° „
100 „ buds of Horse-Chestnut	121.90 „	99.62 „	15° „
„ „ „	59.66 „	154.00 „	30° „
„ branches „	37.33 „	18.57 „	15° „
„ „ „	35.14 „	87.52 „	30° „

A consideration of the foregoing figures shews that the absorption of oxygen and the evolution of carbon dioxide are differently affected by variations of the temperature. This may be stated in a general manner thus: that at a low temperature the absorption of oxygen is more active than the evolution of carbon dioxide, whereas at a high temperature the absorption of oxygen is less active than the evolution of carbon dioxide. This suggests, and Moissan has actually stated, that for every organ there is, generally speaking, a degree of temperature at which the volumes of the oxygen absorbed and of the carbon dioxide exhaled are equal.

Although, as we see, the relation between the absorption of oxygen and the exhalation of carbon dioxide is so variable that we may conclude that the one is independent of the other, yet, under normal conditions, the presence of free oxygen promotes certain processes of destructive metabolism of which the exhalation of carbon dioxide is an expression. For example, Wilson has observed that when seedlings are deprived of oxygen, the amount of carbon dioxide which they exhale is diminished, and similar observations have been made by Broughton and by Wortmann.

We may cite some of the results of these observers in illustration.

Wilson experimented with germinating seeds of *Lupinus luteus*, measuring the CO₂ evolved when the seeds were in air and in hydrogen.

I. Period—Air	{1st half-hour	5·7	mgms of CO ₂ evolved.
	{2nd	6·6	” ”
II. Period—Hydrogen	{3rd	1·5	” ”
	{4th	1·5	” ”
III. Period—Air	{5th	3·9	” ”
	{6th	5·7	” ”

The following are some of Wortmann's results which tend to prove the point in question, but which he has interpreted differently.

1. The mean of a number of experiments made with germinating seeds in the presence or absence of free O, shews that the presence of O promotes the exhalation of CO₂.

Average amount of CO₂ evolved by 1 gramme of seed in 1 hour in presence of free O, '0995 c.cm.

Average amount of CO₂ evolved by 1 gramme of seed in 1 hour in absence of free O, '0855 c.cm.

2. When seeds are deprived of free oxygen the amount of CO_2 which they exhale gradually diminishes.

Seeds of *Vicia Faba* exhaled, in a Torricellian vacuum, for each gramme weight,

During the 1st hour, 0'124 c.cm. CO_2

"	2nd	"	0'117	"
"	3rd	"	0'105	"
"	4th	"	0'098	"
"	5th	"	0'071	"
"	6th	"	0'071	"
"	7th	"	0'066	"

Broughton obtained the following results with leaves of the Box : 5 grammes of leaves were placed under two bell-jars over water, the one containing air, the other nitrogen; the amounts of CO_2 in cubic centimetres evolved in 24 hours are given in the columns headed "Air" and "Nitrogen."

Time.	Air.	Nitrogen.	Difference.
1st 24 hours	7'11	5'97	1'14
2nd "	4'74	3'98	0'76
3rd "	4'38	2'74	1'64
4th "	2'79	2'40	0'39
5th "	1'86	1'61	0'25
6th "	2'32	2'07	0'25
7th "	1'53	1'29	0'24
8th "	1'22	1'13	0'09
9th "	1'09	1'09	0'00

The gradual decrease, in both cases, in the volume of CO_2 exhaled is due to the diminished vitality of the leaves in consequence of their separation from the plant.

In concluding our consideration of respiration, we may enquire whether or not the gaseous interchange of the plant is affected by variations of the proportion of oxygen in the surrounding atmosphere. It appears from the researches of Rischawi and of Godlewski that the relation, whatever it may be, between the amount of oxygen actually absorbed and that of the carbon dioxide evolved, is unaffected by variations in the composition of the atmosphere, except when those variations are so great as materially to affect the absorption of oxygen (see p. 74).

We may briefly mention here that the inorganic substances which are absorbed by a plant may materially affect its respiration. Kellner has observed, for instance, that when germinating seeds were supplied with potassium nitrate, they absorbed it, and they exhaled considerably more carbon dioxide than others which were not supplied with the salt. He concludes that the oxygen which would be set free in the plant in consequence of the reduction of the absorbed nitric acid serves to promote oxidation and thereby the exhalation of carbon dioxide as well.

He determined the relative amounts of carbon dioxide exhaled to be as follows :

10 grammes of peas	in distilled water	in solution of KNO_3 .
Exhaled in 5 days	0.3869	0.4296 grm. CO_2 .

The peas in the solution of KNO_3 absorbed 0.1068 gramme N_2O_5 .

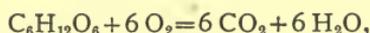
It must be remarked, however, that Kellner's results are not conclusive as regards the effect of the oxygen contained in the nitric acid. It is quite possible that the effect of the salt may have been to promote the metabolic activity of the seeds including the absorption of oxygen from the air.

We have now to endeavour to ascertain what is the relation of the absorbed oxygen and of the evolved carbon dioxide to the metabolic processes, and we will begin with the self-decomposition of the protoplasm. We may, at the outset, make the general statement that the continual absorption of oxygen is essential to the existence of living organisms (with certain exceptions which we shall notice hereafter), and that in the absence of such a supply of oxygen they cease, within a longer or a shorter time, to exhibit those phenomena in virtue of which we call them living, in a word, they die. Death under these circumstances is to be attributed to the arrest of the metabolic processes which are accompanied by the evolution of energy in the organism, and of these by far the most important is the self-decomposition of the protoplasm. It appears, then, that the absorption of oxygen is essential to the self-decomposition of the protoplasm-molecule. It is of course impossible to make any final state-

ment as to the mode in which the oxygen affects this process, but we may provisionally accept Pflüger's view that the absorbed oxygen enters into the protoplasm-molecule as "intramolecular" oxygen, that the molecule is thereby rendered unstable, and that it readily undergoes decomposition, carbon dioxide and water being amongst the products formed. It must not, however, be assumed that the protoplasm-molecule which has taken up oxygen at once undergoes decomposition, and that the carbon dioxide evolved in any given short period of time actually contains oxygen absorbed during that period. It has been shewn above that there is not necessarily any definite relation between the volumes of oxygen absorbed and of carbon dioxide exhaled in a given time, and from this we may infer that there is no definite relation between the taking up of oxygen by the protoplasm-molecule and its decomposition. This independence is well illustrated by the statement made above concerning the nature of the respiratory interchange of gases at different temperatures, to the effect that the absorption of oxygen is relatively greater at low temperatures, and that the evolution of carbon dioxide is relatively greater at high temperatures. Since it is known that a high temperature promotes the processes of destructive metabolism, we find the significance of this statement to be that at a low temperature the storing-up of intramolecular oxygen is relatively more active than the decomposition of the protoplasm-molecules, whereas at a high temperature the converse is the case. We can readily imagine that for each organ there is a temperature at which these processes are equally active, and at which, therefore, the volumes of oxygen absorbed and of carbon dioxide evolved are approximately equal; this equality in the volumes of the gases has been frequently determined as pointed out above (p. 197).

It has been found, however, that the relation between the volumes of the gases depends very much upon the nature of the non-nitrogenous organic substances present in the organ which serve as plastic material for the reconstruction of protoplasm. It is only when the organ contains carbo-

hydrate that the volumes of oxygen absorbed and of carbon dioxide exhaled by it are found to be equal. It has been suggested that this equivalence of volume is due to the oxidation of carbohydrate to carbon dioxide and water, according to the equation,



for it has been found that the loss of weight which a starchy seed, for example, undergoes during germination can be accounted for by the disappearance of starch.

Thus Sachsse made the following determinations with peas :

Dry weight of peas at commencement	100	grammes.
" " after 184 hours' germination	92'54	"
	Loss	7'46
The peas contained	Before germination.	After germination.
Fat	2'27	2'03
Dextrin	6'50	5'41
Cellulose	7'13	8'10
Starch	42'44	33'43
Undetermined substances	13'76	15'74
Proteids	23'82	23'71
Ash	4'08	4'08
	100'00	92'50

If, in the case before us, we deduct from the amount of starch lost (9 grammes) by the germinating seeds the amount of starch which is represented by the gain in cellulose and in the undetermined substances (say 2 grammes), we arrive approximately at the total loss of weight (7'46 grammes).

Though this appears to be a plausible explanation of the loss of weight in these cases, yet it is extremely doubtful if such complete oxidation as that assumed by this mode of reasoning ever occurs in a plant. We should expect to find that respiration would be most active in organs rich in non-nitrogenous organic substances; but this is not the case. Garreau has found, on the contrary, that respiration is most active in organs which are rich in proteids. The following is a view which is more in accordance with our general knowledge of the nature of the metabolic processes. We have

just learned that the evolution of carbon dioxide in normal metabolism is to be attributed to the oxidation and decomposition of protoplasm, the decomposed protoplasm breaking up into nitrogenous and non-nitrogenous (especially carbon dioxide and water) substances of simpler composition, and that, under ordinary conditions, the volume of carbon dioxide evolved in a given time is approximately equal to, or rather smaller than, the volume of oxygen absorbed. But if this process were to go on without any corresponding constructive process, the whole of the protoplasm would in a short time be decomposed. We already know, however, that the plant can construct protoplasm from the nitrogenous residues of previous decomposition together with carbohydrates, and it is shewn by Sachsse's analysis that the amount of proteid matter in the peas was approximately the same after as before germination. It is evident, therefore, that a construction of protoplasm must have accompanied the germination, and it is an obvious inference that this construction of protoplasm was effected at the expense of the starchy reserve-materials. The absorption of oxygen and the evolution of carbon dioxide by the seed is, then, to be attributed to the oxidation and decomposition of protoplasm, and the disappearance of starch is due to its having been used in the reconstruction of protoplasm.

This explanation is not only satisfactory as regards this special case, but it enables us to account also for certain facts which we shall now consider. It has been already mentioned (p. 173) that the germination of an oily seed is accompanied by a disappearance of fat and a formation of starch, and it has been observed, first by de Saussure and subsequently by many others, that, in the course of germination, the absorption of oxygen by these seeds is very much greater than the exhalation of carbon dioxide. In the early stages of germination, according to Godlewski, this is not the case; it is only when fat is being replaced by starch at the time when the radicle is beginning to protrude that the inequality of volume first manifests itself, and it gradually diminishes as the fat disappears from the seed.

Some examples of the gaseous interchange accompanying the germination of oily seeds are given on page 76: we may add some of Dehérain's and Moissan's determinations.

	Time.	O absorbed.	CO ₂ evolved.
Colza	9 days	20 c.c.	11'3 c.c.
Linseed	3 "	29'74 "	14'42 "
"	" "	20'28 "	14'41 "
"	" "	9'79 "	4'91 "

With regard to the replacement of oil by starch we may cite Detmer's analysis of Hemp-seed (see also p. 175)

	Seeds before.	After germination.
Fat	32'65	17'09
Starch	0'00	8'64
Proteids	25'06	23'99
Undetermined substances	21'28	26'13
Cellulose	16'51	16'54
Ash	4'50	4'50
	<hr/>	<hr/>
	100'00	96'89
Loss of weight during germination (CO ₂ and H ₂ O)		3'11
		<hr/>
		100'00

We see, then, that fat which is relatively poor in oxygen (olein contains 10'86 per cent.) is replaced by starch which is relatively rich in oxygen (49'38 per cent.), a process which necessarily involves the fixation of oxygen. Now we already know, and we shall shortly reconsider the point, that starch is formed from protoplasm. The processes which attend the early stages of the germination of an oily seed may be briefly stated thus; protoplasm undergoes decomposition to form starch, and the continued formation of starch depends upon the reconstruction of protoplasm from the nitrogenous residues of previous decomposition together with some form of non-nitrogenous organic substance; the non-nitrogenous substance in question is fat, and, inasmuch as fat contains less oxygen than starch, oxygen is absorbed from without and fixed: at the same time the decomposition of the protoplasm involves an evolution of carbon dioxide. When the fat has been replaced by starch, the volumes of oxygen absorbed and of carbon dioxide exhaled become approximately equal.

We are now in a position to consider the curious abnormal case afforded by de Saussure's *Opuntia*. He found that he could not extract, by means of the air-pump, any appreciable quantity of either oxygen or carbon dioxide from a piece of stem which had absorbed about 80 c.c. of oxygen from the air contained in a receiver. From this it appears that the absorbed oxygen was chemically fixed in the plant, and that the oxidised substance had not undergone any decomposition attended by evolution of carbon dioxide. It is possible to conceive, however, that carbon dioxide may have been formed and retained in the plant in some sort of loose chemical combination, but it is probable, had this been the case, that some considerable amount of this gas would have been given off to the air-pump. We are apparently bound to admit that no carbon dioxide was formed.

In endeavouring to account for this remarkable fact, the explanation which naturally suggests itself is that the absorbed oxygen is retained by the protoplasm as what we have termed intramolecular oxygen. This explanation would, however, involve the assumption that the decomposition of the protoplasm is arrested, inasmuch as no carbon dioxide is evolved. But there are no grounds for such an assumption. The only alternative is to assume that in this instance destructive metabolism is unaccompanied by an evolution of carbon dioxide. It has been ascertained by Mayer, who has carefully investigated this matter, that there is a considerable increase in the amount of organic acid in the organ during the experiment, and this is confirmed by an observation of Dehérain's. It seems, then, that we have before us a case in which the decomposition of protoplasm is accompanied by the formation not of carbon dioxide, but of a more complex acid instead.

The acid which Mayer found in the succulent leaves of the Crassulaceous plants with which he experimented appears to be an isomer of malic acid, whereas in the *Opuntia* it is oxalic acid, according to Dehérain.

We will now pass on to consider those metabolic processes which we have termed fermentative. Of these, some are essentially dependent upon the presence of oxygen, whereas

others take place independently of it. A familiar example of the former kind—of the *oxidative decompositions*, as we may term them—is afforded by the formation of acetic acid from ethyl-alcohol under the influence of the Fungus known as *Mycoderma Aceti*, a plant which is allied to Yeast. The process may be roughly represented by the equation



Another similar Fungus, the *Mycoderma Vini*, induces more complete oxidation and decomposition of alcohol, carbon dioxide and water being the products of its action. It is probable that processes of this kind go on to a greater or less extent in all living cells.

Of the fermentative processes which can go on in the absence of oxygen the most familiar is the decomposition of sugar into alcohol and carbon dioxide which is effected by the Yeast, and which is known as the alcoholic fermentation. It may be roughly represented by the equation



It is seen from the equation that the process does not involve the presence of oxygen, and, as a matter of fact, Pasteur, Hoppe-Seyler, and Brefeld have shewn that when the supply of oxygen is abundant the alcoholic fermentation is reduced to a minimum.

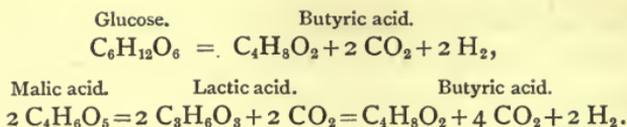
In a series of experiments instituted with the view of determining this point Pasteur found that whereas, in the absence of oxygen, the proportion between the weight of Yeast formed in the fermenting liquid to the weight of sugar decomposed was as 1 : 176, in the presence of oxygen the proportion in an especially successful experiment was as 1 : 4. From this he concludes that in the presence of oxygen the fermentative action of Yeast is diminished.

Although we usually associate the alcoholic fermentation with the Yeast-plant, yet we must not conclude that it is peculiar to it. Pasteur and Brefeld have observed that it is excited, in the absence of oxygen, by various other Fungi (species of *Mucor*, *Penicillium*, *Mycoderma*) growing in saccharine solutions; whereas, when free oxygen is present, no alcoholic fermentation occurs.

Nor is alcoholic fermentation confined to Fungi. Bérard pointed out as long ago as 1821 that ripe fruits continue to exhale carbon dioxide in an atmosphere destitute of oxygen, and that this is accompanied by a diminution of the sugar contained in them. Lechartier and Bellamy, as well as Pasteur, have since shewn that the exhalation of carbon dioxide and the disappearance of sugar is accompanied by a formation of alcohol, that the phenomenon is in fact one of alcoholic fermentation. More recently Brefeld and de Luca have obtained the same results in experiments with fruits, seeds, leaves and branches.

Nor is the alcoholic fermentation the only fermentative process which is induced by the absence of oxygen. So far as we know the conditions of the butyric fermentation, the lactic fermentation, and of the putrid fermentation, fermentations which are effected by certain Schizomycetes, they only take place in the absence of oxygen. It would appear that similar processes may be induced in the cells of any organ. Thus Boehm and de Luca have shewn that if any part of a living plant be insufficiently supplied with oxygen (in these experiments, by keeping it immersed in a limited quantity of water), hydrogen is sooner or later evolved, and, in the case of aquatic plants, marsh gas (CH_4), at a later period. Boussingault observed that leaves and branches evolve combustible gas under these conditions, and Schulz found that when seeds germinated in sealed glass tubes, considerable quantities of hydrogen were given off. Further, an evolution of hydrogen has been observed when parts of plants which contain mannite ($\text{C}_6\text{H}_{14}\text{O}_6$), *e.g.* various Agarics (Müntz), leaves, flowers, and unripe fruits of the Olive, leaves of the Privet (de Luca), are deprived of free oxygen. There can be little doubt that this evolution of hydrogen is accompanied by a diminished formation of watery vapour.

Lactic acid and all substances capable of undergoing lactic fermentation (sugars, starch, many of the more complex organic acids, proteids) are decomposed in such a way as to give rise to butyric acid, carbon dioxide and hydrogen being given off, thus :



De Luca observed, in his experiments, that some acetic acid, which is homologous with butyric acid, was formed in the fruits, flowers and leaves.

The decomposition of mannite mentioned above may be represented by the following equations; it may undergo either

1, alcoholic fermentation, according to the equation,



or 2, lactic fermentation, according to the equation,



butyric and acetic acid are the products of the decomposition of the lactic acid or of the oxidation of the alcohol.

Further, the absence of free oxygen not only modifies the destructive metabolism of the plant as regards the exhalation of carbon dioxide and of watery vapour, but it apparently modifies it also as regards the nitrogenous products of the decomposition of proteid. Boehm found, in the experiments mentioned above, that the water in which the plants were kept gradually acquired an alkaline reaction, and that this was due to the presence of ammonia. The conflicting statements as to the evolution of ammonia by germinating seeds, some observers (Hosæus, Oudemans and Rauwenhoff, Schulz) asserting it, others (especially Detmer) denying it, are probably to be harmonised by the consideration that although it does not take place when free oxygen is present, yet it may do so when the supply of free oxygen is insufficient. Under normal conditions the products of nitrogenous metabolism are principally oxidised substances which are retained by the plant, and if any ammonia is formed it is chemically altered on its formation so that it is not exhaled by the plant: under the abnormal conditions which we are now considering it is apparently formed in such quantity that some of it is exhaled.

From the facts before us we gather that the absence of oxygen profoundly modifies the metabolism of plants. The vast majority of plants are so constituted that they can only thrive

when free oxygen is supplied to them, when their metabolism is what we may term *normal*; but Pasteur has shewn that certain forms of Saccharomycetes and of Schizomycetes thrive best in the absence of oxygen, and that, in certain cases, the access of oxygen proves fatal to the organisms. Pasteur terms plants of the former kind *aërobia*, of the latter *anaërobia*. It is difficult to say whether these anaërobiotic Saccharomycetes and Schizomycetes are distinct species, or whether they are physiological varieties, that is, individuals which have become adapted to a life in the absence of free oxygen: Pasteur inclines to the former of these alternatives. The absence of oxygen does not, however, prove immediately fatal to an aërobiotic plant; it can live for a time without being supplied with free oxygen, and it appears that the more lowly the organism the greater its independence in this respect. Thus, de Saussure observed that seeds do not germinate in an atmosphere destitute of free oxygen, and that, like all other parts of highly organised plants, they die within a comparatively short time. Pasteur, on the other hand, found that a Mould (*Mucor racemosus*) was still alive after having been kept for six months in a vessel containing no free oxygen; but that after being for nearly three years in the vessel it was dead.

We have now to endeavour to account for the modification of the metabolism which is induced by the absence of free oxygen. One conclusion from the facts before us is sufficiently obvious, namely this, that, in the absence of oxygen, the activity of those metabolic processes which we have termed fermentative is largely increased. We may say, indeed, of every living cell what Pasteur has said of Yeast—that in the presence of abundance of free oxygen it is not a ferment, and that it is only in the absence of free oxygen that it exhibits those properties which have earned for it this name. It is evident, too, that fermentative decomposition serves to maintain the life of the plant: this is a simple inference from the fact that anaërobiotic plants exist. The real difficulty is to explain the significance of fermentative decomposition, to determine the mode in which it contributes to the main-

tenance of life. Let us briefly consider the case of an aëro-biotic plant. We have seen that, under normal conditions, the principal features of its metabolism are probably these : it absorbs oxygen ; this oxygen is fixed by the protoplasm as intramolecular oxygen, and the protoplasm undergoes decomposition with evolution of carbon dioxide. It is not too much to assume that, when the supply of oxygen is cut off there is a reserve of intramolecular oxygen, and that the life of the plant is maintained for a time by the decomposition of protoplasm-molecules in which intramolecular oxygen is still present. But now fermentative decomposition becomes energetic. It might be suggested that it is excited and maintained by the decomposition of the protoplasm which is still going on in virtue of the presence of the reserve of intramolecular oxygen, and, as a matter of fact, Pasteur has observed that alcoholic fermentation is most active when the Yeast which excites it has been previously in contact with free oxygen. But this suggestion is untenable for various reasons. In the first place fermentation continues so long that it is impossible to imagine that intramolecular oxygen is present during the whole period. Secondly, if this suggestion be valid, then fermentation ought to go on most actively in the presence of free oxygen, and it has been shewn that this is not the case. Finally, it fails to account for the existence of anaërobiotic plants. Pasteur's view of the significance of fermentative decomposition is this, that it is the expression of the effort of the organism to obtain oxygen from substances which contain it in combination. Another possible view is this, that the organism obtains by the fermentative decomposition of other substances that necessary supply of energy which, in the presence of free oxygen, it obtains by the decomposition of its own protoplasm-molecules. In the case of most aërobiotic plants the end, whatever it is, is only imperfectly attained, for the vitality of the organism becomes gradually diminished, fermentation becomes less and less active, and the organism either dies at once, or passes for a longer or a shorter period into a state of suspended animation from which it can only

be aroused by a timely supply of free oxygen. In the case of anaërobiotic plants, it appears that they can maintain their life so long as there is any substance left for them to decompose.

Finally, the accumulation of the products of metabolism exercises an important influence on the activity of the metabolic processes. In the case of carbon dioxide the accumulation has to be very great before any evident effect is produced. De Luca observed that when, in the course of his experiments, the pressure of the carbon dioxide in the closed receiver became very considerable, the evolution of this gas ceased, and Melsens found that alcoholic fermentation was only arrested when the pressure of the carbon dioxide amounted to twenty-five atmospheres. In the case of other products the effect becomes more quickly apparent. Thus alcoholic fermentation by Yeast is arrested when the fermenting liquid comes to contain about 14 per cent. of alcohol; by *Mucor racemosus*, when the alcohol amounts to 2—5 per cent.; by *Mucor stolonifer*, when the alcohol amounts to 1·3 per cent. (Brefeld). Similarly the lactic and butyric fermentations, which are effected by certain Bacteria, are gradually arrested as the proportion of acid increases, and they are resumed when the acid is neutralised.

With this we complete our consideration of the metabolic processes. In the next lecture we will especially study the physiological significance and the chemical nature of the products which are formed in connexion with these processes.

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LECTURE XII.

METABOLISM (*continued*).

WE have now to enquire more closely into the mode of origin and the chemical nature of the products which, as we have seen, are formed in connexion with the metabolism of the plant.

8. *The Products of Metabolism.*

We gather from what has been said in previous lectures that the products of metabolism may be classified into two groups; those, namely, which can be used in the constructive processes, and those which can not: the former we term *plastic products*, the latter *waste-products*. We find, also, that these may be further subdivided into non-nitrogenous and nitrogenous.

The *plastic products* may be formed in either of two ways: either constructively, when they are built up from simpler substances (as when carbohydrate is formed from carbon dioxide and water, see p. 145), or destructively, when they are formed as the result of the dissociation of the molecules of a more complex substance (as when starch is formed from protoplasm).

Beginning now with the non-nitrogenous plastic substances, we find them to be principally carbohydrates and fats. To these we may perhaps add the more complex

organic acids, but as our knowledge of their significance is at present so incomplete, it will be better to classify them for the present with the non-nitrogenous waste-products.

With regard to the formation of the carbohydrates in the plant we have but little definite information. Of glucose we may say that it is derived by the action of an unorganised ferment from one or other of the carbohydrates, which, as we have seen (p. 170), are stored up as reserve-materials, except in certain plants, the Onion for example (Sachs), in which it appears to be formed in the chlorophyll-corpuscles in the first instance. Of the reserve-carbohydrates, all that we can say is that they are derived, in the case of green plants, from the non-nitrogenous organic substance, whatever it may be, which is formed in the chlorophyll-corpuscles under the influence of light, and, in the case of plants destitute of chlorophyll, from the organic substances supplied to them as food: but the only definite information which we possess as to the mode of this derivation is confined to starch and cellulose.

It has been already stated (p. 180), upon the authority of the observations of Schimper and of Strasburger, that the starch which makes its appearance in chlorophyll-corpuscles or in amyloplasts is formed from protoplasm; that molecules of protoplasm undergo dissociation, and that starch is a conspicuous product of the process. In support of this statement we may now adduce some additional evidence. The cells of the embryo of the Wheat contain, when the seed is quiescent, no trace of starch, but Just has observed that if a seed be kept moist for twenty-four hours, the embryo then contains starch abundantly, although the endosperm has apparently undergone no change, and no trace of sugar can be detected in it. It is difficult to account for this fact in any other way than that suggested by Just, namely, that the starch is formed by dissociation from the protoplasm in the cells of the embryo.

It has also been stated, upon the authority of Schmitz and of Strasburger, that cellulose is likewise formed by dissociation from protoplasm. In support of this statement it may now be pointed out that Schmitz has observed that

when a cell-wall becomes much thickened, that is, when many layers of cellulose are found, the whole of the protoplasmic contents of the cell are gradually used up in the process: and further, that, as has already been stated (pp. 151, 177) no non-nitrogenous plastic substances can be detected in growing-points.

It appears, then, that in these cases the non-nitrogenous organic substance, either formed from carbon dioxide and water or absorbed as food, is not directly converted into starch or cellulose, but goes in the first instance to build up protoplasm, and that it is in consequence of the decomposition of protoplasm that these carbohydrates make their appearance: and we may, perhaps, go so far as to infer that all the reserve-carbohydrates are produced in this way.

With regard to the fats, it is generally assumed that they are formed directly from carbohydrates, because as the fats increase in quantity the carbohydrates diminish. For example, oily seeds contain starch whilst they are unripe, but as they ripen the starch disappears and is replaced by fat.

The first objection to this view is the obvious one that the observed fact does not prove the direct conversion of carbohydrate into fat. And further, we know of no means by which such a conversion could be effected. Hoppe-Seyler, in his investigations on this subject, has found that when carbohydrates are heated with caustic potash, or when they are caused to undergo putrefaction, they yield a series of fatty acids, and he infers that the fats found in animals and plants are derived directly from carbohydrate. But the acids formed in his experiments are only the lower members of the series, and not those which enter into the composition of the more common fats: moreover, he does not suggest how the necessary glycerin is formed from carbohydrate.

The evidence in favour of the view that fats are derived from the protoplasmic cell-contents is of a more satisfactory character. In studying the effects of starvation upon the cells of plants, Cunningham found, in the case of certain Fungi, that if the spores be cultivated in distilled water, the

resulting mycelium, instead of containing an abundance of protoplasm, contains but little, and in this a number of oil-drops are distributed (Fig. 30). It is obvious that, under

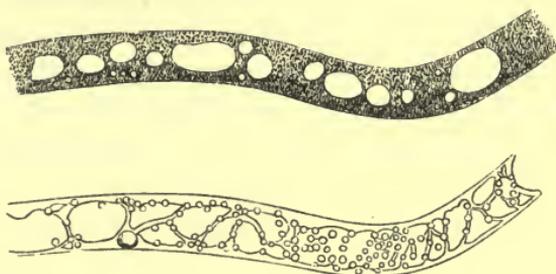


Fig. 30 (after Cunningham). Hyphæ of *Choanephora*, the upper one well-nourished, the lower one starved.

the conditions of the experiment, this oil could not have been formed from any food materials absorbed from without, and, when we note the diminished protoplasmic contents, we cannot but correlate the diminution with the abundance of oil, and conclude that the oil must have been formed at their expense. Similar observations on Fungi have been made by Naegeli. He finds that the nature of the food supplied has but little influence upon the amount of fat formed, and he inclines to the view that fat is formed from the protoplasmic cell-contents.

The experiments of Loew given in Naegeli's paper tend to prove the formation of fat from the protoplasmic cell-contents. Some *Penicillium*-mycelium was left for four weeks in a dilute (1 per cent.) solution of phosphoric acid : analyses before and after gave the following results :

the mycelium contained	before	after the experiment
Proteid	42·7	16·5 per cent.
Fat	18·5	50·5 „
Cellulose	38·8	33·0
Extractives		
Ash		

Admitting that the fats are formed from the protoplasmic cell-contents, we have yet to ascertain whether they are derived from the living protoplasm or organised proteid, or from the dead unorganised proteid. If, as suggested in pre-

vious lectures (pp. 160, 187) we regard the molecule of living protoplasm as a very complex one, it is not improbable that it contains fatty radicles, and that it may undergo decomposition in such a way as to give rise to fats. On the other hand, it has been found that fatty acids are among the products of the artificial decomposition of proteid, and it is therefore possible that fats may be formed in the living cell by the decomposition of the dead proteid which it may contain. In his researches upon the formation of fat in Fungi, Naegeli made the important observation that this process is dependent upon a supply of free oxygen. This fact is, however, susceptible of various interpretations. It may mean that, in the absence of free oxygen, the self-decomposition of the living protoplasm does not take place, and that therefore no fat is formed: or it may mean that, under these conditions, the living protoplasm is incapable of effecting the oxidative decomposition of the unorganised proteid in such a way as to give rise to fat. We must be content to leave this point undecided for the present.

In any case the formation of fat is apparently not direct: fatty acids first make their appearance, and these subsequently combine with glycerin to form fats. Von Rechenberg has found that unripe oily seeds contain a considerable quantity of these acids, and that it gradually diminishes as the seeds become mature. As to the glycerin of the fats, we are unable at present to make any definite statement concerning its mode of origin.

Besides the fats (glycerides) already mentioned, other fatty bodies have been found in plants. These are, cholesterin ($C_{26}H_{44}O$), an alcohol which has been found by Hoppe-Seyler and others in seeds, in buds, and in yeast; lecithin ($C_{44}H_{90}NPO_9$), a complex nitrogenous and phosphorised fat, which has been found by Hoppe-Seyler to be widely distributed in plants. Further, various fatty substances which are generally spoken of as wax, are formed by plants: as these are to be rather regarded as waste-products we shall treat of them subsequently.

The nitrogenous plastic products are unorganised proteid and amides. We have already discussed (p. 150) the possible mode in which these bodies are formed synthetically in

plants. With regard to the possible destructive formation of the proteid, there can be little doubt that it may be derived from living protoplasm. If we regard the molecule of living protoplasm as more complex than that of unorganised proteid, we may infer that proteid may be one of the products of the decomposition of the protoplasm-molecule. The amides, as we have seen (p. 191), are produced from proteid either by the action of an unorganised ferment, or by the fermentative action of the living protoplasm; in the latter case the process would be probably one of oxidative decomposition, for it has been found possible to obtain the amides from proteid in this way by artificial means.

The following is an enumeration of the substances of this kind which have been found in plants.

1. Amides :

Asparagin, $C_4H_8N_2O_3$ probably the amide of succinamic acid, $C_2H_3NH_2$, $CONH_2$, $COOH$.

Glutamin, $C_5H_{10}N_2O_3$, probably the amide of glutaminic acid, C_3H_5 , NH_2 , $CONH_2$, $COOH$.

2. Amidated fatty acids :

Leucin, $C_6H_{13}NO_2$, amidocaproic acid, $C_5H_{10}NH_2COOH$.

Betaïn, $C_5H_{11}NO_2$, possibly trimethyl-glycocoll, $C(CH_3)_3$, $NHCH_3$, $COOH$, or oxynurin $C(CH_3)_3NH_2$, O , CO .

3. Amidated fatty acids containing an aromatic radicle :

Tyrosin, $C_9H_{11}NO_3$, probably α parahydroxyphenylamidopropionic acid, C_2H_3 , NH_2 , C_6H_4 , HO , $COOH$.

A body, $C_9H_{11}NO_2$ allied to Schützenberger's tyroleucin, has been found by Schulze in Lupin-seedlings: it is probably phenylamidopropionic acid, C_2H_3 , NH_2 , C_6H_5 , $COOH$.

4. Bodies belonging to the xanthin-group :

Xanthin, $C_5H_4N_4O_2$, hypoxanthin, $C_5H_4N_4O$, and guanin, $C_5H_5N_5O$, have been found by Schützenberger in Yeast, by Salomon in Lupin-seedlings, by Reinke and Rodewald in *Æthelium*, and Schulze and Eugster believe that they have found them in potatoes. Kossel, who has found them in various plants, is of opinion that they are derived from nucléin. Allantoin, $C_4H_6N_4O_3$, has been found by Schulze in the young leaves of the Plane.

The view that the amides are products of processes of oxidative decomposition is supported by the fact that the

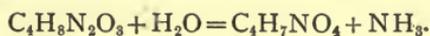
amides are all richer in oxygen than proteid, and by the fact (p. 210)—though much stress cannot be laid upon it at present—that, in the absence of free oxygen, ammonia is evolved by plants. We cannot say at present whether or not all the amides are directly formed in this way. It is possible to imagine that the more highly oxidised of them—the xanthin-bodies, for instance—may be derived from others by further oxidation. On the whole it appears probable that this is not the case, but that the different amides are derived possibly from different forms of proteid, or that the nature of the decomposition may vary under the influence of different external conditions, so as to give rise to amides sometimes of one kind and sometimes of another. In connexion with this point we must bear in mind Kossel's suggestion as to the origin of the xanthin-bodies from nucleïn.

Turning now to the *waste-products*, we find that those with which we have become acquainted in previous lectures (oxygen, carbon dioxide, water) are such as are excreted by the plant; but the majority of the waste-products are retained in the tissues of the plant. Speaking generally we may say that the *excreta* of plants are given off in the gaseous form, though to this statement there are a few exceptions. It was thought at one time that a considerable excretion of waste-products in solution was effected by the roots, and de Candolle went so far as to found upon this supposed excretion a theory of the rotation of crops: but the researches of Bracconot and of Boussingault have conclusively proved that no such excretion takes place. It is true that if the roots of a land-plant be removed from the soil and be immersed in distilled water, small quantities of salts and even traces of organic matter will be extracted from them (Knop), but no inference can be drawn from experiments of this kind in which the conditions are so abnormal.

With regard to the nitrogenous waste-products we may say that the more important of them are compound ammonias. In some comparatively rare cases they are excreted by the plant. Thus, the peculiar odour of certain flowers, notably those of the May (*Cratægus oxyacantha*), depends

upon the excretion of trimethylamin, $N(CH_3)_3$, and the leaves of the Stinking Goosefoot (*Chenopodium Vulvaria*) are constantly giving off this gas. More commonly the compound ammonias are not volatile at ordinary temperatures, and they are then termed *alkaloids*. The presence of these bodies has been determined in a great number of plants, and it is probable that they are more generally present in plants than is usually supposed. They are not excreted by the plant, but they are especially deposited in those parts which become detached, such as the bark, fruits, and seeds, and it is in this way that they are gradually got rid of.

With regard to the origin of alkaloids in the plant, there can be little doubt that they are derived more or less directly from proteid. It is an almost necessary assumption that they are built up from ammonia; we have therefore to enquire into the possibility of the formation of ammonia in the plant. It has been already suggested (p. 150) that ammonia is formed in connexion with the processes of destructive metabolism, and it has also been pointed out (p. 210) that, under abnormal conditions, ammonia may be even excreted. The mode of the formation of ammonia in the plant is not difficult to imagine. It is well known that the amides are readily decomposed into organic acids and ammonia. Thus, when asparagin is boiled with dilute acids or alkalies, aspartic acid is formed and ammonia is evolved according to the equation



It is therefore quite possible that free ammonia may be formed in the plant, and that from this the alkaloids may be built up. It is interesting to note, in connexion with this, that neither urea nor uric acid have ever been found in plants. According to a commonly accepted view it would appear that these bodies may be formed in the animal body from leucin and tyrosin; these substances apparently undergo decomposition into carbon dioxide and ammonia and the carbon dioxide and ammonia combine in other proportions to form urea and uric acid. There is, in fact, a certain amount of evidence to shew that urea is formed synthetically in the animal body,

and it is probable that something of the same kind may take place in the plant, the bodies formed being alkaloids instead of urea and uric acid. As a matter of fact, certain vegetable alkaloids, theïn and theobromine, are allied to uric acid. Further, Broughton has observed that when the Cinchona is manured with highly nitrogenous substances, the amount of alkaloids is very much increased: this is a parallel to the well-known fact that when an animal consumes a large quantity of nitrogenous food, the excretion of urea and of uric acid is increased.

The alkaloids are of two kinds, namely those which do and those which do not contain oxygen. To the former group belong the more familiar alkaloid such as morphin ($C_{17}H_{19}NO_3$) and the other opium-alkaloids; theobromin ($C_7H_8N_4O_2$), theïn ($C_8H_{10}N_4O_2$), strychnin ($C_{21}H_{22}N_2O_2$), atropin ($C_{17}H_{23}NO_3$), quinin ($C_{20}H_{24}N_2O_2$): to the latter belong mercurialin (CH_5, N) probably identical with methylamin (CH_3, H_2N), coniin ($C_8H_{15}N$), nicotin ($C_{10}H_{14}N_2$), and sparteïn ($C_{15}H_{26}N_2$). It has been found that an alkaloid which contains no oxygen can be obtained from one which does: thus Wertheim has succeeded in preparing coniin ($C_8H_{15}N$) from conydrin ($C_{18}H_{17}ON$). It appears that most of the alkaloids can be traced to the compound ammonia pyridin (C_5H_5N). The alkaloids occur in plants in combination with organic acids.

We have every reason to believe that the alkaloids are in reality waste-products, that is, substances which cannot enter into the constructive metabolism of the plant, for the observations of Knop and Wolf shew that the demand for combined nitrogen cannot be met by supplying the plant with it in the form of alkaloids, although, as we have seen (p. 124), the plant can take up urea, uric acid, leucin, tyrosin, or glycocoll.

There is one point which deserves especial mention before we leave this subject, namely this, that, as a rule, the nitrogenous metabolism of plants is not accompanied by any loss of nitrogen when the conditions are normal. In this respect plants differ widely from animals. This difference is due partly to the fact (p. 159) that plants are endowed with a greater constructive capacity than animals; animals excrete the amides formed in the destructive metabolism of the organism in the form of urea, uric acid, etc., whereas plants

are capable of using them in the reconstruction of proteid ; and partly to the fact that any nitrogenous waste-products (alkaloids) which may be formed are not excreted. This important point is illustrated by Boussingault's comparative analyses of seeds and of seedlings given on page 176, and his results agree with those of all other observers.

We must not forget, too, that protoplasm contains sulphur and phosphorus ; we will briefly consider what becomes of these elements in destructive metabolism. It appears that the sulphur is set free as sulphuric acid. Schulze and others have found that the proportion of sulphates gradually increases during the germination of seeds (Lupins, Pumpkins, Vetches), and it seems that the amount of sulphates present bears some relation to the activity of the proteid-metabolism. Probably the same is true of phosphorus.

In certain plants sulphurised ethereal oils are found ; in the Onion, Garlic, Horse-radish, etc., allyl sulphide ($C_3H_5)_2S$; in the seeds of the Black Mustard, allyl sulpho-cyanide, C_3H_5, CN, S . Attention has been already drawn to the fact that a phosphorised fat, lecithin, has been commonly found in plants.

We will now turn our attention to the probable mode of origin of the vast number of other, principally non-nitrogenous, waste-products which have been found in plants, such as the organic acids, the aromatic substances, the colouring-matters, etc.

The organic acids are very generally present in plants, either free, or in combination with inorganic bases, forming frequently acid salts, or in combination with organic bases (alkaloids). It is to the presence of these acids or of their acid salts that the acid reaction of plant-tissues is due.

The following enumeration includes the organic acids most commonly found in plants :

1. Fatty acids ; general formula $C_nH_{2n+1}, COOH$.

Formic acid CH_2O_2 , acetic acid $C_2H_4O_2$, propionic acid $C_3H_6O_2$, butyric acid $C_4H_8O_2$, valerianic acid $C_5H_{10}O_2$, caproic acid $C_6H_{12}O_2$, have been found in various plants by many observers. Bergmann concludes from his researches that formic and acetic acids at least, are always present in living plant-cells.

The higher members of this series such as caprylic acid $C_8H_{16}O_2$,

capric acid $C_{10}H_{20}O_2$, palmitic acid $C_{16}H_{32}O_2$, stearic acid $C_{18}H_{36}O_2$, have only been found to occur in combination with glycerin as fats (glycerides).

2. Acids of the acrylic series ; general formula $C_nH_{2n-1}COOH$.

Angelic acid, $C_5H_8O_2$, has been detected in certain plants (especially in the root of *Angelica Archangelica*) in the free state.

Oleic acid, $C_{18}H_{34}O_2$, occurs in the form of fat (olein) in combination with glycerin.

3. Acids of the lactic series ; general formula $C_nH_{(2n+1-m)}(OH)_mCOOH$.

To this group belongs carbonic acid, H_2CO_3 , which is produced by all plants ; also glycolic acid, $C_2H_4O_3$, which has been found in unripe grapes ; and lactic acid, $C_3H_6O_3$, which is probably produced, by the fermentative action of Bacteria, from sugar and other carbohydrates.

4. Acids of the succinic series ; general formula $C_nH_{2n}(COOH)_2$.

Oxalic acid, $C_2H_2O_4$, is frequently present, combined with sodium or potassium, in solution in the cell-sap of plants, especially in the leaves of the Wood-sorrel, the Dock, and their allies. It is even more commonly found precipitated in the form of crystals of calcium oxalate.

Succinic acid, $C_4H_6O_4$, has only been found in a few plants, but is probably widely distributed. It may be readily obtained from amber which is a fossil resin.

a. Amidated acids of the succinic series :

Aspartic or asparaginic acid (succinamic acid) $C_4H_7NO_4$ and glutamic acid, $C_5H_9NO_4$, have not been found in the free state in plants, but they commonly occur in extracts of plants as products of the decomposition of asparagin and of glutamin respectively.

b. Hydroxy-acids of the succinic series.

Malic acid, $C_4H_6O_6$, very commonly occurs in plants, especially in unripe fruits.

Tartaric acid, $C_4H_6O_6$, is probably (at least dextrotartaric acid) of universal occurrence in plants, and is usually associated with oxalic, malic, and citric acids.

These acids occur either free, or in combination with potassium, or calcium, or with organic bases.

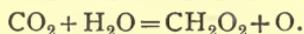
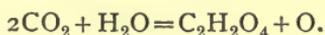
5. Tribasic acids derived from the paraffins.

Citric acid, $C_6H_8O_7$, occurs in the free state in many fruits, and is occasionally met with, in potatoes for example, in the form of acid salts of potassium or calcium.

6. Acids of the maleic series ; general formula, $C_nH_{2n-2}(COOH)_2$.

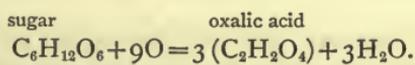
Fumaric acid, $C_4H_4O_4$, has been found in a considerable number of plants.

The mode of formation of acids in the plant is a subject of considerable difficulty. The first attempt to explain it was made by Liebig. He considered that the highly oxidised acids were formed as the first products of constructive metabolism from carbon dioxide and water in the cells containing chlorophyll: that, for example, oxalic and formic acids are produced according to the equations,



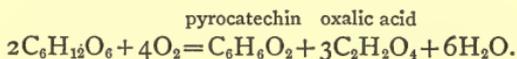
It has been already pointed out (p. 144) that a synthetic formation of formic acid from carbonic dioxide and water may, according to Erlenmayer's view, take place as the first stage in the formation of organic substance, but the formic acid so produced is at once converted into the corresponding aldehyd, and this in turn into a polymer. It is doubtful, therefore, if Liebig's theory will satisfactorily account for the presence of free formic acid, even in cells which contain chlorophyll, and it certainly fails to account for the presence of acids in Fungi and in etiolated plants. We are led to conclude, therefore, that the acids present in plants are products not of constructive but of destructive metabolism.

The next point to be considered is as to the substances from which they are derived. It is commonly held that the acids are produced by the oxidation of carbohydrates, especially sugar, but there is no direct evidence to show that this is actually the case, though, from the facility with which acids can be formed artificially from carbohydrates, it may be assumed to be quite possible. This oxidation is usually supposed to be more or less direct; for instance it is frequently expressed by the equation

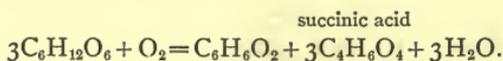


But, even admitting that carbohydrate is thus directly oxidised, it is hardly probable that the process is so simple as this. It was pointed out in the last lecture (p. 202) that the effect of oxidation is to diminish the stability of complex organic substances and thus to facilitate their decomposition,

the products of each successive decomposition being more and more highly oxidised. A suggestion as to the possible nature of this oxidative decomposition in the case of carbohydrates is afforded by Hoppe-Seyler's researches upon the decomposition of carbohydrates by the action of alkalies and by heating in closed tubes with water. He obtained formic and ethylidene-lactic acids, an aromatic substance termed pyrocatechin, and carbon dioxide was evolved. It appears to be probable that oxalic acid is formed in the process, and that it is decomposed into formic acid and carbon dioxide, for the commercial preparation of oxalic acid is effected by heating cellulose (sawdust) with a mixture of potassium and sodium hydrates. We may represent the formation of oxalic acid in this way by the following equation,



It is not probable, however, that so highly oxidised an acid as the oxalic is at once produced; it is more likely that a less highly oxidised acid, such as the succinic, is first formed, and that from this, by successive oxidative decomposition, the more highly oxidised acids are derived. The formation of succinic acid may be represented thus,



Moreover all the more complex acids yield the simpler ones on oxidation; thus, when succinic acid is fused with potassium hydrate, a mixture of potassium propionate and carbonate is formed; when malic, tartaric, or citric acid is similarly treated, it yields a mixture of potassium acetate and oxalate.

It must not be assumed that the decomposition of carbohydrate always takes place in the manner described above; this instance is only cited to illustrate the point that the production of acids from carbohydrates is not effected by simple oxidation.

There is, however, reason to believe that the particular decomposition in question does take place in plants. Karl Kraus has found that the external dry scales of the Onion contain pyrocatechin and crystals of calcium oxalate, but no grape-sugar; whereas the internal succulent

scales contain much grape-sugar, but neither calcium oxalate and pyrocatechin. But if the internal scales be allowed to become dry, they assume the brown colour of the external scales, the grape-sugar disappears from the cells, and pyrocatechin and crystals of calcium oxalate make their appearance. He has also ascertained that pyrocatechin is commonly present in leaves and shoots, especially in the autumn.

But if it be admitted that the carbohydrates undergo oxidative decomposition in the plant, it must be true of other substances also. For instance, the alcohols which are doubtless formed in the plant, would be oxidised to acids. To take glycerin as an example. This alcohol is, as we have seen, set free on the decomposition of glycerides (fats), but free glycerin has never been detected in any plant. It probably undergoes decomposition as soon as it is formed. It is well known that glycerin is readily oxidised to carbon dioxide and water, and that it is susceptible of more gradual oxidation, a number of acids (oxalic, formic, glycolic, etc.) being produced: this is probably its fate in the plant. Again, the amides would yield acids on oxidation. Thus asparagin is readily decomposed into aspartic acid and ammonia, and aspartic acid, when oxidised, yields malic acid.

Aspartic acid is converted into succinic acid on fermentation. It is probable that the succinic acid which is found among the products of the alcoholic fermentation by Yeast, and of the conversion of alcohol into acetic acid by the *Mycoderma aceti*, is derived from asparagin formed in the metabolism of the Fungus.

Again, there can be no doubt that acids are formed by the oxidative decomposition of proteid. It has been found that oxalic acid and amidated acids are formed when proteid is decomposed artificially, that amidated acids, which we have reason to believe are derived from proteids, are present in plants, and that, in the process of fat-formation, fatty acids are produced which doubtless owe their origin to proteids.

Finally, there can be little doubt that the self-decomposition of protoplasm is attended by a formation of acids. This has already been alluded to in discussing de Saussure's observations on *Opuntia* (p. 207), and, if we admit that fat is

formed from protoplasm (p. 218), we necessarily assume that fatty acids are among the products of its decomposition.

It must be borne in mind that acids may be readily derived from each other in various ways. To the examples already given (see p. 228) the following may be added. Under the action of reducing agents, succinic acid is produced from malic or tartaric acid : and conversely, since malic (monohydroxysuccinic) and tartaric (dihydroxysuccinic) acids are oxidised derivatives of succinic acid, it is quite possible that they may be formed from succinic acid in the plant. Again, on heating malic acid fumaric acid is formed, and fumaric acid is converted into succinic acid under the influence of nascent hydrogen. Further, as has already been pointed out, acids undergo decomposition by fermentation : thus malic acid yields on fermentation either (*a*) succinic acid, acetic acid, carbon dioxide and water, or (*b*) propionic acid, acetic acid, and succinic acid, or (*c*) butyric acid, carbon dioxide, and water : the gradual conversion observed by Schindler, of citric into tartaric acid in lemon-juice which had been allowed to stand for a long time, is probably another illustration of the transformation of one acid into others by fermentation.

Now as to the significance of the acids in the metabolism of the plant. It has been already mentioned that Liebig regarded the highly oxidised acids, especially the oxalic, as being the first products of the constructive metabolism of the plant, and he was further of opinion that by gradual reduction of them carbohydrates and even fats were formed. The most important piece of evidence which he offered in support of his views was the fact that, as fruits ripen, they become less sour, a fact which he interprets to mean that acid is converted into sugar. This may, however, be explained in other ways : the sugar may be produced from starch, and the diminution of the acidity may be attributed to the neutralisation of the acid by bases. Still, it appears from Beyer's analyses, that the proportion of mineral matters diminishes in fruits as they ripen, and hence it may be inferred that the acids do not become neutralised ; Beyer also finds that the acids diminish and that the sugar increases in plucked fruits. Again, it seems probable, as stated above (p. 206) that the starch which makes its appearance in the embryo of a germinating oily seed, is formed indirectly, through protoplasm, from the fatty acids set free in the seed by

the decomposition of the fats. Finally, though Schmoeger's observations (see p. 125) tend to prove that highly organised plants cannot take up acids when supplied to their roots, yet Naegeli has shewn that the lower Fungi will flourish when carbonaceous food is supplied to them in the form of various acids, acetic, succinic, and tartaric (p. 125).

But there are certain acids which, so far as our present knowledge goes, cannot be reduced by plants, namely, the formic and the oxalic. Naegeli found that Fungi could not assimilate either of these, and the general occurrence of crystals of calcium oxalate in the tissues of plants, which, according to Hilgers, undergo no alteration after they have been formed, clearly suggest that plants in general are incapable of reducing oxalic acid. Even admitting that some acids may be used in the constructive metabolism of plants, there is a strong presumption that oxalic acid at any rate—and this is of importance, since oxalic acid is the starting-point of Liebig's theory—is of no value for this purpose. It is only of the less highly oxidised acids that plants can avail themselves.

Instances of the solution of calcium oxalate in the plant are, however, on record. Frank has observed it in the mucilaginous cells of the tubers of various Orchids: Sorauer has found that young potatoes abundantly contain crystals of calcium oxalate which disappear as the tuber becomes mature, an observation which has been confirmed by de Vries. Whilst admitting the accuracy of these observations it must not be overlooked that they do not prove that the oxalic acid enters into the constructive metabolism of the plants: they only prove that the oxalate has been brought into solution, or that it has undergone decomposition so as to give rise to soluble salts.

In connexion with Liebig's view as to the reduction of acids in the plant, we may recall the facts mentioned in the last lecture (p. 197) with reference to succulent plants. De Saussure observed, namely, that when a piece of *Opuntia*-stem which had been absorbing oxygen during the night, was exposed to sunlight on the following day in an atmosphere containing no carbon dioxide, it exhaled a volume of oxygen which slightly exceeded that of the oxygen absorbed during the preceding night (in one experiment the volume of O absorbed = 74 c.c., the volume exhaled = 79 c.c.). Mayer observed, in his experiments, that, under these circumstances, starch-grains make their appearance in the chlorophyll-corpules, care being taken to prevent any absorption of carbon dioxide

from without. Mayer is of opinion that the oxygen absorbed whilst the plant is in darkness is retained in the form of an organic acid, and that it is in consequence of the reduction of this acid (he believes it to be an isomer of malic acid) that oxygen is evolved and starch is formed in the chlorophyll-corpuscles when the plant is exposed to light. He conceives the mode of this decomposition to be the following. Relying upon the fact that when uranium succinate is exposed to light it is decomposed into uranium propionate and carbonate, he infers that when this malic acid is exposed to light in a cell containing chlorophyll, lactic acid and carbon dioxide are formed, and he points out that sugar may be produced by polymerisation from the lactic acid. He actually found that a mixture of malic acid and calcium malate was decomposed when exposed to sunlight; carbon dioxide was abundantly evolved, but neither lactic acid nor sugar could be detected in the liquid: it appears that, under the conditions of the experiment, the lactic acid underwent further decomposition. The evolution of oxygen by the plant under the influence of light is doubtless due to the decomposition of the carbon dioxide thus formed, and with this the appearance of starch-grains in the chlorophyll-corpuscles is to be connected.

In addition to their possible significance in the constructive metabolism of plants, the organic acids are of use in other ways. We have seen, for instance (p. 41), that it is probably to the presence of them that the turgidity is to be ascribed; that the presence of acid sap in the root-hairs (p. 55) renders possible the solution and absorption of mineral substances which are insoluble in water; that oxalic acid, at least, decomposes the salts absorbed by the roots (p. 149).

We will now pass on to the consideration of the origin of the aromatic substances. We have learned already (p. 21) that an aromatic substance (lignin) may be formed from a carbohydrate (cellulose), and Hoppe-Seyler's observations (p. 228) suggest a mode in which this may take place. Hartig observed, and his observations have been confirmed and extended by Wiesner, that the parenchymatous cells of the trunks of many trees (Beech, Elm, Sycamore, Oak) contain grains of resin. They conclude that these resin-grains are derived from starch-grains, and it appears very probable that tannin, an aromatic glucoside, is formed as an antecedent of the resin. We would have then, in the process of

lignification, the conversion of cellulose into an aromatic cellulide; in the formation of resin-grains, the conversion of starch into an aromatic glucoside. But it must not be forgotten, as Müller points out, that the simultaneous presence of starch and of tannin or resin in a cell does not prove that the latter are directly derived from the former. It is possible that tannin is a product of the metabolism of the protoplasm, and that the starch-grains present in a cell in which tannin is being formed become impregnated with it, giving rise to the so-called tannin-grains and eventually to resin-grains. It is true that the starch gradually disappears, but this does not prove the direct conversion of starch into tannin; the tannin may be formed indirectly from the starch through the protoplasm. The fact that tannin is constantly present in the cells of parts in which destructive metabolism is active—growing-points, motile organs of leaves, galls, for example—tends to prove that it is, in fact, derived from protoplasm. Further, we must not overlook the fact that substances like tyrosin, which contain an aromatic radical, occur in plants, and that they are probably derived more or less directly from protoplasm: it is also quite possible that these substances may take part in the formation of some of the more familiar aromatic bodies which occur in plants.

It is possible, as Cross and Bevan point out, that the benzoic residue which enters into the composition of the hippuric acid present in the urine of the Herbivora is derived from the aromatic substances present in the lignified cell-walls of the plants consumed. It may be, however, that the aromatic body is also formed from cellulose in the manner suggested by Hoppe-Seyler's observations (p. 228).

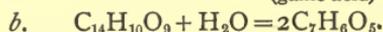
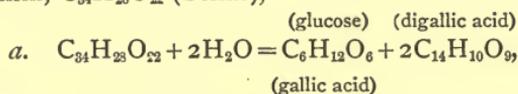
We are already in possession of some information respecting the conditions under which the formation of the cellulides takes place. It was pointed out in a former lecture (p. 18) that lignification may take place in a cell-wall after the protoplasm has disappeared from the cell, but that the cell must still form part of a living plant. But it is scarcely possible to make any definite statement as to the chemical nature of the process. Inasmuch as lignin, for example, contains relatively less oxygen than cellulose (taking Erdmann's formula for

lignose, $C_{18}H_{26}O_{11}$ as a basis) (p. 21), we may infer with Sachs that it is a residue of the oxidative decomposition of cellulose, carbon dioxide, water, and possibly a highly oxidised acid such as the oxalic, being the other products. This view harmonises with what has been said above (p. 228) with reference to the oxidative decomposition of carbohydrates in the plant, though in the illustrations there given the oxidation is represented as being more complete.

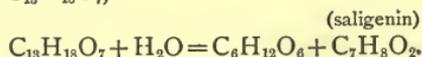
In view of the facts mentioned above with regard to tannin, we must regard the glucosides as being, most probably, products of the destructive metabolism of protoplasm. They occur normally in the cell-sap, but they can commonly be detected in the cell-wall by which they are gradually absorbed as the cell grows old and loses its protoplasmic and watery contents.

The more common glucosides are tannin, salicin, phloridzin, coniferin. They are decomposed by ferments according to the following equations.

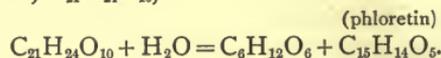
1. Tannin, $C_{34}H_{28}O_{22}$ (Schiff),



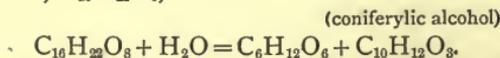
2. Salicin, $C_{13}H_{18}O_7$,



3. Phloridzin, $C_{21}H_{24}O_{10}$,



4. Coniferin, $C_{16}H_{22}O_8$,



It will be seen, from the foregoing decompositions, that the glucosides yield various aromatic substances; they may be regarded, therefore, as substances intermediate between the carbohydrates and the purely aromatic bodies. Though they are products of destructive metabolism, yet they are still of some use in the economy: by their decomposition energy is evolved, and the plant may avail itself of the produced glucose.

It is still a debated question whether or not the plant is capable of making any use of the glucosides. The researches which have been made on the subject refer only to tannin. It must be remembered that micromechanical methods do not enable us to distinguish between the glucoside tannin, and tannic (digallic) acid : it is quite possible that the glucoside is of use in that it yields glucose, and that the acid is not. We will recur to this point below.

We will now treat of the aromatic substances other than the glucosides. The following are those which commonly occur in plants :

Pyrocatechin, Phloroglucin, Saligenin,
Benzoic acid, cinnamic acid, tannic acid, gallic acid, salicylic acid,
Resins, Balsams, and Ethereal Oils.

Pyrocatechin, $C_6H_4(OH)_2$ and phloroglucin, $C_6H_3(OH)_3$, are derivatives of benzene, the former being orthodioxybenzene, the latter probably paratrioxybenzene. Pyrocatechin has been found in various parts of plants, more especially in fading leaves : the mode of its origin has been suggested above.

Phloroglucin (paratrioxybenzene), $C_6H_3(OH)_3$ is a substance of common occurrence in the bark of trees : it is a product of the decomposition of substances like phloretin and quercitrin which are derived from glucosides.

Saligenin $C_7H_8O_2 = C_6H_4(OH), CH_2(OH)$, is a derivative of toluene ; it is orthomethoxyphenol ; it is formed as shewn above, by the decomposition of the salicin and of the populin which are present in the bark of Willows and Poplars respectively.

The aromatic acids are of common occurrence in plants. Benzoic acid ($C_7H_6O_2$) is prepared from gum-benzoin, the produce of *Styrax Benzoin*, but it is present in small quantity in many other plants, and together with cinnamic acid ($C_9H_8O_2$) in various balsams, such as storax and balsam of Peru. These acids are probably formed by the oxidative decomposition of glucosides which, like amygdalin, yield benzoic aldehyde (oil of bitter almonds) under the action of ferments.

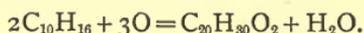
Salicylic acid ($C_7H_6O_2$) occurs in various flowers, especially in those of the genus *Spiræa* : it is probably formed by the oxidation of its corresponding alcohol saligenin.

Tannic and gallic acids are very generally present in plants. Tannic acid ($C_{14}H_{10}O_9$) occurs in two somewhat different chemical forms, in the tissues of almost all plants ; it is found, according to the observations of Sachs and of Pétzold, in the immediate neighbourhood of those parts of the plant, growing-points for instance, in which metabolism is most active. It is doubtless derived from tannin as indicated above. Gallic acid ($C_7H_6O_5$), though not so universally present as tannic acid, has been

found in various parts of many plants : its derivation from tannic acid has been mentioned above.

The resins are substances which are nearly always to be found in plants and in all parts of them. Three kinds of resins may be distinguished, (*a*) True resins ; (*b*) Balsams, mixture of resins and ethereal oils, together with aromatic acids ; (*c*) Gum-resins, mixture of resins, gums, and ethereal oils.

Ordinary resin (colophony) obtained from the Conifers appears to be a mixture of resinous acids, the most important of these being Abietic anhydride, $C_{44}H_{82}O_4$ (Maly). Resin is produced in cells, and it is excreted into intercellular spaces termed *resin-passages*. According to the researches of Wiesner, of Franchimont, and of Hlasiwetz, it appears that the first step towards the production of resin is the formation of a glucoside, probably tannin ; the tannin then undergoes decomposition, and from the tannic acid resin is derived. Franchimont, especially, draws attention to the relation of the cells containing tannin to the resin-passages in Conifers. He is of opinion that the decomposition of the glucoside is attended by the formation of oxalic acid. He also points out that the secreting cells lining the resin-ducts do not themselves contain resin, but that they excrete into the ducts a substance which becomes converted by oxidation into resin. It seems probable that from the tannic acid an ethereal oil (terpene) is formed in the cells, that this is excreted into the ducts, and that it then undergoes partial oxidation into resin, the turpentine which the ducts contain being a solution of resin in an ethereal oil. Hlasiwetz represents the process of oxidation of terpene into resin thus,



The group of ethereal oils includes a great number of substances of very various chemical composition, which are present to a greater or less extent in all parts of Flowering Plants : it is to the presence of volatile ethereal oils that the odours of plants are due. These oils may be classified into those which do and those which do not contain oxygen.

a. Ethereal oils containing oxygen ; the following are the more common :

Aldehydes : oil of cinnamon, C_9H_8O ; oil of bitter almonds C_7H_6O .

Ketones : oil of rue, methylonyl ketone, $C_{11}H_{22}O$: camphor, $C_{10}H_{16}O$ is probably a ketone.

Acids : oil of cloves or eugenol, $C_{10}H_{12}O_2$; coumarin, $C_9H_6O_2$, to which the odour of the Tonka Bean, and of new-mown hay is due, is probably the anhydride of coumaric acid : eugenol is also regarded as being an ether-alcohol.

Mixed ethers: anethol or oil of anise, $C_{10}H_{12}O = CH_3, C_6H_4 (C_3H_5), O$.
 Compound ethers: benzyl benzoate, $C_{14}H_{12}O_2$, and benzyl cinnamate, $C_{16}H_{14}O_2$, in various balsams; methyl salicylate, $C_8H_8O_2 = CH_3, C_7H_5O_3$, in the Winter-green (*Gaultheria procumbens*).

b. Ethereal oils not containing oxygen :

These oils are hydrocarbons of the formula $C_{10}H_{16}$; but though they have the same ultimate chemical composition they are not all identical, but some are isomers and polymers; they are commonly termed terpenes.

Terebenthene is the terpene which is present in turpentine; a terpene is also present in the essential oils of plants, such as oil of Neroli obtained from Orange-flowers, oil of Lemons, oil of Peppermint, etc.

In connexion with the terpenes we may consider two hydrocarbons, Caoutchouc and Gutta Percha which have the formula $(C_8H_8)_x$. Caoutchouc is obtained from the latex of the Urticaceæ, Euphorbiaceæ, and Apocynaceæ: Gutta Percha from the latex of various species of Isonandra (*Dichopsis*) and other Sapotaceæ.

With regard to the function and fate of these aromatic substances, it appears that they are of no use in the constructive processes; they are to be regarded as waste-products, destined, for the most part, to be thrown off. Even when they actually remain in the plant, in resin-ducts or in laticiferous vessels, they are outside the sphere of the metabolism of the plant. Hartig was led, by his observations on the oak, to the conclusion that tannin (tannic acid?) is used in the constructive processes, but Sachs and others do not find that this is the case. According to Schell, tannin can only serve as a plastic substance when the plant possesses insufficient stores of carbohydrates and of fats: this amounts to saying that, under ordinary circumstances, tannin is merely a waste-product. Again, it has been found (Wagner), that when hippuric acid is presented to the roots of one of the higher plants, it is decomposed into glycocoll and benzoic acid, and that only the former of these bodies is absorbed. On the other hand, we must not forget that tyrosin is absorbed when presented to the roots, but we cannot conclude from this that the aromatic radical which it contains is actually used in the constructive processes. Nor must we overlook the fact that Naegeli has succeeded in cultivating

Fungi on dilute solutions of aromatic substances such as carbolic, salicylic, and benzoic acids (p. 125). Taking all this into consideration, we may venture upon the general statement that the higher plants, at least, cannot avail themselves of carbon when combined in an aromatic molecule for the purposes of their constructive metabolism.

Although the aromatic substances are probably to be regarded simply as waste-products, yet some of them are indirectly of use to the plant. We have seen that the odours of plants are due to the presence of volatile ethereal oils, and it has been ascertained that the odours of flowers serve to attract insects and thus contribute to ensure fertilisation.

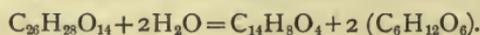
We have yet the group of colouring-matters to consider. These may be conveniently classed as follows:

1. Phlobaphenes, or colouring-matters of the bark.
2. Colouring-matters of woods, etc.
3. Colouring-matters of leaves, flowers, and of Thallophytes.

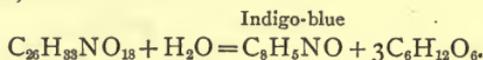
The phlobaphenes are brown amorphous colouring-matters which are present in the walls of the bark-cells of trees and shrubs. They closely resemble the brown products of the oxidation of tannin and other glucosides, and it seems probable that they are in fact formed in the plant in this way. When they are fused with caustic potash they yield protocatechuic acid as one of the products, and this acid is also formed when the brown products of the oxidation of tannin are treated in the same way (Hlasiwetz).

The colouring-matters of woods occur, like the phlobaphenes, in the cell-walls, and, although nothing is definitely known as to their origin, it is probable that they are formed in much the same way. There is, however, reason for believing that they are not formed in the cell-wall, but in the cavity of the cell, and that as the cells lose their contents and become dry the colouring-matters are taken up by the cell-wall. Such are Brasilin, $C_6H_{14}O_5 + H_2O$, obtained from Brazil-wood (*Casalpinia brasiliensis*), and Hæmatoxylin, $C_{16}H_{14}O_6 + 3H_2O$, obtained from the wood of *Hæmatoxylon campechianum*.

In some plants glucosides are present which, after extraction, undergo decomposition, giving rise to colouring matters. Thus the root of *Rubia Tinctorum* (Madder) contains a substance termed ruberythric acid, $C_{26}H_{28}O_{14}$, which decomposes, under the action of a ferment contained in the root, into a colouring matter, alizarin, and glucose, according to the equation,



Again, indigo is formed by the decomposition of a nitrogenous glucoside termed indican, $C_{26}H_{33}NO_{13}$ which is present in various plants, *Nerium tinctorium*, *Polygonum tinctorium*, *Isatis tinctoria*, and especially in *Indigofera tinctoria* a Leguminous plant. The decomposition may be represented thus ;



The colouring-matter obtained from the indican of *Isatis tinctoria* has the formula $C_8H_5NO_2$, and is termed Isatin or Woad.

Other colouring-matters occur in the cavities of cells ; for example alcannin ($C_{18}H_{20}O_4$) in the root of *Anchusa tinctoria*, and curcumin in the root of *Curcuma longa*.

The green colouring-matter of plants, chlorophyll, always occurs in intimate relation with the protoplasmic cell-contents, and, as we have seen, it is confined in the higher plants to certain specialised portions of the protoplasm which are termed chlorophyll-corpuscles. We have already discussed the chemical composition and the physical properties of this substance ; it only remains now to consider the conditions of its formation, and the probable source from which it is derived.

The general conditions upon which the formation of chlorophyll depends are three : 1, exposure to light ; 2, a sufficiently high temperature ; 3, a supply of iron. Of these, the two first will be further discussed in a subsequent lecture, in which we will consider the influence of heat and light on the metabolism of the plant. The significance of the third condition is not understood at present. It was thought that iron entered into the composition of chlorophyll much in the same way that it enters into the composition of the colouring-matter (hæmatin) of the red-blood corpuscles : but it appears from the analysis of chlorophyll (see p. 154) that no iron can be detected in it. It may be urged that the chlorophyll when extracted is not identical with the green colouring-matter in the living plant ; but the extracted chlorophyll has the green colour and the characteristic spectrum, so we may conclude that neither of these important properties depends upon the actual presence of iron in the chlorophyll-molecule. Arthur Gris came to the conclusion

that the absence of iron not only prevents the formation of chlorophyll, but even the differentiation of the corpuscles (see p. 136). The recent researches of Schimper and of A. Mayer prove, however, that this view is quite untenable.

Plants, then, which are normally green, are not green if they have been grown in the dark, or if the temperature has been too low, or if they have not been supplied with iron: but the resulting colour is not the same in all these cases. A plant which has been growing in the dark or at a low temperature is usually of a yellow colour; a colouring-matter has been formed in it, but instead of being a green it is a yellow colouring-matter termed *etiolin*. A normally green plant which has been grown in the dark is said to be *etiolated*. On the other hand, a plant which has been deprived of a supply of iron becomes perfectly colourless, and is said to be *chlorotic*. When an etiolated plant is exposed to light and the temperature is sufficiently high it rapidly becomes green: similarly when a chlorotic plant is supplied with iron it also becomes green.

It appears that the formation of chlorophyll in the plant under ordinary conditions is mediate, that is, that it is not directly formed, but that etiolin is first formed, and that from etiolin chlorophyll is produced. In endeavouring to ascertain the mode of formation of chlorophyll, the first step will be to enquire into the origin of etiolin, and the second, to determine the nature of the process by which etiolin is converted into chlorophyll.

The process of the formation of etiolin appears, from the researches of Gris, of Mikosch, and others, to be as follows. When the protoplasmic corpuscle is fully formed, it produces a starch-grain in the manner described in the case of the amyloplasts in a previous lecture (p. 180); it then gradually assumes a yellow colour, and, at the same time, the included starch-grain diminishes in size and finally disappears; if now the etiolin-corpuscle, as it may be termed, is exposed to light, it assumes a green colour, the etiolin being converted into chlorophyll.

With regard to the chemical nature of this process,

Sachsse is of opinion that the starch is converted into etiolin, that the starch undergoes oxidative decomposition, that fatty aldehydes and aromatic substances (*e.g.* pyrocatechin) are among the products, and that these combine to form etiolin; under the influence of light etiolin is reduced to chlorophyll.

It is not probable, however, that this is an accurate account of the chemical changes in process. It has been shewn (p. 154) that chlorophyll contains not only C, H, and O, but also N, and probably also P, in its molecule; and reference has been made to Hoppe-Seyler's suggestion that chlorophyll is a body allied to the lecithins. It is true that we have no trustworthy analysis of etiolin, but all that is known on the subject tends to shew that etiolin and chlorophyll are closely-allied bodies: what is here said about chlorophyll may therefore be regarded as true of etiolin also. In consideration of the complex composition of these colouring-matters, it is probably nearer the truth to regard them as derivatives, not of the starch, but of the protoplasm of the corpuscle. From this point of view the correlated disappearance of the starch and the formation of the colouring-matter is to be explained thus: that as protoplasm is consumed in the formation of the colouring-matter, the starch is used in the construction of fresh protoplasm. With regard to the nature of the change which etiolin undergoes on its conversion into chlorophyll, we have no definite information. (The spectrum of etiolin is given in the plate.)

It has been ascertained by Pringsheim, Wiesner, and others, that green parts of plants always contain both etiolin and chlorophyll. Besides these, a third substance, xanthophyll, is commonly present. Pringsheim has shewn that xanthophyll is probably a derivative of chlorophyll, though the exact relation between the two is not determined. It is to xanthophyll that the autumnal colouration of leaves is principally due: in many cases the leaves also contain a red colouring-matter, *erythrophyll*, dissolved in the cell-sap.

The colouring-matters of flowers and of fruits are sometimes confined to protoplasmic corpuscles, and sometimes they are dissolved in the cell-sap: the former is the case with the yellow, orange, and brown

colouring-matters (in rare cases also the blue), the latter with the white, violet, blue, and red (rarely the yellow). According to the researches of Weiss, in particular, the fixed colouring-matters are derivatives of chlorophyll; the corpuscles in which they are present are first of all green, and gradually change colour as the flower opens, or as the fruit ripens. The best-known of these is *anthoxanthin*, the colouring-matter of yellow flowers. The dissolved colouring-matters are, in white flowers, *antholeucin*, in blue *anthocyanin*. The violet red and violet colours are probably due to the presence of acids or acid salts in the cell-sap which act upon the anthocyanin. In some instances colouring-matters are present in both these forms, for instance, yellow corpuscles in a cell with a red, blue, or violet cell-sap: in certain leaves, those of the Copper-Beech, the Copper-Hazel, etc., the cells contain chlorophyll-corpuscles and purple cell-sap. It is probable that the dissolved colouring-matters are derived from tannin or other glucosides.

Among the Thallophytes, chlorophyll is always present in the Algæ, and it is always absent in the Fungi. Many of the Algæ are, however, not of a green colour. For instance, the Phycocromaceæ or Cyanophyceæ, are bluish-green, this colour being due to the presence of a blue colouring matter, *phycocyanin*, in addition to chlorophyll: again the Diatomaceæ and the Fucoideæ are yellow or brown; this is due to the presence of a brown colouring-matter, *phycoxanthin*, which masks the green colour of the chlorophyll which is present: finally, the red Seaweeds or Florideæ contain, in addition to chlorophyll, a red colouring-matter termed *phycoerythrin*. Phycocyanin and phycoerythrin are both soluble in water.

Although the Fungi do not contain chlorophyll, yet other colouring-matters are frequently present in them. These occur in all Fungi, from the Bacteria to the Agarics, and they are of different hues, yellow, green, red, brown, and blue. The Lichens are especially rich in these substances: the Algæ which from part of their structure (gonidia) contain of course chlorophyll, but the Fungus-part of the Lichen often contains other colouring-matters in quantity. The Lichens which are used for the commercial preparation of certain pigments, such as Litmus (blue), do not contain these substances as such, but colourless bodies, such as erythrin, lecanorin, etc., which, on decomposition give rise to substance orcin (a dihydroxyl derivative of toluene), and it is from this that the pigments are obtained by various processes.

With regard to their chemical nature, the colouring-matters of plants are considered to be closely connected with the aromatic group of substances. As to their physiological significance, they may be regarded simply as waste-products in so far as their direct use in constructive metabolism is

concerned ; but indirectly they are, in many cases, of great importance. The fact that chlorophyll is essential to the process of the formation of organic substance from carbon dioxide and water has been already dwelt upon at length (p. 151). The colours of flowers play an important part in attracting insects to visit the flower, and by this means cross-fertilization is ensured.

In addition to the substances already enumerated, certain others, known as *bitter principles*, are frequently present in plants. It has been ascertained that some of these are glucosides, and some alkaloids, but the chemical nature of many of them is still undetermined. Such are Santonin ($C_{15}H_{18}O_3$), Aloin ($C_{15}H_{16}O_7$), Quassiin ($C_{10}H_{12}O_3$). It is of course impossible to say anything as the possible mode of their origin or as to their physiological significance in the plant.

We have, finally, to consider certain fatty bodies. It has been already pointed out (p. 216) that the ordinary fats are plastic products, but there are certain fatty bodies of which we cannot make this statement : such are cholesterin, lecithin, and wax. We do not know how these substances are formed, though we may regard it as probable that they, like the ordinary fats (glycerides), are derived from protoplasm : this view is especially probable in the case of lecithin, which is a nitrogenous and phosphorised fat. Nor do we know much about their fate in the plant. It is possible that cholesterin and lecithin may be used in the constructive metabolism of the plant, but wax is to be regarded as a waste-product. Wax occurs especially, and perhaps exclusively, in the external cell-walls or on the surface of those parts of plants which have a cuticularised epidermis. The "bloom" on fruits, for example, is a layer of wax, and it is in the presence of such a layer that the glaucous appearance of many succulent leaves and stems is due. In some cases, more particularly in Palms, the layer of wax is so thick that it is collected for commercial purposes : the Palms which especially yield wax are the Carnauba Palm of Brazil (*Copernicia cerifera*), and the Wax-Palm of New Granada (*Ceroxylon Andicola*).

The waxes are not, like the fats, compound ethers of glycerin, but they are compound ethers of monohydric alcohols with the higher members of the fatty acid series: with these, free acids, alcohols and fats are mixed. Thus the Carnauba wax has been found by Maskelyne and by Berard to consist of

Melissin or Melissyl alcohol	$C_{30}H_{62}O$
Cerotic acid or Cerin	$C_{27}H_{54}O_2$
Cerotin or Ceryl alcohol	$C_{27}H_{56}O$
Palmitin, Stearin, Laurostearin etc. (fats).	

We will enquire, in conclusion, into the fate of the waste-products. Some of these, such as oxygen, water, and methylamin, are excreted in the gaseous form; the greater part of the carbon dioxide is also excreted as a gas, but some of it combines with earthy bases to form carbonates, which are either retained in the plant, or are excreted in solution: the resins and ethereal oils, as well as wax, are frequently excreted.

The mechanism of excretion is widely different in different cases. The resins and ethereal oils are excreted usually by means of special glandular organs. The gland may be a hair on the surface, and it is then commonly the terminal cell at the free end which is secretory (Fig. 32); or it may be a group of epidermal cells between which large intercellular spaces are formed which serve as receptacles for the excreted substance; or the gland is formed by the absorption of the adjoining walls of a group of cells belonging partly to the epidermis and partly to the underlying ground tissue, a cavity being thus formed which contains the excreted substance: or again, strands of cells may become separated so as to enclose an elongated intercellular space into which they excrete; it is in this way that resin-ducts are formed. In many cases the substance to be excreted may be detected in the glandular cells; not unfrequently, however (always in the case of wax), no trace of it can be observed in the cells themselves; it is first to be found in the cell-walls between the cuticular and the deeper layers. We must not conclude from this, as de Bary points out, that the excretion is actually formed at the expense of the

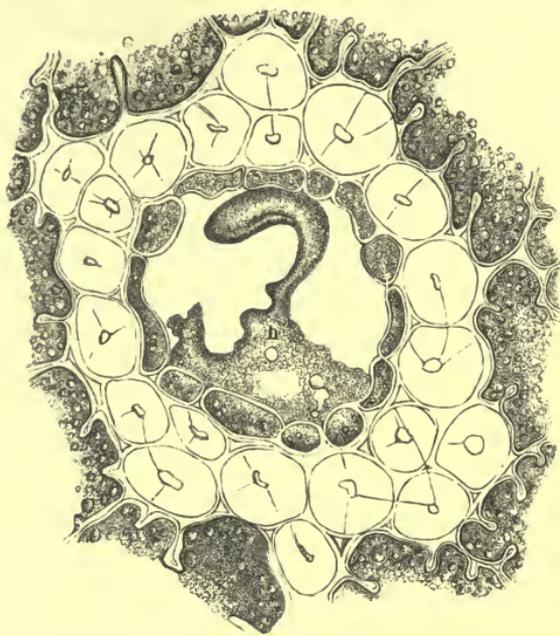


Fig. 31 (after Kreuz). Section of a resin-duct containing resin (*h*) from a leaf of *Pinus sylvestris*.

cellulose of the cell-wall; it is probably derived from the protoplasm, and is merely deposited in the cell-wall. The actual excretion is usually effected, in the case of superficial glands, by the rupture of the cuticle which is continuous over the gland, and the consequent escape of the contents (Fig. 32): in some cases the gland remains closed, and any volatile substances (ethereal oils) which may be present escape by evaporation.

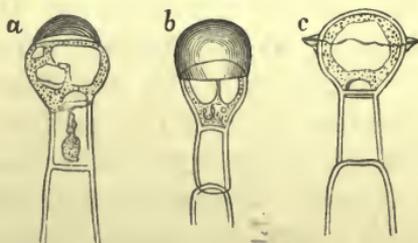


Fig. 32. (after de Bary.) Glandular hairs of *Primula sinensis*. The secretion collects between the cuticle and the deeper layer of the cell-wall. In *a* the accumulation of the secretion is commencing: in *b* it has become considerable: in *c* the cuticle has ruptured, allowing the secretion to escape.

The excretion of salts in solution (principally calcium and magnesium carbonates) is most commonly effected by means of a well-developed gland. A gland of this kind, from the leaf of *Saxifraga crustata*, is shewn in Fig. 19 (p. 91). The gland consists of a group of modified mesophyll-cells in connexion with the termination of a fibrovascular bundle: one or two water-pores are present in the epidermis immediately over it. We have seen that, under the action of the root-pressure, the gland excretes water. The excreted water collects in the depression at the margin of the leaf at the bottom of which the gland lies, and as the water evaporates the salts which it holds in solution are left behind in the solid form. This solid residue is prevented, for a time at least, from filling up the water-pores (Fig. 19, *b*), which are present upon the surface of the pit and upon which the salts are especially deposited. The margin of the leaf of this plant is marked by a series of mineral aggregations formed in this way, resembling beads, each of which corresponds to a gland. Glands of this kind are commonly present, though they are not so well-developed, in many allied plants belonging to the Saxifragaceæ and Crassulaceæ.

In other cases these salts appear to be excreted by ordinary epidermal cells. In certain Ferns (various species of *Polypodium* and *Aspidium*) scales of calcium carbonate are formed on the surface of depressions in the surface which are situated immediately over the terminations of fibrovascular bundles. Similar scales occur also on the leaves and herbaceous stems of various Plumbaginaceous plants, but in these they bear no relation to the fibrovascular bundles. In these cases no glands, like that described above, are present; it is therefore to be concluded that the epidermal cells themselves excrete the calcium carbonate.

It not unfrequently happens, however, that plants excrete substances other than waste-products, but this has the effect of securing indirect advantage to the plant. In the great majority of flowers there are glandular organs which excrete a watery fluid holding principally sugar in solution; the organs are termed *nectaries*, and the excretion *nectar*. A

nectary has essentially the same structure as the water-gland described above. It consists of a group of glandular cells situated in close relation to the terminations of one or more fibrovascular bundles, the only important difference in structure being this, that whereas the water-gland is sunk in the tissue and is covered by the epidermis, the nectary has a large free surface, so that the nectar is at once poured out on the surface. The difference in function, to which attention has already been directed (p. 101), is this, that the excretion of the nectar is independent of the root-pressure, whereas the excretion by the water-gland can only take place under the influence of the root-pressure.

Another instance of an excretion of this kind is afforded by the carnivorous plants. The glands of the leaves of these plants excrete a watery liquid which holds in solution a peptic ferment and one or more organic acids. The structure of the glands is different in different plants. In *Drosera* the gland is borne at the end of a filament (tentacle). It consists (Fig. 33) of a group of tracheïdes which are connected with the fibrovascular tissue of the leaf by a bundle which runs up the filament: the group of tracheïdes is surrounded by one or two layers of parenchymatous cells, and over these is the epidermis. In *Dionæa*, *Pinguicula*, the gland is a modified hair consisting of a group of cells borne upon a short stalk; in *Nepenthes* it is sessile (Kurtz, Wunschmann). In *Darlingtonia* and *Sarracenia* there are, according to Batalin, no specialised glands, but the effect of the contact of organic matter (insects, meat, etc.) with the cells of the lower part of the pitcher is to cause the excretion of some substance (probably the digestive excretion) between the cuticular and the deeper layers of the cell-wall of the cells which have been touched, and this is followed by the rupture of the cuticular layer. This rupture has the effect not only of bringing the excretion into relation with the introduced organic matter, but also of enabling the cells which have thus lost their cuticle to absorb the organic matter.

The use of the nectar is to attract insects, and thus to secure cross-fertilisation. The position of the nectary in a flower is usually such

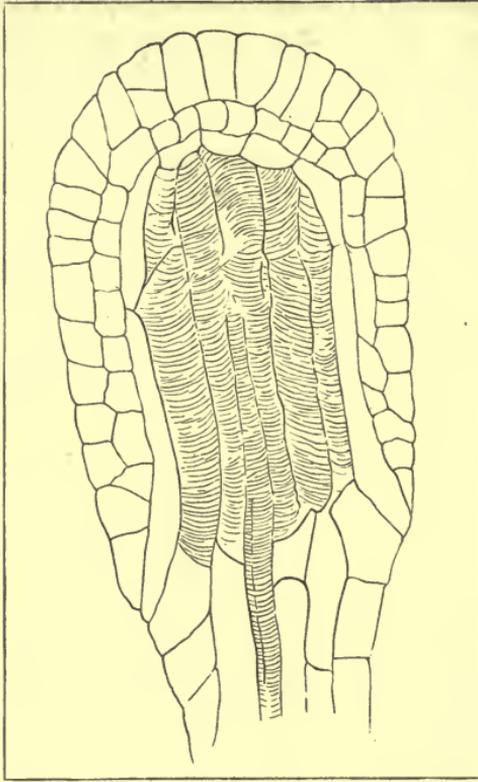


Fig. 33 (after Warming). Gland of *Drosera*.

that when an insect visits the flower, it must, in order to reach the nectary, touch the anthers and carry off with it some of the pollen, and that, when the insect visits another flower of the same kind, the pollen which it carries with it must be rubbed off upon the stigma.

The use of the excretions of carnivorous plants is to dissolve the organic matter (usually insects) which has been deposited on the leaves or in the pitchers, so to bring it into a form in which it can be absorbed.

Many of the waste-products are not excreted, but remain in the plant. Thus the resins are indeed excreted by the cells which line the resin-passages, but these passages have no aperture on to the surface. Similarly, the caoutchouc and gutta-percha which are contained in the laticiferous tissue of certain plants have no means of egress. This is true of the tannic acid, of the calcium carbonate (to some extent) and oxalate, of the alkaloids, and of silica.

The waste-products are usually deposited in the cells in which they are produced, or in intercellular spaces (*e.g.* resin passages): there are thus two kinds of *receptacles for excretions*, cellular and intercellular. Some of them (calcium carbonate and oxalate, alkaloids) are especially deposited in parts of the plant which are deciduous, such as leaves, fruits, seeds, and bark. Calcium carbonate and oxalate are deposited usually in the form of crystals either in the cell-wall or in the cell-cavity, and silica in the cell-wall. Allusion has already been made (p. 22) to the presence of these substances in the cell-wall, especially to the deposition of calcium carbonate in crystaloliths (Fig. 34); these bodies are apparently peculiar

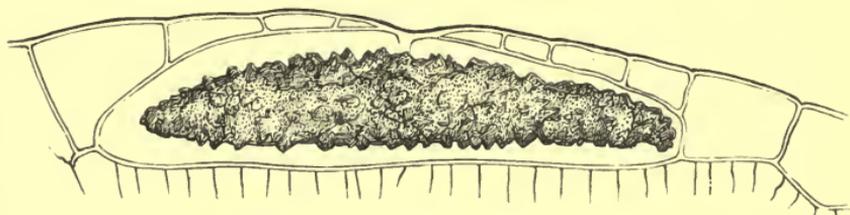


Fig. 34 (after de Bary). Cystolith from the leaf of *Urtica macrophylla*.

to the orders Urticaceæ, Euphorbiaceæ, and Acanthaceæ. Molisch has observed that calcium carbonate is commonly to be found in the cells and vessels of the heart-wood (duramen) of dicotyledonous trees. Calcium oxalate is deposited in cells as either single crystals or a cluster of crystals belonging to the quadratic system ($\text{CaC}_2\text{O}_4 + 2\text{H}_2\text{O}$), or in groups of parallel prismatic crystals (raphides), resembling a bundle of needles, belonging to the clinorhombic system ($\text{CaC}_2\text{O}_4 + 6\text{H}_2\text{O}$). Sometimes the crystals, belonging to either system, are arranged in a radiate manner so as to form a sphero-crystal, as in the hyphæ of *Phallus caninus*, a Basidiomycetous Fungus.

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LECTURE XIII.

METABOLISM (*continued*).

8. *The Supply of Energy.*

OUR consideration of the metabolism of plants will have made it evident that the various chemical processes involve an expenditure of energy: from this it follows that the continuance of these processes, in other words, the maintenance of the life of the plant, is dependent upon a supply of energy. The supply of energy will form the main subject of the present lecture, but we may conveniently consider in connexion with it the general relations of light and of heat to plant-life.

In the case of animals, the food affords the principal supply of energy. It consists for the most part of complex organic substances which represent a considerable amount of potential energy, and when these substances are decomposed in the body, this potential energy appears in the kinetic form. This holds good also with reference to plants which are destitute of chlorophyll, for their food necessarily includes, like that of animals, complex organic substances. But with plants which possess chlorophyll the case is entirely different. We have learned (p. 121) that their food consists of simple inorganic substances which do not represent any considerable amount of potential energy; from these simple substances green plants build up complex organic substances which do represent a considerable amount of potential energy, substances which serve directly or indirectly as the food of all living organisms whatsoever which do not contain chloro-

phyll: it is evident, therefore, that green plants must be largely supplied from without with kinetic energy in some form or other.

We have already noticed more than once that the metabolic processes of plants are materially affected by external conditions, especially by the presence or absence of light, and by variations in the temperature of the surrounding medium. A somewhat elevated temperature is, in fact, essential to the active life of all plants, but light is essential only to the life of those plants which contain chlorophyll. This naturally suggests that the energy requisite for the life of plants is obtained by them either in the form of heat or of light. With regard to heat, its importance is not that it affords a continuous supply of energy to be converted into work in the plant, but that it determines the initiation of chemical processes which are carried on by means of energy obtained from other sources: hence the supply of energy in the form of heat is relatively small, as compared, on the one hand, with the supply of (potential) energy afforded by their food to plants which do not possess chlorophyll, and on the other hand, with the supply obtained in the form of light by plants which do possess chlorophyll. With regard to light, we know of a mechanism in plants, but only in plants possessing chlorophyll, by which the radiant energy of the sun's light is converted into work: light then is the special form in which kinetic energy is supplied to green plants. But in addition to its importance in the constructive metabolism of green plants, light has, as we shall see, a modifying influence upon certain of the metabolic processes, the nature of which is not in all cases perfectly understood. We will now study in detail the relation of light and heat to the metabolism of plants.

Light. We learned in a previous lecture (p. 157) that a green plant is incapable of constructing organic substance from the materials of its food unless it is exposed to light: and not only does it not increase in weight, when in darkness, but it loses weight in consequence of the exhalation of carbon dioxide and aqueous vapour in respiration (p. 195). Prolonged

exposure to darkness must, therefore, eventually prove fatal to the plant, the length of the time being determined by the amount of reserve plastic material which the plant possesses. On the other hand, adequate exposure to light enables the green plant to assimilate its food, and thus not only to make good the loss due to respiration, but to increase in weight.

The foregoing statements are well illustrated by some experiments of Boussingault and of Sachs.

1. (Boussingault.) Two beans of known weight were sown in moistened pumice-stone on June 26; they were allowed to grow until July 22, the one exposed to daylight, the other in the dark. The weights of the seedlings were then determined.

<i>Plant in light.</i>			<i>Plant in darkness.</i>		
Weight of seed	...	0·922 grme.	Weight of seed	...	0·926 grme.
„ seedling	...	1·293 „	„ seedling	...	0·566 „
Gain		0·371 „	Loss		0·360 „

2. Boussingault ascertained with Oleander-leaves that for one square metre of leaf-surface 6336 cub. centim. of carbon dioxide were decomposed during 12 hours' exposure to daylight, whereas only 396 c.c. of carbon dioxide were exhaled during twelve hours' darkness. It is evident from this that the gain in weight during the twelve hours of daylight was greater than the loss during the twelve hours of darkness.

3. Sachs sowed four seeds of *Tropæolum majus* in each of ten pots; the seedlings appeared above the soil on April 28. They were then treated as follows: I. two pots were placed in a dark cupboard; II. two pots were so placed in a room that they received only diffuse daylight; III. two pots were so placed in a window that they received diffuse daylight for seven hours daily; IV. two pots were so placed in a window that they received diffuse daylight and often direct sunlight for about six hours daily; V. two pots were so placed in a window that they received as much light, both diffuse daylight and direct sunlight, as possible. On May 22 the weights of the plants in the different pots were determined.

	I.	II.	III.	IV.	V.
Weight of seeds	0·394	0·394	0·394	0·394	0·394 grme.
„ seedlings	0·238	0·264	0·301	0·480	1·292 „
Loss	0·156	0·130	0·093	Gain 0·086	0·898 „

A plant which does not possess chlorophyll is capable, on the contrary, of assimilating its food in the absence of light.

The reason of this is that the food, consisting as it does largely of complex organic substances, supplies, on being decomposed in the body, the necessary energy for the carrying on of the assimilative or constructive processes. Such a plant is therefore independent of any supply of kinetic energy from without, except in so far as it is dependent upon an adequate temperature for the initiation of the decomposition of its organic food. A plant which does possess chlorophyll is incapable of constructing complex organic substances out of the materials of its food in darkness, for it then has no supply of energy by means of which the necessary chemical processes could be effected. It can only do this when it is exposed to light, and can absorb the necessary radiant energy. It is true that a green seedling or a shoot can live for a time in darkness, and also increase in weight, but it does so, not by assimilating *food-materials*, but at the expense of complex organic *reserve-materials* stored up in some depository with which it is in connexion. Thus, a shoot may grow from a potato-tuber to a great length in the dark, but this is accompanied by a decrease in absolute weight; that is, that the dry weight of the shoot and of the tuber, taken together, is less than the original dry weight of the tuber. The same is true, as shewn above, of seeds and seedlings.

In a previous lecture (IX. p. 157) it was pointed out that it is by means of their chlorophyll that green plants are enabled to avail themselves of the kinetic energy of the sun's rays; we will now discuss this point more fully than we did then. It was then mentioned that there are two principal conflicting views as to which of the rays of the spectrum are the most efficacious in promoting the decomposition of carbon dioxide by the chlorophyll-corpuscles of plants, that, namely, of Draper and of Pfeffer, according to which the yellow rays are the most active, and that of Lommel, Timiriaseff, and others, according to which it is the rays which correspond to the most conspicuous absorption-band (band I, see plate) of the chlorophyll-spectrum, the rays, that is, between the lines B and C of the solar spectrum, at the junction of the orange and of the red, which are the most active. The obvious difficulty

which presents itself in considering Draper's and Pfeffer's view is that, inasmuch as the yellow rays are not absorbed by chlorophyll, it is difficult to see in what way chlorophyll assists in the conversion of these rays into work in the chlorophyll-corpuscle. This is a difficulty which has never yet been explained, and it is one which appears to be hardly susceptible of any satisfactory physical explanation. The view held by Lommel and by Timiriaseff is, *a priori*, intelligible, for the rays in question are absorbed by the chlorophyll, and it may be inferred that they are converted into chemical work after absorption. Moreover, the experimental evidence is decisively in favour of the latter view. In his experiments Timiriaseff was careful to work with a pure spectrum, that is, he endeavoured to prevent as far as possible any admixture of the rays of different colours, so that the red portion of his spectrum consisted almost exclusively of red rays, the yellow of yellow rays, and so on. Draper and Pfeffer clearly worked with impure spectra, for in their experiments the aperture of the slit by which the light was admitted was very wide in order to increase the intensity of the illumination. Hence in their spectra there was a considerable admixture of rays of different colours. Their observations are doubtless accurate enough, but their conclusions as to the relative efficacy of the different rays of the spectrum in the decomposition of carbon dioxide are vitiated by the imperfection of the method by which their data were obtained. Timiriaseff's results have received important confirmation by the ingenious experiments of Engelmann, to which reference has been already made (p. 156).

Engelmann ascertained that certain Schizomycetes (*Bacterium termo*, Cohn) only exhibit their movements in the presence of free oxygen; if a drop of water containing these organisms be examined under the microscope, the Bacteria collect especially at the edges of the cover-glass and there continue their movements, and those which remain at some distance from the edges soon cease to move. He observed also that if a cell containing chlorophyll, such as a small Alga, be introduced into such a preparation, the Bacteria collect around it, provided, of course, that the illumination is sufficiently intense to ensure the evolution of oxygen by the chlorophyll. By observing the green Alga in the different regions of

a relatively pure spectrum produced by means of a microspectroscope, he ascertained that the Bacteria collected especially in the region between the lines B and C, that is, at the junction of the orange and red, and that there was a secondary maximum of aggregation in the blue just beyond the line F: these regions coincide with the most marked absorption-bands of the chlorophyll-spectrum. Inasmuch as the collection of the Bacteria in these regions is an indication that oxygen is being evolved there, these observations afford most valuable support to the view that those rays are the most active in the decomposition of carbon dioxide which correspond in position to the most conspicuous absorption-bands in the chlorophyll-spectrum.

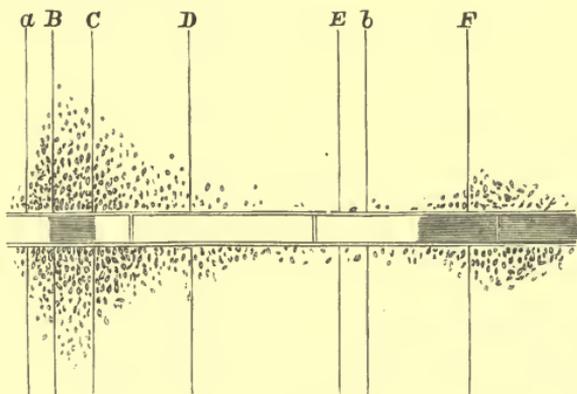


FIG. 35 (after Engelmann). A portion of a *Cladophora*-filament seen under the microscope in the solar spectrum, the chlorophyll-corpuscles being omitted from the drawing. The principal lines of the spectrum are indicated. The aggregation of the motile Bacteria about the filament is seen to be greatest between the lines B and C.

It has been mentioned (p. 152) that Engelmann is of opinion that some of the colouring-matters which are characteristic of certain Algæ (*phycoxanthin*, *phycocyanin*, and *phycoerythrin*) have the same function as chlorophyll. He obtained with various brown, bluish-green, and red Algæ, results similar to those given above with reference to chlorophyll, though the points of maximum aggregation were not the same inasmuch as the absorption-spectrum of these colouring-matters is not the same as that of chlorophyll. Thus in the case of blue-green Algæ the maximum of aggregation is not in the red-orange, but in the yellow, and in the case of red Algæ, in the green.

Engelmann was enabled to estimate quantitatively the relative activity of the different rays of the spectrum by the following method. He observed the moment when, in each successive region of the spectrum, the movement of the Bacteria in the neighbourhood of the Alga began, and then ascertained the width of the slit. The width of the slit is a measure of the intensity of the light; therefore the wider the slit the

greater is the intensity of light required to produce the movements of the Bacteria in any given region of the spectrum, or, in other words, to cause an evolution of oxygen. Assuming that the evolution of oxygen is proportional to the intensity of the light, that is, to the width of the slit, the relative activity of the various regions of the spectrum will be inversely proportional to the width of the slit. The maximum may be taken as 100.

The following are some of the results obtained in this way. The observations were made with a prism-spectrum, but they are reduced to the diffraction-spectrum.

I. Green Cells (Sunlight).

a	$B\frac{1}{2}C$	$C\frac{1}{2}D$	D	$D\frac{1}{2}E$	$E\frac{1}{2}b$	$E\frac{1}{2}F$	F	$F\frac{1}{2}G$	G
6.38	100	81.2	55.1	41.2	36.3	69.9	86.1	80.9	47.2

II. Brown Cells (*Diatoms*) (Sunlight).

13.3	94.6	77.0	77.1	100	89.3	79.3	75.9	53.8	36.6
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III. Bluish-green Cells (*Oscillatoria*, *Nostoc*) (Sunlight).

—	85.3	96.7	100	—	44.4	—	21.2	—	—
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IV. Red Cells (*Florideæ*) (Gaslight, calculated to Sunlight).

a	$B\frac{1}{2}C$	$C\frac{1}{2}D$	D	$D\frac{1}{4}E$	$D\frac{1}{2}E$	$E\frac{1}{2}b$	$E\frac{1}{2}F$	F	G
1.9	15.4	31.8	50.5	100	79.4	62.2	36.5	46.4	19.1

We learn, then, that the chlorophyll (and the other colouring matters above alluded to) absorbs certain rays in different parts of the visible solar spectrum, some to a greater and some to a less extent, and that this absorption is the means by which the kinetic energy of the rays is made available for the work of constructive metabolism. It is of interest to note, as Timiriaseff does, that the maximum absorption of chlorophyll coincides exactly with that portion of the spectrum in which, according to Langley, the maximum of energy falls. The whole of the kinetic energy thus absorbed is not transformed into work, but still the chlorophyll-corpuscule appears to be a very perfect machine in this respect, for, according to Timiriaseff's calculations, it transforms into work as much as forty per cent. of the absorbed energy.

In concluding this part of the subject we will briefly consider the relation between the intensity of the light and the decomposition of carbon dioxide. It is obvious that there must be a minimum intensity at which this process first

begins to take place, and the results of a great number of observers all tend to prove that a feeble light is less active than one of greater intensity. It is probable, as Sachs points out, that there is an optimum intensity above which the activity of the process decreases, but it is a question whether or not, in the case of any given plant, this optimum intensity is ever reached or surpassed by the sunlight: it appears, however, that, in some of his experiments, this optimum was observed by Famintzin.

In the preceding remarks upon the action of light in enabling plants to decompose carbon dioxide, our attention has been confined to sunlight; a few words may be added with regard to light derived from artificial sources. The experiments of Déhérain and Maquenne, of Famintzin, and of Engelmann, made with light supplied by various forms of lamps, shew that, provided the light is sufficiently intense, carbon dioxide is decomposed and oxygen evolved; this is doubtless true also of the electric light, according to Siemen's observations.

Inasmuch as light exercises so great an influence upon the constructive metabolism of green plants, it may be inferred that it must indirectly affect the absorption of mineral food-materials by the roots. This has been shewn to be the case by Rudolph Weber, and he finds further, as might be expected, that rays of different degrees of refrangibility have different effects in this respect. The greatest absorption of ash-constituents took place, he found, in white light, it was considerable in (impure) yellow light, very slight in (impure) violet light, and least of all in green light.

Weber experimented by growing peas in cases covered with glasses of different colours, having ascertained in each case by means of the spectroscope the composition of the light which passed through the glass, which was never monochromatic.

The following is a brief summary of the most important of his results:

Plants grown in	Increase in organic substance	Increase in ash-constituents
Sunlight	100	100
Red light	35.5	41.4
Yellow "	82.6	62.0
Blue "	22.4	33.3
Violet "	14.5	5.3

The following table gives an account of the different kinds of ash-constituents absorbed in light of different colours. In each case 100 seedlings were analysed, and the weights given are in grammes.

Light	Total dry weight	Total Ash	Potash	Soda	Lime	Magnesia	Ferric oxide	Phosphoric acid	Sulphuric acid
White	21.506	2.746	1.044	0.023	0.689	0.220	0.020	0.359	0.352
Red	12.573	1.683	0.710	0.018	0.306	0.119	0.017	0.289	0.224
Yellow	14.992	2.007	0.797	0.014	0.454	0.143	0.034	0.342	0.223
Green	7.603	1.032	0.430	0.015	0.138	0.064	0.011	0.224	0.150
Blue	10.850	1.556	0.663	0.014	0.328	0.095	0.023	0.235	0.198
Violet	9.453	1.116	0.431	0.014	0.191	0.081	0.016	0.225	0.158
Darkness	10.514	1.064	0.473	0.015	0.130	0.070	0.022	0.216	0.138
100 Seeds	22.565	0.659	0.333	0.014	0.017	0.051	0.001	0.215	0.028

It will be noticed that when the plants were exposed to those rays of light (impure yellow) which, as we have seen, are the most active in promoting constructive metabolism, the essential ash-constituents are absorbed in largest quantity.

We will now pass on to consider the relation of light to the destructive metabolism of plants.

Inasmuch as the respiration of a plant affords an indication of the activity of its destructive metabolism, we will enquire, in the first instance, if it has been discovered that respiration proceeds more or less actively in light than in darkness. With regard to the absorption of oxygen, it appears from the researches of Mayer and von Wolkoff—and theirs seem to be the only direct observations bearing upon this point—that the absorption of oxygen by seedlings of various plants (wheat, Buckwheat, *Tropæolum*), is slightly more considerable in light than in darkness. Similar results have also been obtained by Pauchon. From this we may infer that light does not promote the taking up of oxygen by the living protoplasm, for, were this the case, the increase in the amount of oxygen absorbed would be much more marked: the slight increase in the amount of oxygen absorbed in the light is probably to be ascribed to the influence of light in promoting the oxidation or oxidative decomposition of any readily oxidisable substances which may be present in the cells. To these latter points we shall return in a short time. Coming now to the other factor in respiration, the exhalation of carbon dioxide, we find that, so far as plants which do not possess chlorophyll are concerned, there is no evidence that light has any material influence upon it. Cahours found a slight increase in the amount of carbon dioxide exhaled by flowers when exposed to light, and Drude observed in his experiments with *Monotropa* that in many instances more carbon dioxide was evolved during the night than during the day. Detmer and Wilson, however, both failed to find that the exhalation of carbon dioxide in light is more active than it is in darkness. In the case of a plant which possesses chlorophyll, it is difficult to determine directly the effect of light upon the exhalation of carbon dioxide on account of the decomposition of carbon dioxide which is of course going on in the chlorophyll-corpuscles. It would appear at first sight from Borodin's researches that the exhalation of carbon dioxide by green plants is much

more active in light than in darkness. He ascertained, namely, that when a branch with green leaves is placed in the dark after having been previously exposed to light, the exhalation of carbon dioxide rapidly diminishes until it becomes very inconsiderable, and it then remains approximately constant. After a short re-exposure to light, the activity of the exhalation of carbon dioxide by the branch is perceptibly increased. It might be concluded from this that light affects the destructive metabolism of plants and parts of plants which do not possess chlorophyll otherwise than it affects that of plants and parts of plants which do possess chlorophyll. But such a difference does not really exist: the apparent paradox is susceptible of a simple explanation. In a branch, such as those with which Borodin experimented, there is no considerable deposit of reserve-material; destructive metabolism is carried on at the expense of the organic substances which are being formed in the leaves; hence the activity of the destructive metabolism is determined by the activity of the constructive metabolism: in the dark the latter cannot be carried on, and hence the activity of the former, as indicated by the evolution of carbon dioxide, must soon diminish.

We learn, then, that light has very little effect upon the respiration of plants; it appears to be slightly favourable to the absorption of oxygen, but it has no direct effect in promoting the exhalation of carbon dioxide. We may go on to say that the destructive metabolism of plants, as a whole, is not materially affected by light, though, as we shall shortly see, light has some influence upon certain of the processes of destructive metabolism.

We may digress for a moment to consider the bearing of the conclusion to which we have just come upon Pringsheim's theory of the function of chlorophyll (p. 157). Pringsheim is of opinion that light promotes the respiration, in other words, the destructive metabolism of plants, and he believes that the function of chlorophyll is to absorb those rays which are most active in promoting destructive metabolism, and thus to render possible the performance of the various constructive

processes. But, as we have just learned, there is no evidence to shew that light has any such influence on destructive metabolism, still less is there any evidence to shew that the rays which are absorbed by chlorophyll are especially active in this respect.

The most obvious effect of light upon the metabolism of plants is its influence in causing the formation of colouring-matters. The most conspicuous example of this is afforded by chlorophyll. Chlorophyll is usually not formed in the absence of light (see p. 239); I say, usually, for, according to Sachs, chlorophyll is formed in the cotyledons of some Conifers and in the leaves of Ferns in complete darkness, provided that the temperature is sufficiently high. If a seed of a green plant be made to germinate in the dark, the seedling will present, amongst others, this peculiarity, that it is not green, but is of a pale yellow colour, or it may be quite white. Such a plant is said to be *etiolated*. The yellow colour of an etiolated plant is due to the presence of a yellow colouring-matter, *etiolin*, in its corpuscles; the white colour may be due to the absence of any colouring-matter, but it appears probable that the corpuscles contain a colourless chromogen, termed by Sachs, *leucophyll*, which under appropriate conditions gives rise to chlorophyll.

The formation of chlorophyll will take place in light of very low intensity, but still, as Wiesner's experiments shew, there is a lower limit of intensity below which light is inactive. It is true that a great many observers agree in stating that the requisite degree of intensity is different for different plants, but this difference must not be taken to mean that the chemical process of the formation of chlorophyll can go on at a low intensity of light in some plants and only at a relatively high intensity in others: it is due, as Wiesner points out, to the fact that other conditions are not the same in all cases; for instance, leaves differ in the thickness of their epidermis, in the presence or absence of hairs, in their mode of veneration, etc., and in proportion as the access of light to the mesophyll cells is interfered with by any of these structural peculiarities the formation of chlorophyll will be

retarded. On the other hand it appears that the process is retarded when the light is very intense, for it has been frequently observed that the leaves of etiolated plants become green more rapidly in diffuse daylight than in sunshine.

It appears from the researches of Wiesner and of Mikosch that the formation of chlorophyll in an etiolated plant does not commence directly the plant is exposed to light, but that a longer or shorter time must elapse before any perceptible amount of chlorophyll is produced. They found also, in harmony with the foregoing, that the effect of exposure to light does not cease directly a plant is placed in darkness, but that the formation of chlorophyll is continued for a time in the dark. This mode of action of light they term photo-chemical-induction, an expression suggested by Bunsen and Roscoe.

With regard to the relative efficacy of the different rays of the spectrum in the formation of chlorophyll, it appears, from Wiesner's researches, that all the rays between Fraunhofer's lines B and H promote it to a greater or a less extent. Both Gardner and Guillemin found that seedlings turned green more rapidly in the yellow than in any other part of the spectrum, and this result has been confirmed by Wiesner. Wiesner has observed, namely, that, in diffuse daylight, chlorophyll is formed first in plants exposed to white light, then in those in yellow light, then in those in green light, then in those in red light, and finally in those in blue light. But these results hold only for light of low intensity, for he observed that when the light is very intense the formation of chlorophyll takes place earlier in blue than in yellow light. The reason of this is that in intense light chlorophyll undergoes decomposition, and this decomposition goes on most actively in yellow light. We shall recur to this point subsequently.

Guillemin states that the invisible rays of the spectrum, both the ultra-red and the ultra-violet, induce the formation of chlorophyll. Wiesner, who has re-investigated this point, fails to confirm Guillemin's statement as regards the ultra-red rays, and leaves it still uncertain whether or not it holds with reference to the ultra-violet rays.

The relation of light to the formation of chlorophyll has been investigated chiefly by means of experiments with etiolated seedlings, but it must not be assumed that the process takes place once and for all in the life of a plant. There can be little doubt that the chlorophyll of a plant is always undergoing decomposition, and it is therefore necessary that the formation of chlorophyll should also be continually going on. Sachs has pointed out that when green plants are kept for some time in darkness the leaves gradually turn yellow. The explanation of this fact is this, that, in the dark, the decomposition of the chlorophyll continues, a yellow colouring-matter (see *infra*) being the product, whereas no formation of fresh chlorophyll can take place. Light is necessary, therefore, not only for the first formation of chlorophyll in an organ, but also for the maintenance of the green colour during the whole life of the organ.

It appears probable, as Wiesner and others suggest, that chlorophyll is formed from etiolin. Wiesner, amongst other experiments on the subject, observed that young Pumpkin-seedlings which contain no etiolin turn green, when exposed to light, much more slowly than older seedlings which contained etiolin abundantly.

Elfvig has made the interesting observation that light promotes the formation of etiolin. On exposing etiolated seedlings to light for short periods at a temperature which was too low to admit of the formation of chlorophyll, he noticed that their leaves assumed a deeper yellow colour, and he ascertained that the change of colour was due to the presence of a larger quantity of etiolin. He found that the rays of low refrangibility (yellow, orange, and red) are those which are especially active in the process. From this we may infer that the formation of etiolin is always going on in actively living chlorophyll-corpules; this accounts for the fact mentioned in previous lectures (pp. 154, 241) that etiolin is always found to be present in alcoholic solutions of chlorophyll; and it is probable that chlorophyll is formed from the etiolin when the conditions are favourable.

Although light is, as we have seen, in most cases an

essential condition for the formation of chlorophyll, yet it also promotes its decomposition. This is proved to a certain extent by some of the facts with which we have recently become acquainted, namely, that the leaves of etiolated plants become green more rapidly in diffuse daylight than in direct sunlight, and that, when the light is intense, the formation of chlorophyll takes place earlier in blue than in yellow light; but more direct evidence is not wanting. It has been frequently observed, especially in the case of Conifers, that those leaves of the plant which are most exposed to sunlight in summer have a yellowish tinge when compared with leaves which are shaded to some extent, and they may become quite yellow. The green colour of these yellow leaves may however be restored, as Batalin has shewn, by covering them with something, a sheet of white paper for example, which diminishes the intensity of the light which reaches them. The yellow colour which leaves assume in the autumn is doubtless due to the alteration of the chlorophyll under the influence of light, for it has been observed that the autumn colouration makes its appearance first in those leaves which are most fully exposed to light (see, for instance Haberlandt, Askenasy). We have, then, two processes going on in the chlorophyll-corpuscle under the influence of light, the formation of chlorophyll, and the decomposition of chlorophyll: when the former is the more active then the corpuscle is green, when the latter, then the corpuscle becomes more and more yellow. The summer yellowness, as we may term it, appears to be due solely to the fact that intense light promotes rather the decomposition than the formation of chlorophyll; the autumnal yellowness, on the other hand, appears to be due to other causes, for in the autumn the light is not usually so intense that it would cause the decomposition of the chlorophyll to exceed its formation in the corpuscle. The first of these other causes is, in the case of deciduous leaves at least, that the vitality of the leaf is diminishing as it approaches the term of its existence, that is, that all its various functions, including of course the formation of chlorophyll in its corpuscles, are being carried on with a rapidly decreasing activity.

In the case of persistent leaves, the vitality is also diminishing, but the diminution is due rather to the unfavourable external conditions, especially the low temperature, which prevail in autumn. It has been already mentioned (p. 239) that a certain temperature is necessary to the formation of chlorophyll, and if this condition is not complied with, as is usually the case in autumn and winter, no chlorophyll will be formed and the leaves will become and remain yellow. When the temperature rises in the spring the yellow leaves become green again, as von Mohl first observed, that is, the formation of chlorophyll is resumed. This may be effected even in the winter by placing the plants in a warm atmosphere; Askenasy found, for example, that when a branch of Thuja with yellow leaves was kept in a warm place they slowly became green.

It appears that the conversion of chlorophyll into the yellow colouring-matter xanthophyll or phylloxanthin (see p. 241) is effected by a process of oxidation. S n bier observed long ago that solutions of chlorophyll when exposed to light lose their green colour, and Gerland and N. J. C. M ller, in repeating this observation, have found that the presence of oxygen is essential to the process. The influence of light in promoting the oxidation of the chlorophyll is well illustrated by Pringsheim's observation that when chlorophyll-corpuscles are exposed to intense light they completely lose their colour in a few minutes provided that oxygen is present. It is doubtless to the continuous oxidation of chlorophyll in the plant that the constant presence of xanthophyll in solutions of chlorophyll is due. Sachs and Wiesner have further ascertained that the decolouration of a solution of chlorophyll goes on much more rapidly in intense than in feeble light, and that the rays of low refrangibility are more active in producing it than those of high refrangibility.

In many cases leaves assume other colours than yellow in the autumn. Very commonly they become red. This is due to the presence of a red colouring-matter (erythrophyll) or probably of a mixture of colouring-matters, in solution in the cell-sap. The formation of erythrophyll appears to be dependent to some extent upon light, but the exact conditions have not been fully investigated (see von Mohl, Treviranus, Wiesner,

Batalin, G. Haberlandt). In other cases leaves assume a leathery brown colour: this is well-marked in some Conifers, such as various species of Thuja, Yew, *Sequoia gigantea*. This colouration is only produced after the plants have been exposed to frost (Kraus, Haberlandt), but it is also in some way connected with the influence of light. It appears to be due to a chemical alteration of the chlorophyll by the action of some substance (possibly an acid) contained in the cell-sap.

Sénébier observed that if strips of tin-foil be fastened on pears and apples, the natural red colour which these fruits assume on ripening is not produced in those parts which have been covered.

It will be remembered that, when we were considering the effect of light upon respiration, it was mentioned that it tends to promote the absorption of oxygen. The oxidation of chlorophyll is one instance of this, but it is probably only one of many. De Saussure observed that light is favourable to the absorption of oxygen by oil of Lavender, and Jodin has found this to be also the case with ethereal oils and solutions of tannin. It has been suggested (p. 236) that resin is formed in the living plant by the oxidation of an ethereal oil (terpene), but nothing is known as to the influence of light upon the process.

The formation of the other colouring-matters of plants, those of flowers for example, appears to be less dependent upon the action of light than is the formation of chlorophyll. Sachs observed, in his experiments upon etiolation, that in all the plants which came under his observation, the flowers which were produced in darkness were coloured in much the same manner as those produced in light. Askenasy has however found that this is by no means always the case, but that the colouration of flowers is in many cases much modified or even absent when the plants bearing them are kept in darkness. There are not at present sufficient data upon which to base an explanation of the diversity of behaviour of flowers in this respect, but it appears to depend upon their particular hue. Sorby has observed that the red colouring-matter of flowers (which is probably identical with erythrophyll) is formed in smaller quantity in relatively weak than in relatively strong light.

Comparatively little is known as to the influence of light

upon the formation of any other waste-products. It seems to be a well-established fact that light is of importance in the formation of alkaloids, for tropical plants which produce these substances in abundance in their normal habitat produce only small quantities when grown in hot-houses in this country. On the other hand it appears that too intense light is unfavourable to the accumulation of alkaloids for it has been observed in certain cases that plants which have grown in the shade are richer in alkaloids than others which have been exposed to the full glare of the tropical sun. This is probably due to some decomposition of the alkaloids under the influence of intense light. Similarly light appears to be unfavourable to the accumulation of organic acids in the plant, for both Wiesner and de Vries have observed that etiolated plants are richer in organic acids than plants of the same kind which have been grown in light. This is in harmony with the facts mentioned in a previous lecture with reference to Mayer's observations on succulent plants (p. 232), from which it appears that light causes the decomposition of organic acids in the plant. Further, Rauwenhoff found that the cells of an etiolated *Polygonum cuspidatum* contained no crystals of calcium oxalate whereas they are abundant in green plants, and that the amount of tannin in etiolated leaves and branches of *Polygonum Bistorta*, *Rosa centifolia*, and *Vicia Faba* was much smaller than in similar organs which had been developed in the light.

Finally, it appears probable that light also influences the metabolism of plants by affecting the action of unorganised ferments. Nièpce de St Victor and Corvisart found that starch was converted into sugar more rapidly in light than in darkness, and Mayer observed that whereas the action of invertin and of pepsin was unaffected by light, the action of rennet (chymosin) was distinctly retarded. It is however impossible at present to form any estimate of the importance of these facts in the metabolism of plants.

Heat. It is a well-established fact that the temperature of the surrounding medium has an important influence upon

the activity of the metabolism of living organisms. This is especially evident in the case of animals. The metabolic activity of cold-blooded animals is directly dependent upon the temperature to which they are exposed, and Pflüger has shewn that even in warm-blooded animals the activity of metabolism varies with variations in the temperature of the surrounding medium. A remarkable illustration is afforded by the phenomenon known as "hibernation", exhibited even by certain warm-blooded animals, that is, that when the animal is exposed to a persistently low temperature its metabolism is reduced to a minimum. Plants behave in relation to temperature like the cold-blooded animals. When they are maintained at a low temperature they cease to exhibit any signs of life. The meaning of this is that, at a low temperature, the metabolic processes are arrested; but this arrest is not death, nor does it necessarily involve it, but, if the exposure to the low temperature be long continued, it may eventuate in death.

We may cite the following examples in illustration of the depressing effect of a low temperature upon the metabolic processes. De Candolle found that of the seeds of ten species of plants, those of one species only (*Sinapis alba*) germinated at 0° C.; and even in this case germination was much retarded, for whereas these seeds germinated at 0° C. after seventeen days, similar seeds germinated in sixteen days at a temperature of 1·90 C., and in four days at 5·70 C. Similar observations have been made by Sachs.

The minimum temperature for germination has been ascertained in certain cases. Sachs has made the following determinations, the minimum temperature being that at which a small proportion only of the total number of seeds germinated:

	Minimum
<i>Zea Mais</i>	9·4° C.
<i>Phaseolus multiflorus</i> ...	9·4 "
<i>Cucurbita Pepo</i>	14·0 "
Wheat	5·0 "
Barley.	5·0 "

The following determinations were made by Haberlandt :

	Minimum between
Buckwheat, Hemp, Oat, Rye, Rape, Wheat, } Barley, Flax, Pea	0°—4·8° C.
Sunflower, Maize	4·8°—10·5 „
Pumpkin, Tobacco	10·5°—15·6 „
Melon, Cucumber	15·6°—18·5 „

Hoffmann observed that the spores of many Fungi do not germinate when the temperature is near the freezing-point, and that those which do germinate do so very slowly : thus, spores of *Uredo Segetum* germinated at a temperature of 0·4—0·8 R. in six days, whereas they germinated in half a day at 13° R. Wiesner ascertained that the spores of *Penicillium glaucum* can germinate at 1·5° C., but that germination at that temperature is not followed by the development of a mycelium.

The effect of a low temperature upon individual metabolic processes is also well marked. It is well known, for instance, that the unorganised ferments are only active at a temperature considerably above 0° C. (Schützenberger). With regard to respiration it has been already pointed out (p. 198) that the absorption of oxygen and the evolution of carbon dioxide is less considerable at a low than at a relatively high temperature, and that the former process goes on more actively at low temperature than does the latter ; it appears that the zero-point for the absorption of oxygen is lower than that for the evolution of carbon dioxide. The actual zero-points for these processes have not been determined, but they are undoubtedly lower than that for growth in the case of any given plant. It was mentioned in a previous lecture (p. 239) that when normally green plants are exposed to a low temperature the newly-formed organs are yellow, that is, that chlorophyll is not formed in them. Sachs has determined the lowest temperature at which the chlorophyll-corpuscles turn green in the following plants : in *Phaseolus multiflorus*, in *Zea Mais*, in *Sinapis alba*, and in *Brassica Napus* at above 6° C. ; in *Pinus Pinea* and *canadensis* between 7° and 11° C. Again, the decomposition of carbon

dioxide with evolution of oxygen will not go on below a certain degree of temperature. Cloez and Gratiolet observed that it began in *Potamogeton* between 10° and 15° C., and in *Vallisneria* above 6° C., an observation which has been confirmed by Sachs. Boussingault detected an evolution of oxygen from leaves of the Larch at 0.5° — 2.5° C., and from those of meadow grasses at 1.5° — 3.5° C.: in the case of *Hottonia palustris* Heinrich found that bubbles of oxygen were first given off at 2.7° C. We may just repeat here that the absorbent activity of the roots and the activity of transpiration depend very much upon temperature (see Lectures IV. p. 52, and VII. p. 108).

We will now consider the modes in which exposure to cold causes the death of plants. It has been found, in the first place, that long continued exposure to a not very low temperature proves fatal. This fact has been ascertained by experiments made with seeds. It has been already pointed out (p. 172) that if seeds be kept for a long time they lose their vitality, and it appears that the same effect is produced by exposing them for a comparatively short time to a low temperature.

Haberlandt kept seeds of a number of plants for four months in a vessel surrounded by melting ice, and then sowed them at a temperature of 16° C. He found that seeds of the following plants had germinated to a certain extent during the four months :

Out of 300	Rye	seeds nearly all had germinated.
"	213 Hemp	" 30 " "
"	150 Vetch	" 3 " "
"	100 Pea	" 6 " "
"	245 Mustard	" 30 " "
"	305 Red Clover	" 29 " "
"	361 Lucerne	" 138 " "
"	200 Gold-of-Pleasure	" 1 " "

- a. Very slight elongation of radicle ; Rye, Hemp, Vetch, Pea.
- b. Considerable elongation of radicle ; Mustard, Red Clover, Lucerne, Gold-of-Pleasure,

and that seeds of the following had not germinated at all :

Wheat, Barley, Oat, Rye-grass, Buckwheat, Beet, Rape, Poppy, Flax, White Clover, Bean.

The seeds of the following plants germinated at the end of the four months at a temperature of 16°C . :

Out of 215 Rye	seeds	...	4 germinated.
„ 205 Hemp	„	...	76 „
„ 205 Mustard	„	...	2 „
„ 280 Lucerne	„	...	3 „
„ 452 White Clover	„	...	23 „

The seeds of the following did not germinate at this temperature :

Wheat, Barley, Oat, Rye-grass, Buckwheat, Beet, Gold-of-Pleasure, Rape, Flax, Poppy, Vetch, Lentil, Pea.

It has been found, in the second place, that exposure to a very low temperature for a short time is not necessarily fatal, and that the injury which a plant or any part of a plant sustains depends very much upon the proportion of water which it contains. The relation between the injurious effect of frost and the proportion of water in the cells exposed to it has been long known: it was definitely stated by A. P. de Candolle so long ago as 1832, but the first experimental determination of it appears to have been made by Göppert in 1830. He exposed seeds, some of which were dry, whereas others had been previously soaked in water, to a temperature of from -25°C . to -40°C ., and he found that only the moistened seeds were deprived of their germinating power by this treatment. Detmer has made similar observations with the same results.

A remarkable illustration of the extent to which dry seeds can withstand the injurious influence of extreme cold is afforded by C. de Candolle's observations. He exposed seeds of a number of species of plants for about two hours to a temperature of -80°C ., obtained by the evaporation of liquid sulphur dioxide and nitrous oxide, and he found that none of them lost their power of germinating.

With regard to other plants, Cagniard de la Tour ascertained that dry Yeast may be exposed to the temperature of solid carbon dioxide (-60°C .) without being killed, whereas, in the moist state, a temperature below -50°C . proves fatal to it: Cohn found that Bacteria were not killed by exposure for five hours to a temperature of -10°C . which sank, sometimes, as low as -18°C . Probably the Schizomycetes and Saccharomycetes cannot be killed by cold, for Schumacher has found that they survive exposure to a temperature of -113.7°C .

The death of cells which contain much water when exposed to a very low temperature, appears to depend upon the conversion of the water into ice. The effect of freezing is, as Sachs has shewn, that the parenchymatous tissues become ruptured, and that on the surface of the isolated masses of tissue radially arranged prisms of ice are formed. The effect upon each individual cell is then this, that the water which is present in it, either as cell-sap or as saturating the protoplasm and the cell-wall, is gradually attracted to the surface. This process necessarily involves a considerable disturbance of what we may term the equilibrium of the cell, in that the cell-sap becomes diminished in quantity, and that what of it remains is very concentrated, that is, that it holds in solution a relatively larger quantity of the substances present in it than is normally the case. Further, it appears from the observations of Kunisch that the lowering of the temperature of the cell-sap may be accompanied by chemical changes in the substances which it holds in solution, and it is possible that these changes may be prejudicial. There can be little doubt that the leathery brown colour which is assumed after exposure to frost by the persistent leaves of certain plants is due to changes of this kind (see p. 267). Finally, if the exposure be long continued, it will lead to the actual disorganisation of the protoplasm, and therefore also to the death of the cell.

Provided that the protoplasm has not undergone disorganisation, the formation of ice does not necessarily involve the death of the cell. If a frozen organ be thawed slowly, so that its cells can gradually absorb the water which they have lost, equilibrium will be restored in the cells and they may continue to live. If, on the contrary, the thawing be rapid, so that the water, instead of being absorbed by the cells, escapes into the intercellular spaces, then the organ is killed.

Sachs found, for instance, that leaves of the Beet and of the Cabbage frozen at from -4° C. to -6° C. and thawed either in air at 2° — 3° C. or in water at 6° — 10° C. were killed, whereas, when they were slowly thawed in

water at 0°C ., they survived: even the very sensitive leaves of the Tobacco were not killed by freezing when they were slowly thawed.

A good illustration of this is afforded by Tautphoeus' experiments with seeds. He exposed the seeds for a night to a temperature of -5°C ., and, after either slow or quick thawing, sowed them. The percentage of the seeds which germinated in the two cases is given in the following table:

1. After slow thawing:

	<i>Not frozen.</i>		<i>Frozen.</i>	
Wheat	100	86 germinated.
Rye	97	88 "
Rape	100	97 "

2. After rapid thawing:

	<i>Not frozen.</i>		<i>Frozen.</i>	
Wheat	100	18 germinated.
Rye	97	35 "
Rape	100	66.5 "

The greater tolerance of cold which is exhibited by organs which contain little as compared with those which contain much water, is to be attributed to various causes. In the first place, organs which contain a relatively large quantity of water are in a more actively living condition than those which contain but little; the protoplasm is, in the former case, more susceptible than in the latter to the injurious effect of that disturbance of the equilibrium of the cells which we have spoken of as the result of the freezing of the water which is present in them. Secondly, the cell-sap in relatively dry organs is more concentrated than that of watery organs; as a consequence the formation of ice involves a lower temperature in the former case than in the latter, and the resulting disturbance is less considerable in the one case than in the other.

Müller-Thurgau gives the following illustrations of the difference in the freezing-point for various organs. The succulent labellum of *Phajus* freezes at -0.56°C .; the succulent leaf of *Sempervivum* at -0.7° ; the Potato-tuber at -1° ; the leaf of *Tradescantia mexicana* at -1.16° ; the Ivy-leaf at -1.5° ; the leaves of *Pinus austriaca* at -3.5° ; young shoots of *Thuopsis* at -4°C .

The effect of freezing is to make the organs hard and brittle, and, in the case of succulent organs, to give them a transparent glassy appearance. The destructive effect of freezing upon succulent organs is very clearly exhibited when they have been rapidly thawed; they are quite flaccid, because the protoplasm of the cells is now no longer capable of maintaining their turgidity (p. 40). The permeability of the protoplasm is demonstrated by the fact that in cells in which coloured cell-sap is present, the protoplasm becomes stained by the colouring matters when the cells have been killed by freezing (p. 44).

From the various facts with which we have now become acquainted we may draw some general conclusions as to the relation of cold to the life of plants. We see, in the first place, that the power of enduring extreme cold is possessed in different degrees by one and the same organ in different plants. Martins compares each plant to a thermometer, the zero-point of which is the minimum-temperature at which its life is possible. Secondly, we learn that the different metabolic processes do not all stand in the same relation to temperature; that, in any given plant, some of the processes can go on at lower temperatures than others, each process having its own zero-point. Thirdly, that the larger the proportion of water in an organ, the more liable it is to be injured by frost: hence the zero-point for the life of any given organ will vary according to the amount of water which it contains at different times.

We have learned, so far, that a certain temperature is essential to the maintenance of the life of the plant, and we have now to study the effect of different and relatively high temperatures upon it. The relation of temperature to the metabolic and other processes of plants may be generally stated thus; that, as the temperature rises above the zero-point for any given process, that process is performed with greater activity. Some illustrations of this have been already given with reference to absorption (p. 52), transpiration (p. 108), respiration (p. 198) and germination; to these the following may be added. Sachs found that whereas the roots

of a Tobacco-plant and of a Gourd in a moist soil at a temperature of 3° — 5° C. did not absorb sufficient water to compensate for the loss by transpiration, they did so when the temperature of the soil was raised to 12 — 18° C. Heinrich found that the number of bubbles of oxygen given off by *Hottonia palustris* (immersed in water and exposed to light) at a temperature of 10.6° — 11.2° C. was 145—160 in a unit of time, the number given off at 31° C. was 547—580.

It must not be assumed, however, that there is an exact proportion between the rise of the temperature and the increased activity of any particular metabolic process. The nearest approach to such a proportion is afforded by Mayer's observations (p. 198) on the absorption of oxygen by seedlings at different temperatures, but even in this case it is not exact.

The activity of the metabolic processes cannot be indefinitely increased by a rise of temperature. As the temperature rises from the zero-point for any one process, the activity of that process is increased until a certain degree of temperature is reached, and any further rise of temperature leads to a diminished activity of the process in question, until, at a certain temperature, it ceases altogether. We see, then, that for each metabolic process there are three *cardinal* points of temperature; the *minimum-* or *zero-point* at which the performance of the process is just possible, the *optimum-point* at which it is carried on with the greatest activity, the *maximum-point* at which it is arrested. In our study of respiration we met with two cases which illustrate this statement. In the table of Mayer's observations on seedlings of *Tropæolum majus* (p. 198), it appears that the absorption of oxygen gradually increased as the temperature was raised from 22.4° C. to 35° C., but that it was less considerable at 38.2° C. than at 35° C.; from this it is evident that the optimum degree of temperature is lower than 38.2° C. The other case, which is of a similar nature, but refers to the evolution of carbon dioxide, occurs in the tables of Dehérain and Moissan's experiments with leaves (*Sinapis alba*, p. 199). With regard to the decomposition of carbon dioxide and the evolution of

oxygen by green plants exposed to light, Heinrich found that, in the case of *Hottonia palustris*, the number of bubbles given off in a unit of time gradually increased as the temperature rose up to 31° C., and that a further rise in the temperature diminished the number of the bubbles evolved until, at 56° C., the evolution of gas ceased altogether: 31° C. is then the optimum-temperature for this process in this plant, and 56° C. is the maximum temperature. The optimum-temperature for alcoholic fermentation appears, according to Mayer, to lie between 25° and 30° C. It is not possible to make any general statement as to the optimum-temperature for the action of the various unorganised ferments, for it has been found that the temperature is different for the different kinds of ferments, and for the same kind of ferment obtained from different sources, and that the nature of the liquid in which any given ferment is dissolved affects the position of the optimum-point. Mayer mentions that this point is about 50° C. for Emulsin, and for various specimens of Invertin he determined optimum-points between 31° and 48° C. The optimum- and maximum-points for germination have been ascertained by Haberlandt, Sachs, and Just for a number of seeds.

Haberlandt's determinations are as follows :

	Optimum between	Maximum between
Wheat, Rye, Barley, Oat, Flax, Pea	25° — 31° C.	31° — 37° C.
Buckwheat	25° — 31° „	37° — 44° „
Red Clover, Sunflower, Lucerne	31° — 37° „	37° — 44° „
Maize, Hemp, Pumpkin	37° — 44° „	44° — 50° „
Melon, Cucumber	31° — 37° „	44° — 50° „

Sachs determined the following temperatures :

	Optimum	Maximum
<i>Zea Mais</i>	$34^{\circ}0'$ C.	$46^{\circ}2'$ C.
<i>Phaseolus multiflorus</i>	$34^{\circ}0'$ „	$46^{\circ}2'$ „
<i>Cucurbita Pepo</i>	$34^{\circ}0'$ „	$46^{\circ}2'$ „
Wheat	$29^{\circ}0'$ „	$42^{\circ}5'$ „
Barley	$29^{\circ}0'$ „	$37^{\circ}5'$ „

Just found the maxima for Wheat and Barley to be 37° — $38^{\circ}5'$ C.

We have seen that exposure to a temperature higher than the optimum exercises a depressing influence upon the various metabolic processes, and we shall now learn that a considerable rise of temperature is fatal. We shall find, moreover, that the conditions for the fatal action of an excessively high temperature and the mode of that action are very much the same as in the case of an excessively low temperature. The higher the temperature, the longer the exposure to it; and the larger the proportion of water which the plant or organ contains, the more actively will the prejudicial effect be produced. The following facts will illustrate these statements.

In the case of entire plants Sachs found that an exposure to air at a temperature slightly above 51° C. for ten minutes sufficed to injure them, and, in many instances, to kill them, and that immersion for ten minutes in water at 51° C. proved fatal in all cases. The plants with which he experimented were *Nicotiana rustica*, *Cucurbita Pepo*, *Zea Mais*, *Mimosa pudica*, *Tropæolum majus*, *Brassica Napus*. Similar experiments with water plants (*Vallisneria spiralis*, *Ceratophyllum demersum*, *Chara sp.*, and *Cladophora*) shewed that immersion in water at 50° C. for ten minutes was fatal; *Vallisneria* and *Chara* were killed when the water had a temperature of 45° C.

The following determinations of fatal temperatures are due to de Vries :

I. Roots, and branches with leaves :

	Roots		Leafy branches
	in water	in dry earth	in water
<i>Zea Mais</i>	$47^{\circ}0'$ C.	$52^{\circ}2'$ C.	$46^{\circ}8'$ C.
<i>Tropæolum majus</i>	$47^{\circ}0'$ "	$52^{\circ}0'$ "	$46^{\circ}8'$ "
<i>Citrus Aurantium</i>	$50^{\circ}5'$ "		$52^{\circ}5'$ "
<i>Phaseolus vulgaris</i>	$47^{\circ}0'$ "	$51^{\circ}5'$ "	
<i>Brassica Napus</i>	$47^{\circ}0'$ "	$52^{\circ}8'$ "	
<i>Lupinus albus</i>			$45^{\circ}8'$ "

2. Leaves :

	in water	in air
<i>Vinca minor</i>		
young leaves	47·8° C.	53·3° C.
old "	50·1 "	
<i>Erica carnea</i>		
young leaves	50·6 "	
<i>Taxus baccata</i>		
young leaves	52·0 "	

3. Cryptogams (entire plant in water) :

<i>Funaria hygrometrica</i>	43·4° C.
<i>Marchantia polymorpha</i>	46·4 "
Oedogonium sp.	44·2 "
Spirogyra sp.	44·2 "
Oscillatoria (various species)	45·1 "

According to Mayer and others the fatal temperature for moist Yeast is about 53° C. ; but the temperature is not the same for all species of Saccharomyces, and it varies with the nature of the liquid in which the Yeast is warmed. Schützenberger states that dry Yeast may be heated to nearly 100° C. without losing its vitality. Cohn has found that Bacteria, in his normal solution, are killed when the liquid is heated up to or above 60° C. for an hour, and that an exposure of 14 hours to a temperature of 45° C. or of 3 hours to a temperature of 50° C. proves fatal. Kühne found that the plasmodium of *Æthelium septicum* were killed by an exposure of two minutes to a temperature of 40° C.

Some plants exhibit a remarkable tolerance of high temperatures. De Candolle mentions that Oscillatorias grow in hot-springs such as those of Plombières, at 51° C., of Dax, at 49° C., of Carlsbad, at 50° C. Cohn found *Leptothrix lamellosa* growing in the hot-springs of Carlsbad at temperatures of from 54° C.—44° C. In these cases there seems to be a certain adaptation of the organisms to the conditions of their environment.

The most striking illustration of the fact that when organs contain a relatively small proportion of water they are better able to endure exposure to high temperatures than when they contain a relatively large proportion of water, is

afforded by seeds. In a series of experiments made upon the seeds of a great number of plants (88 species) Haberlandt found that the dry seeds were not in any case injured by being exposed for forty-eight hours to a temperature of 77° C., and that in some cases the seeds survived an exposure of the same duration to a temperature of 100° C. He found, indeed, that previous warming, if not excessive, was beneficial to the seeds inasmuch as it shortened the period of germination.

Thus, seeds warmed for 48 hours at temperatures of

37.5° C., 56° C., 75° C., 87.5° C.,

germinated in

5.45, 5.2, 5.2, 5.03 days.

Again, von Höhnelt found that most seeds, provided that they are quite dry, survive an exposure of one hour to a temperature of 110° C. He considers that the maximum-temperature which dry seeds can bear for at least a quarter of an hour without being killed, lies between 110° and 125° C.

When seeds are exposed to a moist heat, or when they are heated in water, they are killed at lower temperatures than those mentioned above, and in a shorter time. Edwards and Colin observed that an exposure of fifteen minutes to watery vapour at 62° C. sufficed to kill more than half the number of the seeds (of Leguminous and Cereal plants) experimented with, and an exposure of the same duration to watery vapour at 72° C. killed them all. Just found that an exposure of four days duration to watery vapour at 40° C. was injurious to Oat- and Barley-seeds; that an exposure for 24 hours at a temperature of 50° C. was more injurious than the exposure for four days at 40° C.: that exposure for 24 hours at a temperature of 60° C. was fatal. With regard to the effect of heating seeds in water, it must be borne in mind that a prolonged soaking in water at ordinary temperatures is in itself prejudicial. The prejudicial effect is remarkably increased as the temperature of the water is raised. Edwards and Colin found that if seeds are kept for a long time in water at a temperature of 35° C. they are killed. This observation has been confirmed and extended by Haberlandt and by Just.

The following are some of Haberlandt's results: the temperatures given are those of the water in which the seeds were soaked.

	Without previous soaking		Previously soaked for 24 hours in water at ordinary temperatures 12°—15° C.	
	Percentage of seeds germinated	Mean duration of germination; in days	Percentage of seeds germinated	Mean duration of germination; in days
I. WHEAT.				
Control experiment	98	1'6	97	1'7
5 hours at 30° C.	96	1'7	96	1'57
10 " " "	97	1'55	90	1'43
5 " 40° C.	88	2'25	80	2'18
10 " " "	90	2'36	44	2'5
5 " 50° C.	60	2'9	22	3'0
10 " " "	1	3'5	0	—
II. BARLEY.				
Control experiment	98	2'72	63	2'84
5 hours at 30° C.	58	3'17	16	3'87
10 " " "	36	3'00	8	4'25
5 " 40° C.	5	3'80	0	—
10 " " "	1	3'60	0	—
5 " 50° C.	0	—	0	—
III. HEMP.				
Control experiment	96	2'43		
10 hours at 30° C.	58	1'17	42	1'21
" 40 "	46	1'26	41	1'22
" 50 "	37	1'94	30	1'96
5 " 55 "	0	—	0	—
IV. BUCKWHEAT.				
Control experiment	79	3'62		
10 hours at 30° C.	24	4'16	23	5'09
" 40 "	16	3'75	0	—
" 50 "	2	3'50	0	—
5 " 55 "	0	—	—	—

It will be seen that the effect of the warm water was most marked in the case of those seeds which had been previously soaked in water.

Fiedler made the following important observations upon the relation between the presence of a considerable quantity of water in seeds and the temperatures which prove fatal to them.

He made comparative experiments on seeds which were dry, and on similar seeds which had been previously soaked for 24 hours in water:

they were exposed to a dry heat for an hour. They were afterwards sown in earth. In the table, *A* indicates that the seedlings appeared above the surface of the soil; *B* that, though the seeds germinated, the seedlings did not reach the surface: the blank spaces indicate that no germination took place: a dash indicates that no determination was made. The numbers are percentages.

1. Dry seeds :

	Not heated		59°—60° C.		64°—65° C.		69°—70° C.		74° C.	
	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>
Pea	88	10	—	—	75	20	85	10	1	
Rye	96	2	—	—	40	36				
Barley	96		90	2	6					
Wheat	100		—	—	98		1	1		
Maize	100		86	8	25	28				

2. Soaked seeds :

	Not heated		49°—50° C.		51°—52° C.		53°—54° C.		54°—55° C.	
	<i>A</i>	<i>B</i>								
Pea	96		75	10	30	4	20			
Rye	96		30	20	18	8				
Barley	90		3	4						
Wheat	98		40	12	8	8				
Maize	88		2	1						

It has been occasionally observed that seeds survive prolonged boiling in water, for example, that the seeds in the stones of plums which have been made into jam may germinate. This is due to the fact that the seeds are protected from the action of the hot water by the thick endocarp.

The observations which have been made as to the effect of high temperatures upon spores fully accord with those stated above with reference to seeds. Pasteur has shewn that dry spores of *Penicillium glaucum* can endure, without injury, a temperature of 108° C., and that the majority germinate after being exposed to a temperature of 119°—121° C. for half-an-hour. They are all killed by half-an-hour's exposure to a

temperature of 127°—132°C. Hoffman found that the dry spores of *Uredo destruens* and *segetum* (*Ustilago Carbo*) can survive being heated for an hour to 128° C., whereas if they are moist they are killed in the case of *Uredo destruens* at 70°—73° C., and in the case of *Uredo segetum* at 58·5°—62°C. by an exposure of two hours.

Schindler made the following determinations with spores of *Tilletia Caries* :

1. Dry heat (2 hours)

		Heated.	Unheated.
at 50° C.	germination began in	4	4 days.
„ 65 „	„	6	„
„ 80 „	„	8	„
„ 95 „	„	8	„
„ 100 „	no germination.		

2. Moist heat (2 hours)

at 30° C.	germination began in	4	4 days.
„ 35 „	„	4	„
„ 40 „	„	5	„
„ 45 „	„	5	„
„ 50 „	no germination.		

Cohn has found that the spores of *Bacillus subtilis* survive prolonged boiling. This is due, as in the case of seeds mentioned above, to the fact that water penetrates them with difficulty.

We have to enquire, finally, into the cause of death consequent on exposure to high temperatures. It might be imagined that, since a rise of temperature promotes the activity of the metabolic processes, a high temperature would make them excessively active and that the cell would die in consequence of living, as it were, too fast. But such an explanation is inadmissible, for, as we have seen, a rise of temperature above the optimum-point has a depressing effect upon the activity of the metabolic processes. Many physiologists are inclined to believe that the fatal effect of a high temperature is due to the coagulation of the coagulable proteids in the cell, but this connexion cannot be regarded as established. It is doubtless upon the living protoplasm of the cell that the temperature

acts: the effect first manifests itself by a diminution of the metabolic activity of the protoplasm, and ultimately effects its disorganisation.

Plants or parts of plants which have been killed by exposure to high temperatures present the same appearances as those which have been killed by exposure to low temperatures. They are flaccid because their cells are incapable of becoming turgid. This is due to the fact that the protoplasm has become permeable as a result of death, and this may or may not be accompanied by its separation from the cell-walls so as to form amorphous masses.

The foregoing facts suffice to shew that, as in the case of low temperatures so also in the case of high temperatures, the power of endurance is different in different kinds of plants, and, we may add, in individuals of the same species. The figures given above must therefore be regarded as true only with regard to the individual plants or organs experimented upon. A variety of conditions may affect the power which a plant or an organ possesses of enduring exposure to extreme temperatures, and it is on account of the influence of these conditions that the results of different observers in any one case are not always quite in accord. For instance, in experiments made with seeds, the seeds, though they may be stated to be dry, are not necessarily equally dry in all cases; hence the results of different observers as to the extremes of temperature which any particular kind of seed can endure will vary according to the relative dryness of the seeds. Age, too, doubtless exerts an important influence in experiments of this kind: the younger the plant, the more it suffers. The conditions under which the plant had been previously living must also be taken into consideration. G. Haberlandt concludes from his experiments that the lower the temperature at which a seed can germinate, the more capable is the seedling of enduring exposure to low temperatures. Still it is possible to base some generalisations upon the ascertained facts. Attention has already been drawn to the most important of these, namely, that the more water an organ contains the more does it suffer in consequence of exposure to extremes of tempera-

ture. It appears, further, at least as far as high temperatures are concerned, that some organs which are saturated with water are more tolerant than others. Soaked seeds, for instance, can endure exposure to higher temperatures than can stems, leaves, or roots.

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LECTURE XIV.

METABOLISM (*continued*).

9. *The Expenditure of Energy.*

IN entering upon the subject of the expenditure of energy by the plant we must bear in mind that it is with kinetic energy that we are directly concerned, and we must therefore begin by ascertaining what are the sources from which kinetic energy is obtained. We have already learned that the income of all plants includes a certain amount of kinetic energy in the form of heat, and that, in the case of plants possessing chlorophyll, it includes a large amount of kinetic energy in the form of light. But in addition to the kinetic energy absorbed from without, there is a constant evolution of kinetic energy going on in every actively living plant in connexion with the decomposition of more or less complex organic substances which have either been formed in the plant, or, as in the case more particularly of plants destitute of chlorophyll, have been absorbed as food, in connexion, that is, with destructive metabolism. It was pointed out in a previous lecture (Lecture I. p. 5) that as the constructive metabolism of plants involves the conversion of kinetic into potential energy, so their destructive metabolism involves the conversion of potential into kinetic energy. For the processes of destructive metabolism consist in the decomposition of relatively complex and unstable compounds into others which are relatively simple and stable, and, to quote the words of Her-

mann, "in every chemical process in which stronger affinities are saturated than were saturated before its occurrence, potential energy becomes kinetic." The simpler and the more stable the waste-products of any destructive process, the greater is the amount of energy evolved. For instance, in the self-decomposition of protoplasm (p. 188), if the decomposition were as complete as it would be on combustion, and the only waste-products were carbon dioxide, water, and some comparatively simple nitrogenous substance or even nitrogen itself, a relatively large amount of energy would be evolved; whereas, as a matter of fact, though carbon dioxide and water are formed, yet various more or less complex substances are formed as well, so that only a relatively small amount of energy is set free.

We have now especially to consider what becomes of kinetic energy in the plant. The matter may be briefly stated thus: a portion of the kinetic energy is stored up by the plant in the form of potential energy: the remainder is lost to the plant; it is either spent in the performance of mechanical work in connexion with growth or movement, or it is given off most generally in the form of heat, occasionally in the form of light, and possibly in the form of electricity. We shall speak of the storing up of energy in the plant as the *accumulation of energy*; and of the loss of energy as the *dissipation of energy*.

I. *The Accumulation of Energy.* We know already that the accumulation of energy is the necessary accompaniment of constructive metabolism, that the formation of more and more complex organic substances involves the conversion of kinetic into potential energy. We know also that constructive metabolism is being constantly carried on in the plant. We learned in a previous lecture (p. 202) that so long as a plant is living its protoplasm is undergoing active decomposition. Hence, if the life of the plant is to be maintained, the repair, or as we may term it the *Nutrition*, of its protoplasm must be carried on at least as actively as its decomposition. This continual construction of protoplasm involves a continual conversion of kinetic into potential energy: hence

any increase of the protoplasm of a plant means an accumulation of energy in the potential form.

But it is not so much to an increase of its protoplasm that the gain in organic substance by a plant is due. It is principally due to the accumulation of substances which are directly or indirectly the products of the decomposition of protoplasm, such as cellulose, starch, fats, proteids, etc. These represent a certain proportion of the energy which became potential in the construction of the protoplasm from which they were derived, and it is in these substances chiefly that the potential energy accumulated by the plant is stored up.

The proportion of the kinetic energy which is stored up in the form of potential energy in connexion with the production of organic substance in the plant is large, if we compare plants with animals. If we consider the enormous amount of organic and organised substance formed by a plant from the time of its development from a seed to its death, in the development of an oak from an acorn, for example, and we bear in mind the amount of potential energy which all this organic and organised substance represents, we can form some idea of the amount of kinetic energy which has been stored up in the potential form. The heat which is given out by burning wood or coal is but the conversion into kinetic energy of the potential energy which was stored up by the plant which produced the wood or the coal. The reason of the difference between plants and animals in this respect is that whereas the increase in bulk of an animal is limited, that the animal soon ceases to increase the dry weight of its organised substance, the increase in bulk of a plant goes on during its whole life. The plant therefore produces a very large dry weight of organised substance, and this represents a large amount of energy.

II. *The Dissipation of Energy.* We turn now to the loss of energy by the plant. In dealing with this subject we have first of all to shew that the expenditure of energy in connexion with growth and movement and with the evolution of heat, light, and electricity, is dependent upon destructive metabolism. That this is the case will be fully proved in our

detailed consideration of these various phenomena; it will suffice for the present to state generally that the conditions which are essential to destructive metabolism are also essential to the exhibition of these phenomena. We have seen, for example, that temperature has an important influence upon the processes of destructive metabolism, and we shall find that it has a marked effect upon growth and movement. Again, the absorption of free oxygen is of importance in destructive metabolism, and we shall find that the evolution of heat and light by plants, their growth, and their movements, are likewise dependent upon the absorption of free oxygen, excepting, of course, in those plants which, as we have seen (p. 211), are capable of living in the absence of oxygen. We will now consider these phenomena individually and in detail, and we will begin with growth.

Growth. Before we can enter upon a detailed consideration of the relation of growth to destructive metabolism we must understand what we mean by "growth." By growth we mean permanent change of form accompanied usually by increase in bulk. We must clearly distinguish between growth and constructive metabolism. Growth can, it is true, only go on when the necessary material is supplied by the processes of constructive metabolism, but a mere increase in the dry weight of the organic substance of a plant does not necessarily imply that it is growing, for increase in weight may take place without increase in bulk or change of form. When, for instance, in the development of the seed, the cells of the endosperm, or of the perisperm, or of the cotyledons, become filled with reserve-materials in the form of aleurone-grains, starch-grains, etc., we have a great increase in the dry weight of the organic substance without a corresponding growth of the organ. Nor does an increase even of the organised structures of an organ, that is, of the protoplasm and the cell-wall, necessarily imply that it is growing. Thus, an increase of the cell-wall may take place without any perceptible enlargement of the cell, as, for instance, when a cell-wall thickens: in fact it appears from the researches of Strasburger that the cell-wall does not become thickened so long as the cell is

growing. The consideration of the mechanics of growth may be conveniently deferred for the present: that subject will be treated of in a subsequent lecture.

It is easy to prove that growth involves an expenditure of energy, inasmuch as it will only go on when destructive metabolism is active, that is, when the evolution of energy is considerable. It is a well-known fact that the higher plants do not grow in the absence of free oxygen. Malpighi found that seeds would not germinate in water which was covered with a layer of oil, under conditions, that is, in which they could obtain no oxygen: Sénéquier and de Saussure ascertained that branches will not grow *in vacuo*, nor in an atmosphere which does not contain oxygen: more recently Detmer has shewn that the growth of seedlings is arrested when they are deprived of oxygen, and his results have been confirmed by Wortmann. We know that oxygen is essential to the normal destructive metabolism of these plants; the obvious inference is that growth does not go on in the absence of oxygen because the destructive metabolism is too feeble, that is, that the evolution of energy is inadequate. In the case of plants which can live without oxygen, growth will proceed provided that the destructive metabolism is sufficiently energetic. With regard to Yeast (*Saccharomyces cerevisiæ*) it has been much debated whether or not the cells can grow and multiply in the absence of oxygen. Considering the activity of the fermentation which it can excite, it would seem probable *a priori* that it can. This assumption is on the whole confirmed by the experimental evidence. It appears, from the researches of Pasteur, of Brefeld, and of Nägeli, that, as a matter of fact, the Yeast-cells do grow in the absence of oxygen, provided that they are supplied with fermentable material (sugar), and that the alcohol, the principal waste-product of the metabolism of the cells, is not allowed to accumulate. Amongst the Schizomycetes many forms are, as we have seen (p. 211), anaërotic. *Clostridium butyricum*, for example, the plant which causes butyric fermentation, not only grows and multiplies in the absence of oxygen, but, as Pasteur and Prazmowski have ascertained, it dies when free

oxygen has access to it. With regard to the higher Fungi Brefeld has observed that though *Mucor Mucedo* and *stolonifer*, *Penicillium crustaceum* and others, can live in the absence of oxygen, they do not grow, because they can excite only comparatively feeble alcoholic fermentation. *Mucor racemosus*, on the other hand, excites active alcoholic fermentation, and accordingly it can grow in the absence of oxygen.

We have already learned (p. 203) that temperature has an important influence upon metabolism, and we shall find, in harmony with this, that it materially affects growth. In discussing, in the previous lecture, the general relations between temperature and the metabolic processes, we found that there are three cardinal points to be noted; the *minimum* temperature at which the process first begins, the *optimum* at which it is most active, the *maximum* at which it ceases. These points we have also to note in considering the relations between temperature and growth.

The following tables illustrate the relation of growth to temperature. In the first table are given the results obtained by Köppen and de Vries which illustrate the relation in a detailed manner. The measurements refer to increments in length of hypocotyls in periods of 48 hours.

Temperature	Köppen			de Vries		
	<i>Lupinus albus</i>	<i>Pisum sativum</i>	<i>Zea Mais</i>	<i>Sinapis alba</i>	<i>Lepidium sativum</i>	<i>Linum usitatissimum</i>
14.1° C.	9.1 mm.	5.0 mm.				
15.1				3.8 mm.	5.9 mm.	1.5 mm.
18.0	11.6	8.3	1.1 mm.			
21.6				24.9	38.0	20.5
23.5	31.0	30.0	10.8			
26.6	54.1	53.9	29.6			
27.4				52.0	71.9	44.8
28.5	50.1	40.4	26.5			
30.2	43.8	38.5	64.6			
30.6				44.1	44.6	39.9
33.5	14.2	23.0	69.5			
33.9				30.2	26.9	28.1
36.5	12.6	8.7	20.7			
37.2				10.0	0.0	9.2

In the second, which was compiled by Pfeffer, are given determinations of the cardinal points made by Sachs (S), de Candolle (C), Köppen (K), de Vries (V). The observations were made on seedlings: the minima and maxima were determined in some cases by the non-germination of the seed, in others (de Vries) by the actual arrest of the growth of the seedling: the optima were determined by the growth of the root (including the hypocotyl) of the seedlings.

Plant	Minimum temperature	Optimum temperature	Maximum temperature	Observer
<i>Triticum vulgare</i>	{5.0 ⁰ C.	28.7 ⁰ C.	42.5 ⁰ C.	S
	{7.5	29.7		K
<i>Hordeum vulgare</i>	5.0	28.7	37.7	S
<i>Sinapis alba</i>	0.0	{21.0	28.0	C
		{27.4	above 37.2	V
<i>Lepidium sativum</i>	1.8	{21.0	28.0	C
		{27.4	below 37.2	V
<i>Linum usitatissimum</i>	1.8	{21.0	28.0	C
		{27.4	above 37.2	V
<i>Trifolium repens</i>	5.7	21—25	below 28.0	C
<i>Phaseolus multiflorus</i>	9.5	33.7	46.2	S
<i>Pisum sativum</i>	6.7	26.6		K
<i>Lupinus albus</i>	7.5	28.0		K
	{9.5	33.7	46.2	S
<i>Zea Mais</i>	{9.6	30.2—33.5		K
	{9.0	21—28	35.0	C
<i>Cucurbita Pepo</i>	13.7	33.7	46.2	S
<i>Sesamum orientale</i>	13.0	25—28	below 45.0	C

It may be stated as a general rule that the minimum temperature is higher for plants belonging to warm climates than for those which belong to cold climates, but this does not hold good with regard to the maximum.

Since, as we have been endeavouring to make clear, growth is dependent upon the activity of destructive metabolism, it might be expected that the relation of growth to temperature would be the same as that of respiration, for, as has been pointed out in a previous lecture (p. 195), the respiratory interchange of gases affords an indication of the activity of normal destructive metabolism. There is, it is true, some sort of parallelism between the relation of growth to temperature and that of respiration to temperature, but the two are

not quite identical. In the first place, the minimum temperature for respiration (including both the absorption of oxygen and the exhalation of carbon dioxide) is lower than that for growth. It is true that growth may take place at very low temperatures, but this does not affect the truth of the general statement just made. In the second place the optimum temperature for growth is reached much earlier than that for respiration (Rischawi, Mayer); that is, that in the case of any given plant, the optimum temperature for respiration lies very near the maximum temperature which is compatible with the maintenance of life, whereas the optimum temperature for growth lies considerably below this limit. If these facts were expressed graphically, we should find that the curve of growth begins to rise rather later than the curve of respiration, and that the former begins to fall whilst the latter still continues to rise.

In endeavouring to account for the difference in the curves of growth and of respiration, we can readily explain why they do not begin to rise at the same point, in other words, why the minima of temperature are not the same in the two cases. Growth, we have already seen, can only take place when the evolution of energy in the plant is considerable; at the minimum temperature for respiration the destructive metabolism is feeble, too feeble to admit of growth; it is therefore only at a higher temperature, a temperature at which destructive metabolism is more active, that growth begins. The only explanation which we can offer of the fact that the curve of growth falls at temperatures at which the curve of respiration continues to rise, is this, that the process of growth itself is affected prejudicially by high temperatures. At these temperatures the evolution of energy is adequate, but the processes upon which increase in bulk directly depends are in some way interfered with.

We see, then, that though growth is dependent upon an evolution of energy, that is, upon destructive metabolism, it is nevertheless a distinct process which is not always affected by variations in external conditions in the same way as destructive metabolism; in fact, it may be affected by conditions

which do not affect destructive metabolism at all. We have just learned, for instance, that growth is restricted to narrower limits of temperature than is destructive metabolism. Again, we saw, in the last lecture (p. 261), that light does not materially affect destructive metabolism as estimated by respiration: but, as we shall learn in a subsequent lecture when we are studying the mechanics of growth, light has a remarkable effect upon growth.

Movement. Without entering for the present into the mechanics of the movements exhibited by plants, we will consider those facts relating to movement which prove that it is dependent upon destructive metabolism and that it involves a loss of energy to the plant. We may, however, briefly enumerate the different ways in which movement manifests itself. The lowest expression of it is the streaming movement of the protoplasm in closed cells; this is known as the "rotation" or the "circulation" of the protoplasm: then there is the contraction of contractile vesicles; ciliary movement; amoeboid movement; and finally the movement of entire organs in the higher plants.

We have to shew, in the first place, that movement is dependent upon destructive metabolism, and we shall do this in the same manner as in the case of growth: we shall, namely, adduce evidence to prove that conditions which are unfavourable to destructive metabolism also act prejudicially upon the power of movement.

In regard to growth we found that the presence of oxygen is an essential condition in the case of truly aërobiotic plants; this holds good, and for the same reasons, with regard to movement. Dutrochet observed that the motile leaves of *Mimosa pudica*, the Sensitive Plant, lose their power of movement *in vacuo*: Kabsch confirmed these observations and extended them to the motile stamens of *Berberis*, *Mahonia*, and *Helianthemum*, and found further that their movements are arrested in an atmosphere of nitrogen or of hydrogen: Pfeffer, too, observed that the stamens of *Centaurea Facca* lost their power of movement after being kept for one minute in an atmosphere of carbon dioxide: Kühne ascertained that

the amoeboid movements of the plasmodium of *Myxomycetes* and the rotation of the protoplasm in the cells of the staminal hairs of *Tradescantia* cease in the absence of oxygen: and finally, it was mentioned in a previous lecture (p. 255), in describing Engelmann's experiments on the action of light upon the exhalation of oxygen by cells containing chlorophyll, that it is only when supplied with oxygen that *Bacterium Termo* is motile.

On the other hand, just as anaërobic plants are capable of growth in the absence of oxygen, so also they are capable of movement. Grossmann and Mayerhausen have observed, for instance, that certain *Schizomycetes* are motile in the absence of oxygen.

Further, movement, like growth, is affected by temperature, and in much the same way; its curve presents the same cardinal points, and it probably bears much the same relation to the curve of respiration as that of growth does. Thus, with regard to the rotation of the protoplasm, Velten found, in the case of *Chara fætida*, that the minimum temperature was 0°C ., the optimum temperature, that namely at which the movement was most rapid, was 38.1°C ., the maximum temperature, that namely at which the movement ceased, was 42.81°C .; in the case of *Vallisneria spiralis* the minimum was $0-1^{\circ}\text{C}$., the optimum 38.75°C ., the maximum 45°C .: in the case of *Elodea canadensis* the cardinal points were 0°C ., 36.25°C ., and 38.75°C .

In the cells of *Chara fragilis* Dutrochet detected rotation at $0-1^{\circ}\text{C}$., and Cohn in *Nitella syncarpa* at -2°C . Sachs observed, in the cells of the hairs of *Cucurbita Pepo*, *Solanum Lycopersicum*, and of *Tradescantia*, slow rotation at $12-16^{\circ}\text{C}$., rapid rotation at $30-40^{\circ}\text{C}$., and slow rotation again at $40-50^{\circ}\text{C}$. Many other observations might be quoted (Jürgensen, Max Schultze, Kühne), but it is not necessary to do so, for they agree with those which have been given in proving that a rise of temperature from the minimum to the optimum accelerates rotation, and that a further rise from the optimum to the maximum retards and finally arrests it. With regard to amœboid movement, Kühne found that the

movements of the plasmodium of *Didymium Serpula* were arrested when the temperature was raised to 30° C., and that they also ceased at a low temperature. With regard to ciliary movement, Strasburger has found that the zoospores of *Hæmatococcus lacustris* tend to come to rest at from 8—4° C., but he has observed them in movement even in water containing ice; he fixes the optimum temperature for these zoospores at 30—40° C., and the maximum at 50° C. He also observed that the zoospores of *Botrydium* ceased to move when the temperature sank to 6° C. The minima and maxima for the zoospores of marine Algæ are lower than those for fresh-water Algæ. Kjellmann observed the formation of zoospores going on in the Algæ of the coast of Spitzbergen when the temperature of the sea was -1.5° C. to -1.8° C.: and Strasburger found that the zoospores of the marine Algæ which he observed were killed at 35°—40° C. Finally, with regard to the movements of organs in the higher plants, Kabsch observed that the spontaneous movements of the lateral leaflets of the Telegraph-plant {*Desmodium (Hedysarum) gyrans*} ceased when the temperature sank to 22° C., that they went on slowly at 28—30° C. (a complete up and down movement in 4 minutes), and that they were more rapid at 35° C. (a complete movement in 85—90 seconds): in the case of the Sensitive Plant (*Mimosa pudica*) Sachs observed that if the plant be kept for some hours at a temperature of about 15° C., its leaves gradually lose their motility; the lower the temperature below this degree the more rapidly does the power of movement disappear; he found also that the power of movement is lost within an hour when the plant is kept in damp air at 40° C., within half an hour in air at 45° C., and in a few minutes in air at 49—50° C.

Again, movement, like growth, is affected by light. In some cases light appears to promote movement, in others to arrest it. Thus Engelmann has discovered a form of Bacterium, termed by him *Bacterium photometricum*, which is only motile when exposed to light; and Sachs has found that if plants with motile leaves (*Mimosa*, *Acacia*, *Trifolium*, *Phaseolus*, *Oxalis*) are kept for some days in darkness, or even

in feeble light, they lose their power of movement. On the other hand, exposure to light arrests the spontaneous movements of the motile leaves in the majority of plants which possess them.

A remarkable instance of the influence of light in causing movement is afforded by the change in position of the chlorophyll-corpuscles in cells exposed to light. Marquard, and after him Sachs, observed that green leaves exposed to sunlight soon assume a brighter green colour than they have when in the shade: this can be made very evident by covering a portion of a leaf exposed to sunlight with some opaque body, a strip of tinfoil for instance; on the removal of the tinfoil after a few minutes the parts which were covered are seen to have a deeper colour than those which were exposed. The difference of colour is due to the different distribution of the chlorophyll-corpuscles in the cells in the two cases. It appears, from the researches of Famintzin, Borodin, Frank, Stahl, and others, that in diffuse daylight the chlorophyll-corpuscles collect on the free cell-walls, that is, on the walls next the surface in the superficial cells of organs consisting of several layers of cells, and on the upper and lower walls of organs consisting of only one layer of cells: whereas in direct sunlight they collect upon the lateral walls, and in darkness upon the lateral and lower walls. In the former case, which Frank terms *Epistrophe*, the corpuscles lie parallel to the surface of the organ; in the latter, which is termed *Apostrophe*, they lie at right angles to the surface (Fig. 36): hence the green colour of an organ, a leaf for instance, is of a darker hue in epistrophe than in apostrophe. Since the chlorophyll-corpuscles are themselves incapable of movement, their change of position under the influence of light must be attributed to movements of the protoplasm in which they are imbedded. Frank has in fact observed that the collection of the chlorophyll-corpuscles on any of the cell-walls is accompanied by an accumulation of protoplasm. Under unfavourable conditions, for instance when the temperature is low, or when the cells are old, the chlorophyll-corpuscles remain in the position of apostrophe.

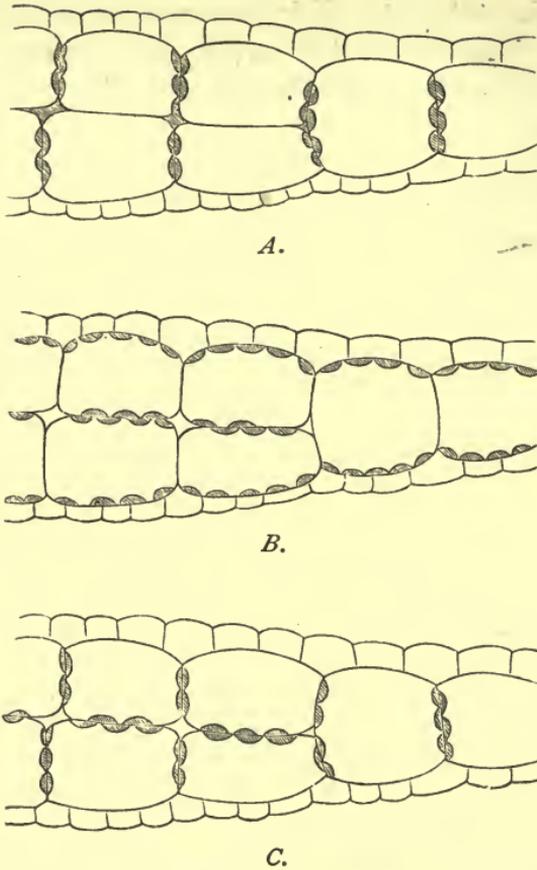


FIG. 36 (after Stahl). Sections of the phylloid stem of *Lemna trisulca*.

- A. Position of the chlorophyll-corpuscles when the stem is exposed to intense light (light-apostrophe).
- B. Position of the corpuscles in diffused daylight (epistrophe).
- C. Position of the corpuscles in darkness (dark-apostrophe).

We come, then, to the same conclusions in the case of movement as in the case of growth. Movement is dependent upon an evolution of energy, that is, upon destructive metabolism, but it is nevertheless a distinct process capable of being affected by conditions which do not affect destructive metabolism.

We will now go on to study the nature and causes of the movements rather more closely. Most of the move-

ments exhibited by plants are discontinuous: the only continuous movement is, apparently, the streaming movement of the protoplasm. Again, most of the movements are spontaneous, but some of them, as in the case of the leaves of the Sensitive Plant, of the stamens of *Berberis*, of *Helianthemum*, of the *Cynareæ*, &c., are induced by some external cause. Continuous movement is the expression of a corresponding continuous evolution of energy; discontinuous movement implies that it is only at certain intervals that the necessary evolution of energy takes place. We have already learned (page 7) that the living protoplasm of certain cells is automatic, that is, that it gives rise to internal stimuli which find their outward expression in spontaneous movement: we may now go further and say that these internal stimuli determine the evolution of energy which makes movement possible. We have also learned that protoplasm is irritable; we can now interpret this by saying that, in the case of organs exhibiting induced movements, the necessary evolution of energy is determined by a stimulus acting from without.

Now with regard to the nature of the stimuli. Concerning the internal stimuli we know nothing. Stimulation from without can be effected in a variety of ways. The external stimulus may be mechanical, simply the contact of a foreign body, or electrical, or chemical; a sudden change from light to darkness, or a variation in the intensity of the illumination, will sometimes act as a stimulus. Then there is the further question, how the stimulus acts upon the protoplasm. To this we can give no definite answer, but since, as we have seen, movement can only take place when destructive metabolism is active, it is very probable that the immediate effect of stimulation is to cause destructive metabolism. We may accept Pflüger's dictum, "stimulation is decomposition"; that is to say that when a stimulus, either internal or external, acts upon irritable protoplasm, it determines the sudden, we may almost say explosive, decomposition of some complex organic substance. This view enables us to give a satisfactory

explanation of the phenomena of Fatigue. It has been found, namely, that if a motile organ, that of the leaf of the Sensitive Plant for example, be repeatedly stimulated at short intervals, it will soon cease to respond to the stimuli, it will lose its irritability; after a short period of rest it again becomes irritable. The loss of irritability we may ascribe to the consumption, in consequence of the repeated stimulation, of the material by the decomposition of which the necessary energy for the performance of a movement is evolved; possibly the accumulation of the waste-products of decomposition may contribute to this result. The regaining of irritability we may ascribe to the accumulation of a fresh store of decomposable material and perhaps, in some degree, to the removal of the waste-products of previous decompositions. Finally, we have to answer the question, what is this decomposable material? We have seen throughout our consideration of this subject that movement is dependent upon the same general conditions as destructive metabolism. Of the processes of destructive metabolism the most conspicuous is the self-decomposition of the protoplasm. We have no reason to suppose that the metabolism of a motile cell differs in kind from that of a non-motile cell. If, then, the evolution of energy in a non-motile cell is mainly due to the self-decomposition of the protoplasm, we may infer that this is also the case in a motile cell.

Heat. An evolution of energy in the form of heat is the inseparable accompaniment of the processes of destructive metabolism; in fact, an organism can only be considered to be living so long as it is setting free energy in the form of heat. Pflüger goes so far as to say that the "intramolecular heat of an organism is its life," that is, that it is only in consequence of the continued evolution of heat in the protoplasm-molecule that the intramolecular vibratory movement is maintained (p. 160). The living protoplasm-molecule is ever undergoing active self-decomposition and evolving heat, the dead protoplasm-molecule has ceased, probably in consequence of some change of molecular

structure, to undergo this active self-decomposition and to evolve heat.

A few instances will suffice to prove that the evolution of heat in the plant is dependent upon destructive metabolism. When we were discussing destructive metabolism we found that it is very active in germinating seeds and in opening flowers, and it is just these that afford the best examples of an evolution of heat by plants. The evolution of heat by germinating seeds is a familiar fact in the process of the malting of Barley, and from the extended observations of Göppert we may conclude that it accompanies germination in all cases.

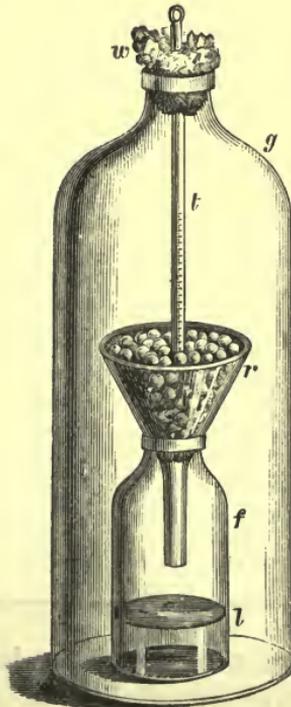


FIG. 37 (from Prantl, after Sachs). The moist seeds are placed in the funnel *r*, which is placed in the neck of the bottle *f* containing some solution of caustic potash *l* to absorb the carbon dioxide evolved. The whole is covered by the bell-jar *g*, through the neck of which passes the thermometer *t*: the bulb of the thermometer is covered by the seeds in the funnel. The cotton-wool *w* which holds the thermometer in the neck of the bell-jar admits air.

By means of an apparatus similar to the above figure, Göppert determined the excess of the temperature among the seeds over that of the surrounding air in the following cases :

Wheat and Oats	11.25—12.50° C.
Peas and Hemp	7.50— 8.75
Maize	6.25— 7.50
Clover	17.50
<i>Spergula arvensis</i>	11.25
<i>Brassica Napus</i>	21.25
<i>Carum Carui</i>	7.50

The evolution of heat in connexion with flowering appears to have been first observed by Lamarck in the case of the spadix of *Arum italicum*, and it is with compact inflorescences of this kind that most of the subsequent observations have been made. Sénébiér was the first to determine by means of the thermometer the difference between the temperature of the spadix and that of the air.

The following is a series of determinations made with *Arum maculatum* :

Time	Temperature of the air	Temperature of the Spadix	Excess
3 p.m.	15.6° C.	16.1° C.	0.5° C.
5 "	14.7	17.9	3.2
5 $\frac{3}{4}$ "	15.0	19.8	4.8
6 $\frac{1}{4}$ "	15.0	21.0	6.0
6 $\frac{3}{4}$ "	14.9	21.8	6.9
7 "	14.3	21.2	6.9
9 $\frac{1}{4}$ "	15.0	18.5	3.5
10 $\frac{1}{2}$ "	14.0	15.7	1.7
5 a.m.	14.1	14.1	0.0

A striking illustration of the dependence of the evolution of heat upon destructive metabolism is afforded by the fact that the evolution of heat and the absorption of oxygen are intimately connected. Hubert observed that when the spadix of *Colocasia odora* was smeared with oil or with honey, that is, when the free access of air was prevented, its temperature sank; Vrolik and de Vriese could detect no rise of temperature in the spadix of *Colocasia odora* in an

atmosphere of nitrogen, and they further observed that when a spadix was kept in a closed receiver containing air, a high temperature was only maintained so long as free oxygen was present: Eriksson found that the temperature of seedlings, of flowers, and of fruits in an atmosphere of hydrogen was only 0.1° — 0.3° C. higher than that of dead objects, whereas in air their temperature was very much higher.

	Excess of temperature in hydrogen	Excess of temperature in air
Seedlings of <i>Raphanus sativus</i>	0.2° C.	5.7° C.
Spadix of <i>Arum maculatum</i>	0.3	16.5
Flowers of <i>Isatis tinctoria</i>	0.1	2.8
Cherries	0.2	0.5

De Saussure observed in the case of *Arum maculatum* there was some relation between the evolution of heat and the absorption of oxygen, but it was left for Garreau to investigate this point with accuracy. He found, in a number of experiments, of which an instance is given below, that, in the case of the spadix of *Arum italicum*, the greater the absorption of oxygen the higher the temperature.

The mean temperature of the air was 18° C.

Time	Excess of temperature of spadix	Mean temperature of spadix	Oxygen absorbed in c.c.
$3\frac{1}{2}$	2.5° C.	3.2° C.	39
$4\frac{1}{2}$	3.9		
$4\frac{1}{2}$	3.9	5.3	57
$5\frac{1}{2}$	6.7		
$5\frac{1}{2}$	6.7	7.8	75
$6\frac{1}{2}$	8.9		
$6\frac{1}{2}$	8.9	8.3	100
$7\frac{1}{2}$	7.7		
$7\frac{1}{2}$	7.7	6.0	50
$8\frac{1}{2}$	4.2		
$8\frac{1}{2}$	4.2	2.7	20
$9\frac{1}{2}$	1.2		

The above determinations were made by means of the apparatus shewn in Fig. 38. *A* is a graduated glass bell-jar standing in a saucer which contains water: *B* is a thermometer, fastened by a cork in the neck of *A*, with its bulb in contact with the spadix which is supported in a test-tube *C* filled with moist sand: the bulb of the thermometer and the spadix are covered by a piece of muslin. The internal surface of the bell-jar is smeared with concentrated solution of potash: hence the CO_2 evolved by the spadix is absorbed, and the absorption of oxygen can be estimated by the rise of the water from the saucer into the graduated bell-jar.

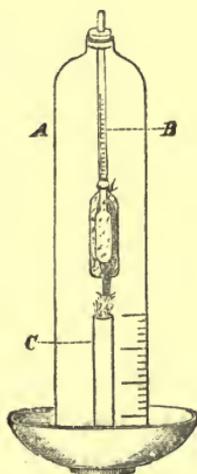


FIG. 38 (after Garreau).

But the evolution of heat is not confined to those processes of destructive metabolism in which oxygen is concerned; it accompanies others as well. We have an instance above, in Eriksson's experiments, of the evolution of heat in the absence of oxygen. One of the most conspicuous examples of destructive metabolism in the absence of oxygen is, as we have seen (p. 208), the alcoholic fermentation effected by Yeast. The fact that a liquid in which this fermentation is going on soon acquires a temperature considerably higher than that of the surrounding air has long been known, but Eriksson has shewn definitely that this rise of temperature takes place also in the absence of oxygen, that it is due, therefore, to the fermentative activity of the Yeast.

Two bottles were taken, and the one filled with water, the other with a fermenting solution of sugar; the temperature of the liquid in each

bottle was observed by means of a thermometer introduced through the cork.

Time	Temperature of water	Temperature of fermenting liquid	Excess
3 p.m.	22·3 ⁰ C.	23·4 ⁰ C.	1·1 ⁰ C.
4 "	22·5	25·1	2·6
5 "	22·6	26·0	3·4
6 "	22·6	26·5	3·9
7 "	22·6	26·3	3·7

Eriksson also ascertained that Yeast evolves heat in the absence both of oxygen and of alcoholic fermentation. Pasteur has pointed out that Yeast can live upon milk-sugar, though it cannot cause it to ferment, and Eriksson availed himself of this fact for the purpose of his experiments.

The apparatus was the same as that described above: one of the bottles (*A*) was filled with small pellets of blotting-paper containing a mass of Yeast moistened with solution of milk-sugar, and the air was removed from the bottle by passing a current of hydrogen through it for half-an-hour; the other bottle (*B*) was filled with pellets of moistened blotting-paper.

Time	Temperature in <i>B</i>	Temperature in <i>A</i>	Excess of temperature in <i>A</i> over <i>B</i>
9 a.m.	18·4 ⁰ C.	18·4 ⁰ C.	0·0
10 "	18·4	18·5	0·1
11 "	18·6	18·7	0·1
12 noon	18·7	18·8	0·1
1—3 p.m.	18·8	19·0	0·2

It is of interest to note in connexion with the foregoing experiment that the admission of air to the Yeast in the bottle *A* was immediately followed by a considerable rise of temperature.

Time	Temperature in <i>B</i>	Temperature in <i>A</i>	Excess in <i>A</i>
3.15 p.m.	18·8 ⁰ C.	19·0 ⁰ C.	0·2 ⁰ C.
4 "	18·9	19·4	0·5
5 "	18·8	19·6	0·8
6 "	18·7	19·8	1·1

We have now sufficiently established the connexion between the evolution of heat and destructive metabolism, but we may briefly consider the fact which is apparent in the tables given above that the evolution of heat is not constant but variable. In opening flowers there is a period, varying in length in different cases, of active destructive metabolism; at the commencement of this period the evolution of heat is small, but it gradually rises to a maximum, and sinks again to a minimum. This we may term the "grand period" of the evolution of heat.

In illustration of this, Kraus' observations, made by means of a thermometer on the temperature of the spadix of *Arum italicum*, may be quoted. It may be mentioned here that the evolution of heat is greatest in the sterile portion of the spadix (Dutrochet, Kraus), less in the portion bearing the staminal flowers, and least in that bearing the pistillate flowers. Only the excess of the temperature of the spadix over that of the atmosphere is given in the table: the temperature of the air varied between 15.3°C . and 16.3°C .

Kraus.

4.15 p.m.— 0.9°C .	7.30 p.m.— 11.3°C .
4.25 " — 1.3	8 " — 11.9
5 " — 2.2	8.15 " — 12.15
5.30 " — 5.4	8.30 " — 12.00
5.45 " — 7.0	8.45 " — 11.8
6 " — 8.2	9.30 " — 11.3
6.30 " — 8.6	10.20 " — 10.6
6.45 " — 9.0	11 " — 10.4
7.2 " — 9.7	1 a.m.— 8.0
7.15 " — 10.5	6.30 " — 0.2

When the period of active destructive metabolism is prolonged the evolution of heat exhibits a diurnal variation, which might be indicated graphically as a secondary curve on the curve of the grand period.

The following are some observations of Dutrochet's on the spadix of *Arum maculatum*, made by means of a thermopile: they extend over the whole grand period, and illustrate the relation of the daily periods to the grand period: the figures give the difference between the temperature in the spadix and that of the air; when a minus sign is used, it means that the temperature of the spadix was lower than that of the air.

Day and hour	Diff. of temperature	Day and hour	Diff. of temperature	Day and hour	Diff. of temperature
<i>May 9</i>		<i>May 10</i>		<i>May 11</i>	
6 a.m.	0'00 ⁰ C.	6 a.m.	0'00 ⁰ C.	6.15 a.m.	0'00 ⁰ C.
7 "	0'00	7 "	0'00	7.30 "	0'00
8 "	0'06	8 "	0'31	8.10 "	0'00
9 "	0'12	9 "	0'37	8.45 "	0'00
10 "	0'18	10 "	0'40	9.30 "	0'00
11 "	0'25	11 "	0'44	9.45 "	0'00
12 noon	0'28	12 noon	0'62	10.15 "	0'00
1 p.m.	0'25	12.20 p.m.	0'81	11.30 "	0'03
2 "	0'25	12.45 "	1'12	12 noon	0'06
3 "	0'21	1 "	1'40	1 p.m.	0'00
4 "	0'18	1.20 "	1'50	2 "	0'00
5 "	0'18	2 "	2'63	3 "	-0'06
6 "	0'18	2.30 "	4'48	4 "	-0'12
7 "	0'12	3 "	5'65	5 "	-0'25
8 "	0'09	3.15 "	6'25	6 "	-0'25
9 "	0'06	3.30 "	6'93		
10 "	0'03	4 "	7'78		
		4.15 "	8'25		
		4.30 "	7'78		
		4.50 "	6'93		
		5.15 "	5'93		
		6 "	4'68		
		7 "	3'34		
		8 "	1'90		
		9 "	1'56		
		10 "	1'06		

According to the results of a large number of observers, the daily period in these inflorescences is of this kind, that the maximum excess of temperature is attained during the day and the minimum during the night. The course of the daily periods, as indicated by the occurrence of the maxima, is the less uniform the shorter the grand period. This is clearly seen on comparing the daily periods of inflorescences which have longer or shorter grand periods. Thus in the case of *Arum maculatum* (see table above) the grand period is rather short, and the daily maximum occurred later in the middle of the grand period than at its beginning or towards its end. In *Philodendron bipinnatifidum*, in which the grand period extends over only 34—36 hours, Warming observed that the maximum excess of temperature (18.5° C.) occurred on the first day at 7 p.m., and on the second day (5°—7° C.) between

9—10 a.m. In the case of *Colocasia odora*, in which the grand period is much longer, the following results have been obtained.

Observer	Day I		II		III	
	Hour	Max. Excess temp.	Hour	Max. Excess temp.	Hour	Max. Excess temp.
Vrolik and de Vriese } ¹	—	—	4 p.m.	4'40 ⁰ C.	5 p.m.	7'20 ⁰ C.
" } ²	—	—	3 "	8'90	12.30 "	8'30
Van Beek and Bergsma } ²	—	—	3 "	14'38	3.30 "	21'87
Brongniart	3.15 p.m.	4'50 ⁰ C.	4.15 "	10'00	5 "	10'20
Hoppe	—	—	2.15 "	3'10	1.45 "	2'75
	IV		V		VI	
Vrolik and de Vriese } ¹	3 p.m.	6'70 ⁰ C.	9 a.m.	8'90 ⁰ C.	2 p.m.	7'80 ⁰ C.
" } ²	2 "	10'00	12 noon	1'70	—	—
Van Beek and Bergsma } ²	—	—	—	—	—	—
Brongniart	4—6 "	11'00	11 a.m.	8'20	10 a.m.	2'5
Hoppe	1.5 "	3'32	1 p.m.	2'44	—	—

Day I is the day on which the spathe opens.

When the grand period extends over a considerable time, as in the case of growing shoots for instance, the course of the daily period is more regular. Dutrochet came to the conclusion from his numerous observations on growing shoots that the hour of the daily occurrence of the maximum excess of temperature is constant for any given plant, but that it is different for different plants.

Dutrochet determined the daily period of the evolution of heat by shoots in the following cases.

These observations were made upon plants in a saturated atmosphere to prevent loss of heat by transpiration.

1. Complete daily period in *Euphorbia Lathyris*:

Day	Hour	Excess of temp. of plant	Day	Hour	Excess of temp. of plant
June 5	6 a.m.	0·09 ⁰ C.	June 6	6 a.m.	0·00 ⁰ C.
	7 "	0·11		7 "	0·03
	8 "	0·12		8 "	0·06
	9 "	0·18		9 "	0·09
	10 "	0·25		10 "	0·11
	11 "	0·28		11 "	0·15
	12 noon	0·31		12 noon	0·15
	1 p.m.	0·34		1 p.m.	0·18
	2 "	0·28		2 "	0·12
	3 "	0·28		3 "	0·12
	4 "	0·18		4 "	0·06
5 "	0·12	5 "	0·03		
6 "	0·06	6 "	0·03		
7 "	0·03	7 "	0·015		
8 "	0·03	8 "	0·00		
9 "	0·015	9 "	0·00		
10 "	0·00	10 "	0·00		

2. Time of occurrence of maximum temperature in various plants:

	Hour	Maximum excess of temperature
<i>Rosa canina</i>	10 a.m.	0·21 ⁰ C.
<i>Allium porrum</i>	11 "	0·12
<i>Borago officinalis</i>	12 noon	0·09
<i>Euphorbia Lathyris</i>	1 p.m.	0·34
<i>Papaver somniferum</i>	1 "	0·21
<i>Cactus flagelliformis</i>	1 "	0·12
<i>Helianthus annuus</i>	1 "	0·22
<i>Impatiens balsamina</i>	1 "	0·11
<i>Ailanthus glandulosa</i>	1 "	0·16
<i>Campanula media</i>	2 "	0·31
<i>Sambucus nigra</i>	2 "	0·21
<i>Lilium candidum</i>	2 "	0·28
<i>Asparagus officinalis</i>	3 "	0·25
<i>Lactuca sativa</i>	3 "	0·09

It is generally admitted that this daily periodicity is entirely due to causes inherent in the plant, to variations in the activity of its destructive metabolism. It is, however, affected by variations in the external conditions. The evolution of heat by the plant is greater when the external

temperature is moderately high, so that, within a certain limit, the excess of the temperature of the plant over that of the air is greater at a higher than at a lower external temperature. We can readily understand this, for we know that destructive metabolism is more active, within a certain limit, the higher the external temperature. When the variations of the external temperature are gradual, the course of the daily period asserts itself even in opposition to them: but when they are sudden and considerable, they give rise, as Hoppe found in the case of *Colocasia odora*, to corresponding variations, but of greater amplitude, in the daily period of the plant. With regard to the influence of light, Dutrochet found that the daily period persists for a time (4 days, *Campanula medium*; 3 days, *Lactuca sativa*; 1 day, *Borago officinalis*) when the plant is kept continuously in darkness, and then disappears, and that it is slowly restored when the plant is again exposed to light. There can be little doubt that this influence of light is an indirect one; that the disappearance of the daily period is due to a diminished destructive metabolic activity in consequence of the arrest of constructive metabolism. We met with a case of this kind in a previous lecture (p. 261).

The observations which we have hitherto selected in illustration of the evolution of heat are all such as have been made on growing organs, for it might be expected, and investigation has fulfilled the expectation, that, inasmuch as growth is accompanied by active destructive metabolism, it would be attended by an evolution of heat. This appears to be true also with regard to movement, for Bert has observed that the movement of the motile organ of the leaf of *Mimosa pudica* is accompanied by a rise of temperature. But it must not be supposed that the evolution of heat in plants is confined to such periods of specially active destructive metabolism. Heat is evolved whenever destructive metabolism is in progress, and the only reason why we cannot in all cases detect an evolution of heat is that the destructive metabolism is not sufficiently active to determine such an evolution of heat as to make good the loss of heat

which is going on, and at the same time to raise perceptibly the temperature of the plant or of the organ. We shall see, when we come to consider the loss of heat by the plant, that a considerable amount of heat must be continually evolved in it, or else its temperature would be found to be lower as compared with that of the surrounding medium than is actually the case.

We may now pass on to the loss of heat by plants. In the first place subaërial organs lose heat by radiation. A conclusive proof of this is afforded by the familiar fact that dew and hoar-frost form so readily on plants. The significance of this is that, in consequence of loss of heat by radiation, the temperature of the plant sinks below that of the atmosphere. It is on this account that plants often suffer from frost when the temperature of the air is actually above the freezing-point. Plants or parts of plants growing in water or in the soil lose heat by conduction.

This subject was first investigated by Wells, and more recently by Boussingault and by Maquenne. Boussingault mentions that a thermometer placed on grass on a clear night often indicates a temperature 7–8° C. below that of the air. Maquenne states that leaves radiate almost as much as lamp-black.

In the second place, subaërial organs lose heat in connexion with transpiration. Transpiration, we have seen (Lecture VII), consists in the exhalation of watery vapour by the plant. This involves the conversion of water into vapour in the plant, and for that a certain amount of heat is necessary; and it involves, further, a transpiration-current through the root, stem, and branches, which has a subsidiary cooling effect. Thus Rameaux found that, when two similar branches, one of which was deprived of its leaves, were exposed to the sun and supplied with water, the temperature of the interior of the branch which bore leaves was 10° C. lower than that of the branch which had been deprived of its leaves.

In conclusion we will briefly consider the temperature of plants. A number of factors cooperate to determine it: first, the activity of the evolution of heat in the plant; secondly, the temperature of the surrounding medium; thirdly, the loss

of heat by the plant. Then the nature of the medium by which an organ is surrounded will materially affect its temperature. Thus plants growing submerged in water, or roots buried in the soil, have approximately the same temperature as the water or the soil, but the mean temperature of roots is somewhat lower than that of the soil on account of the current of water passing through them. This is to be accounted for by considering that the temperature of the water or of the soil is not subject to rapid variations, that it is nearly constant for long periods of time; that the organs lose heat neither by radiation nor in connexion with transpiration, but only slowly by conduction. The temperature of subaërial organs, on the other hand, is often different from that of the air, quite apart from the exceptional cases which have come under our notice, in which, in consequence of a period of active destructive metabolism, the temperature of the organ is higher than that of the air for a considerable time. In the first place, the temperature of the air is liable to rapid variations, and this naturally leads to differences between it and the temperature of the subaërial organs of a plant; again, variations in the temperature of the air have, as we have learned, a considerable effect upon the activity of most of the vital processes of the plant, and in this indirect way they affect its temperature. Finally the form and bulk of a subaërial organ modify its temperature. Small organs, like the mycelium of Fungi or the thallus of Lichens, have approximately the temperature of the air. Dutrochet observed that the temperature of subaërial organs of moderate bulk is in fact always lower than that of the air, and de Saussure noticed in his investigations, that in many cases the temperature of flowers was lower than that of the air. The temperature of leaves is lower than that of the air because of the extent of surface which they offer in proportion to their bulk, and thus radiation and transpiration go on actively in them. Maquenne has shewn, on the other hand, that leaves absorb heat; this contributes to prevent their temperature from falling excessively in consequence of active transpiration. In the case of fleshy leaves Askenasy has found that when they are exposed

to the sun their temperature may be much higher than that of the air: thus the leaves of *Sempervivum alpinum* had a temperature of 52° C., whilst that of the air was 28.1° C. When the organ is bulky, the trunk of a tree for example, the temperature is never the same as that of the air, and it is different in different parts. With regard to the temperature of trees Krutzsch states that in general the temperature of the trunk and main branches is lower than that of the air during the day and higher during the night, and that, during the day, the temperature of the trunk is lower than that of the branches; but neither the trunk nor the larger branches attain within the twenty-four hours either the maximum or the minimum temperature attained by the air: the temperature of the smaller branches is approximately that of the air. Becquerel finds that the maximum temperature of the trunk is attained about sunset, and the minimum about sunrise. The mean temperature of the trunk is higher than that of the air in autumn and in winter, and lower in spring and in summer: but the mean annual temperature of the trunk is, as Becquerel points out, the same as that of the air. We see, then, that the temperature of trunks and branches of a certain bulk depends entirely upon that of the external air. In these organs the proportion of actively living cells to dead cells is so small that the heat evolved in the metabolism of the former is insufficient to affect perceptibly the temperature of the whole organ. In the course of his observations upon the evolution of heat in plants, Dutrochet found that the temperature of stems and branches is highest near the growing point, and that the temperature of the pith when its cells are living is higher than when its cells are dry and dead: these differences of temperature are of course due to the greater metabolic activity in the growing-point and in the young pith than in older parts.

The reason why the differences of temperature, which arise in the different parts of a plant in obedience to internal or to external causes, are sufficiently permanent to be detected is due to the fact that the tissues of plants are bad conductors of heat; and this also explains to some extent why it is that

the temperature of the trunks of trees differs from that of the air, for a change in the temperature of the air is only very slowly responded to in the trunk. Some woods conduct better than others, hence some trunks respond more promptly to variations in the external temperature than others; Krutzsch observed, for instance, that the temperature of the trunk of a Pine changed more rapidly than that of the trunk of a Maple, and he ascertained that the conductivity of the wood of the former is twice as great as that of the wood of the latter. Again, the conductivity of wood is greater in the direction of the length of the fibres than in the transverse direction; hence, in a trunk, the tendency towards the establishment of uniformity of temperature between its different parts is greater than that towards the assumption of the temperature of the external air.

With regard to the relative conductivity of different woods, de la Rive and A. de Candolle find that the denser the wood the better it conducts. They arrange the following trees in the order of the conductivity of their wood: *Cratægus (Pyrus) Aria*, *Fuglans regia*, *Quercus Robur*, *Pinus Abies*, *Populus italica*, *Quercus Suber*.

Knoblauch has determined the relative conductivity in the direction of the fibres and across them in the following woods:

Acacia, Box, Cypress	1'25 : 1.
Elder, Lilac, Hawthorn, Walnut, Beech, Elm, Oak	1'45 : 1.
Apricot, Brazil-wood	1'60 : 1.
Willow, Chestnut, Lime, Alder, Birch, Pine, Fir ...	1'80 : 1.

Sowinsky determined the relation to be, for the Oak 1'15 : 1, for the Hornbeam 1'43 : 1, for the Lime 1'28 : 1, and for the Cherry 1'4 : 1. He finds, in opposition to de Candolle, that the lighter woods are the best conductors: this difference is due to the fact that Sowinsky experimented with fresh woods, whereas de Candolle used dry woods.

Light. The evolution of light by plants is a phenomenon which has been known from the time of Aristotle and Pliny, and is commonly spoken of as phosphorescence. So far as we know at present, this property is confined to Thallophytes. The so-called phosphorescence of decaying wood is due to the presence of the mycelium of *Agaricus melleus* (Rhizomorpha), and that of putrefying meat and vegetables to Schizomycetes of the nature of Micrococci (Pflüger, Lassar). Other luminous

Fungi are the *Agaricus olearius* of Southern Europe, the *Agaricus igneus* of Amboyna (Rumpf), the *Agaricus noctilucentis* of Manilla (Gaudichaud), the *Agaricus Gardneri* of Brazil (Gardner), and various Australian Agarics (Drummond). In all these last-mentioned cases it is the fructification which is luminous and not the mycelium.

Various statements have been made as to the luminosity of flowers (*Tropæolum majus*, *Oenothera macrocarpa*, *Calendula officinalis*, *Lilium bulbiferum*, *Tagetes patula*, Helianthus, Polyantes, *Phytolacca decandra*), but, even admitting the accuracy of the observations, the phenomenon in most of these cases is different from that described above. The luminosity spoken of above is persistent, whereas in the case of most of these flowers it consists of sudden flashes, in fact it suggests an electrical discharge. In some of the cases (*Oenothera*, *Phytolacca*, Polyantes) the luminosity was persistent, but it might have been due to the presence of luminous Fungi. (For Literature of the subject see Fries, Meyen, de Bary, and Pflüger.)

Among Algæ Meyen mentions a species of *Oscillatoria*, occurring in masses in the Atlantic ocean, and Ehrenberg certain species of Diatoms, of the genera *Chaetoceras* and *Discoplea*, as being luminous: Ducluzeau speaks of luminous *Confervæ*, and Brewster states that he observed luminosity in *Chara vulgaris* and *hispida*. But these statements all require investigation; the luminosity of *Chara* mentioned by Brewster is almost certainly due to the phosphorescence of the calcium carbonate with which the plants are encrusted.

The evolution of light is essentially dependent upon the life of the organism; thus Fabre observed that the luminosity of a specimen of *Agaricus olearius* was destroyed when the plant was killed by dipping it into water at 50°C. Further, the evolution of light is dependent upon the destructive metabolism of the plant. Bischoff found, for instance, that the luminosity of *Rhizomorpha* is not exhibited *in vacuo* or in an atmosphere destitute of free oxygen, and his results have been confirmed by all subsequent observers in the case of other Agarics and of Bacteria: thus Ludwig ascertained that *Rhizomorpha* remains luminous in water which has not been boiled, whereas it at once loses its luminosity in boiled water, in water, that is, which holds no air in solution. Fabre found, in one experiment, that a given weight of *Agaricus olearius* exhaled more carbon dioxide than an equal weight of the

Fungus when not luminous. Again, it has been pointed out, especially by Brefeld, that it is only the young growing hyphae of *Rhizomorpha* which are luminous. The dependence of the evolution of light upon destructive metabolism is also shewn by the fact that temperature has an influence on luminosity. Fabre states that 3—4° C. is the minimum temperature for the luminosity of *Agaricus melleus*; Ludwig found that the luminosity of *Rhizomorpha* was very feeble at 4—5° C., and Schmitz observed specimens which were not luminous at 17—18° C. Brefeld, however, found *Rhizomorpha* luminous at a temperature of 1—2° C. The optimum temperature for the luminosity of *Rhizomorpha* lies, according to Ludwig, between 25° and 30° C.: at 50° C. its luminosity was permanently destroyed. The curve of luminosity appears, then, to differ from that of respiration, in that the former begins to fall at a temperature at which the latter continues to rise. Fabre failed to find that the evolution of light was accompanied by a rise of temperature in *Agaricus olearius*.

It is doubtless due to the nature of the light that the luminosity of plants has been termed phosphorescence. Fabre describes the light of *Agaricus olearius* as being white, soft, and uniform, and compares it to that of phosphorus dissolved in oil. Gardner states that the light of *Agaricus Gardneri* has a green tinge, and Rumpf speaks of that of *Agaricus igneus* as being bluish. According to Ludwig, the light emitted by *Rhizomorpha* consists of the blue and the more highly refrangible rays.

We have to attempt, in conclusion, to give some account of the mode in which the luminosity is produced. In the first place it is not a phenomenon of the same nature as true phosphorescence, for the luminosity of a plant is quite independent of any previous exposure to the sun, nor can it be induced, as it can in certain substances (phosphorite, chlorophane) by mere heating. In the second place, it is improbable, as Pflüger has made clear, that it is due to the formation in the plant of some readily oxidisable phosphorus-compound, such as phosphuretted hydrogen. The immediate disappearance of the luminosity on the death of the organism shews

that it is not due to the presence of a substance which, like wax, various oils, quinia sulphate, etc. (Dessaigue), is luminous at a moderate temperature in the presence of free oxygen, but that it is directly connected with the destructive metabolism of the protoplasm. We can only conclude that a portion of the energy set free in the destructive metabolism of the protoplasm is evolved in the form of light. ✕

Electricity. In view of the changes, both chemical and physical, which, as we have seen, are going on with greater or less activity in the various parts of the plant, it has been not unnaturally inferred that the electrical equilibrium of the plant is being constantly disturbed, and that differences of electrical potential in different parts may be observed by means of appropriate instruments. A considerable number of observations have, in fact, been made, all of which tend to shew that electric currents are constantly traversing the different organs of plants, that is, that different organs and different points of one and the same organ exhibit differences of electric potential. We will not attempt to deal with the extensive literature of the subject, but a few of the more important and trustworthy observations may be cited in illustration. Buff found, for example, that the exterior subaërial parts of plants are in a state of permanent positive electrification, whereas the roots and the internal tissue are electrically negative; that is, that when one electrode is placed on the surface of the stem or of a leaf and the other electrode on the root or on the section of the stem, the deflection exhibited by the galvanometer indicates the existence of a current passing, through the plant, from the root or the section of the stem to the surface of the stem or leaf, and through the galvanometer, from the surface of the stem or leaf to the root or to the section of the stem. When both the electrodes were placed upon the surface of the stem, currents could be detected passing irregularly sometimes in one direction and sometimes in the other: and Ranke found that when both the electrodes were placed upon points on the surface of the section, a point relatively remote from the centre of the section was always negative to all points relatively near the centre. Similar results were obtained by

Jürgensen and by Heidenhain. Ranke not only succeeded in detecting the above-mentioned currents which, as he points out, resemble the so-called "normal currents" of du Bois-Reymond in muscle and nerve, but he detected others as well. He found, namely, that if the epidermis of a piece of a stem or of a petiole be removed and one electrode be placed upon this artificial longitudinal section and the other on the transverse section, a current passes through the galvanometer from the transverse to the longitudinal section. This current he distinguishes, as the "true current," from the current mentioned above as passing from the uninjured surface to the transverse section which he calls the "false current."

A series of minute observations of this kind has been made by Munk on the leaf of *Dionæa muscipula* (Venus' fly-trap). He finds, first, that the mid-rib is positive to all points of the lamina on either surface: secondly, that a point on the mid-rib, at the junction of its proximal third with its distal two-thirds, is positive as regards all other points on the mid-rib; this is, therefore, the point of greatest positivity of the whole surface: thirdly, that in any transverse strip taken right across the leaf, the most positive point lies in the portion of the mid-rib included in the strip, and there are two points on the portion of lamina included in the strip which are negative with regard to all other points on the strip; these points, the points of greatest negativity of the strip, are situated in the lamina, one on each side of the mid-rib, about half-way between it and the margin: by imagining the leaf to be divided into a number of such strips, and by joining the negative points of the successive strips the two negative lines are obtained; all points in the two negative lines are isoelectric: fourthly, that all points situated symmetrically with regard to the mid-rib are isoelectric: fifthly, that a point on the mid-rib which is relatively near the point of greatest positivity is positive as regards all points which are relatively distant from that point; in the lamina, a point which is relatively near to one of the lines of negativity is negative as regards all points which are relatively distant from it: sixthly and lastly, that the distribution of

potential is the same on both surfaces of the leaf, and that symmetrically placed points, one on the upper and the other on the lower surface, are isoelectric.

The accompanying diagram will make this description more intelligible.

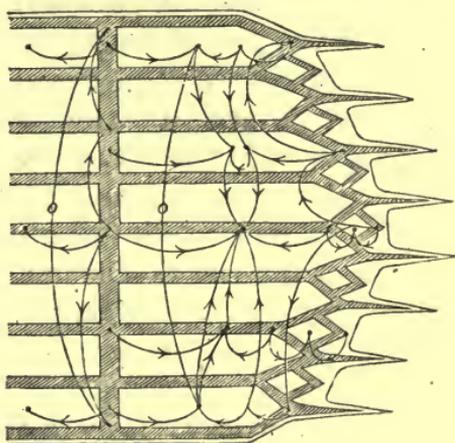


FIG. 39 (after Munk). Distribution of potential on the surface of the leaf of *Dionaea muscipula*. The shaded vertical portion represents the mid-rib. The curves with arrow-heads mark the directions of the currents passing through the galvanometer from relatively positive to relatively negative points of the surface of the leaf.

Burdon-Sanderson however finds that any point on the upper (ventral) surface of the leaf of *Dionaea* is usually negative to the corresponding point on the lower (dorsal) surface. He has also made the interesting observation that when a voltaic current is passed through the petiole near its junction with the lamina, it affects any "normal" current in the mid-rib in such a way that the normal current is strengthened when the current led through the petiole travels in the same direction as the normal current, and that the normal current is weakened when the current led through the petiole travels in the opposite direction. He draws attention to the similarity between these phenomena and those exhibited by nerves (electrotonus) under the same conditions.

The question now arises whether or not these currents are dependent upon the metabolism of the plant, that is, whether they indicate a real dissipation of energy in the form of elec-

tricity, or whether they are due to purely physical causes. Buff considers them to be quite independent of the vital processes of the plant, and in this opinion Jürgensen, Heidenhain, and Ranke agree. Kunkel offers the following explanation of the phenomena. He ascertained, by a number of experiments of different kinds, that whenever a current of water is set up between one part of an organ and another, it is accompanied by a disturbance of electrical equilibrium of such a nature that a current travels (through the galvanometer) in the same direction as that in which the current of water is travelling. Let us consider one case from this point of view. In speaking of Munk's experiments it was mentioned that all points on the mid-rib of the leaf of *Dionæa* are positive as compared with all points on the lamina, and Kunkel found this relation to hold in the considerable number of leaves of dicotyledonous plants which he investigated. Now it is well known that the nervature of leaves is more easily wetted by water than the rest of the surface. When, then, a moist non-polarisable electrode is placed on a nerve and another on the surface of the lamina, the point of the nerve touched by the electrode will become moist more rapidly than the point of the surface, and diffusion-currents will be set up which are more active at the one point than at the other: these diffusion-currents are accompanied by electrical disturbances, as is well known in Physics, and the result is a difference of electrical potential at the two points which is indicated by a current passing from the former to the latter through the galvanometer with which the electrodes are connected. We can apply this explanation to the above-mentioned results of Buff, Jürgensen, Heidenhain, and Ranke. The greater the amount of water present in a mass of tissue the less active will be the diffusion-currents when water is placed on its surface, and the less considerable will be the accompanying electrical disturbance. In the experiments with roots, the root had been previously well washed in water, so that it was saturated; hence, when the moist electrode was laid upon it, or when, as in Buff's method, the root was dipped in water, the diffusion-currents set up were less active than those set

up in the stem, and, as a consequence, the former was found to be electrically negative as regards the latter. Again, in the experiments with stems which had been cut across, the section was covered with moisture which had escaped from the injured cells, and the cells in the immediate neighbourhood of the section were saturated with water; hence the diffusion-currents were more active at the point of the uninjured surface touched by the one electrode than at the section touched by the other, and consequently the former was positive as compared with the latter. With regard to Ranke's "true current," there can be little doubt that it is susceptible of explanation in much the same way. Hermann mentions that the artificial longitudinal section is often positive to the artificial transverse section, especially when the organ consists for the most part of cells elongated in the direction of its length. It might be suggested that this current is due to some chemical difference in the cell-sap of the cells in contact with the electrodes on the longitudinal and transverse sections respectively, but Velten has shewn that this is not the case. He prepared a piece of the stem of *Sida napaea* which shewed the "true current," and he found that both the longitudinal and transverse sections were strongly acid. He then washed the longitudinal section with dilute solution of soda until its reaction was slightly alkaline, and in another instance he treated the transverse section in the same way. On examination it was found that, in these pieces of stem, with one acid and one alkaline surface in contact with the electrodes, the current remained the same as when both the surfaces were acid.

We see that there is some reason for accepting the view that the electrical currents which have been observed in plants do not indicate a dissipation of the energy of the plant, but are due to physical causes, and are even induced by the apparatus employed for the purpose of detecting them. The crucial test lies in the comparison of living and dead organs. Ranke observed that parts of plants which had slowly died no longer shewed the "true current," though irregular "false currents" could be detected for some time. Munk found that

no currents could be detected in leaves of *Dionæa* which had either died slowly, or had been suddenly killed. Velten was however able to detect currents in leaves and portions of stems which had been suddenly killed by immersion in boiling water or in alcohol. Though these results are contradictory, yet this one fact is clear that, in certain organs at least, when death is suddenly induced in such a way that the organisation is not materially injured, the currents persist.

Some further light is thrown upon this point by the observations which have been made on the currents in motile organs when quiescent and when stimulated. Burdon-Sanderson and Munk have found that when the leaf of *Dionæa* is stimulated, any current which may be observed between any two points when the leaf is unexcited exhibits a variation. For instance, let us suppose the electrodes to be placed on opposite points of the upper and under surfaces of an unexcited leaf, and that the point on the lower surface is then found to be positive with regard to the point on the upper surface. On stimulation, either mechanical or electrical, of the irritable upper surface, the under surface becomes suddenly negative to the upper, and then gradually becomes positive to the upper, more positive than in the unexcited leaf, the first (negative) variation being less considerable than the second (positive) variation. Kunkel obtained similar results in his experiments on the pulvinus of the leaf of *Mimosa pudica*. When we come to study the mechanics of these organs, we shall learn that stimulation of them gives rise to the passage of currents of water through their tissues. The passage of currents of water through the tissues leads, as we have seen above, to a disturbance of electrical equilibrium, and Kunkel and Burdon-Sanderson agree in referring to this cause the positive variation which they observed: currents of water pass from the cells near the point of stimulation to others more remote, and the latter become positive to the former. With regard to the negative variation which follows almost immediately upon stimulation, their opinions differ. Kunkel considers it to be due to alterations in the protoplasm which cause a disturbance of the diffusion-currents in the resting

leaf: Burdon-Sanderson regards it as "a visible sign of an unknown molecular process," which he considers to be "an explosive molecular change," and as of the same nature as the negative variation which follows upon the stimulation of muscles and nerves.

The stimulation of the leaf of *Dionæa* may or may not be followed by the closing of the leaf, but in either case the electrical phenomena above described are manifested. This shews that the electrical changes observed in connexion with the stimulation of motile organs are not due to movement of the organs, but are the expression of preliminary changes taking place in their cells.

Summing up the evidence which is now before us we come to the following conclusions: (1) that the so-called "normal" currents (including Ranke's "true" and "false" currents) are not the expressions of a dissipation of the energy of the plant; (2) that the electrical disturbances exhibited by motile organs on stimulation, or at least the negative variation, are the expression of the dissipation of a portion of the energy set free as the result of molecular change in the protoplasm.

We have now concluded our study of the metabolism of plants, and it only remains for us to bring together the most important points. The best means of stating them clearly will be to draw up an account of the income and expenditure of a plant.

In the case of a plant possessing chlorophyll, the income of matter consists, as we have seen, of the food (salts, water, carbon dioxide, free oxygen), and the income of energy of kinetic energy in the form of light and heat, the former being the more important of the two items. The great bulk of the food absorbed is converted into organic matter, which is retained by the plant in the form of organised structures, of reserve-materials, and of waste-products which are not excreted. At the same time a loss of matter, in the form of the

carbon dioxide and water exhaled in respiration, of oxygen exhaled by green parts in sunlight, and of excreted organic or inorganic matter, has been going on. Besides these items of loss we must mention some others to which we have as yet paid little attention. All plants lose a certain amount of matter in connexion with reproduction, for all plants throw off from themselves in the course of their lives, certain portions of their structure, in the form of seeds, spores, antherozoids, etc., for this purpose. Again, plants which persist for more than one period of growth, lose matter by the falling off of certain of their organs and of portions of their structure; for example, by the falling of the leaves in autumn, and by the shedding of bark, fruits, etc. With reference to the expenditure of energy, we have seen that a large proportion of the income of energy is employed in the processes of constructive metabolism and of nutrition, and remains stored up as potential energy in the organic matter which the plant accumulates. A dissipation of energy in the form of heat and in connexion with growth is common to all plants: in some, there is dissipation of energy in the form of motion: in some, in the form of light: in some, probably, in the form of electricity. A loss of energy, potential energy, occurs also when the plant loses organic matter in any of the ways mentioned above. We may now proceed to tabulate these various items. They will be arranged under the two heads of (1) Income, and (2) Expenditure. The water lost in transpiration is not considered, inasmuch as it simply traverses the plant: only that amount of water is considered which may be assumed to enter into the processes of constructive metabolism or to be produced in the processes of destructive metabolism.

PLANT POSSESSING CHLOROPHYLL.

INCOME.	EXPENDITURE.
<i>Matter.</i>	<i>Matter.</i>
Food.	Organic matter.
Inorganic salts.	Carbon dioxide } Respiration.
Carbon dioxide.	Water }
Water.	Free oxygen—in decomposition of CO ₂ in light.
Free oxygen.	

INCOME.

Energy.

Rays of light absorbed by chlorophyll.

Heat.

EXPENDITURE.

Matter.

Excreted substances (organic or inorganic).

Reproduction (spores, seeds, etc.).

Other losses (leaves, fruits, bark, etc.).

Energy.

Constructive metabolism.

Growth.

Heat.

Motion (in some cases).

Light ”

Electricity ”

Potential energy (when organic matter is excreted or thrown off).

BALANCE in favour of plant.

Matter.

Organic matter, including

Tissues.

Reserve-materials.

Unexcreted waste-products.

Energy.

Potential energy represented by the organic matter.

In the case of a plant which does not possess chlorophyll the items must be altered as follows.

INCOME.

Matter.

Food.

Inorganic salts.

Organic matter.

Water.

Free oxygen (in most cases).

Energy.

Potential energy of organic food.

Heat.

EXPENDITURE.

Same as above, except that no free oxygen is given off.

BALANCE in favour of plant.

Same as above.

It may be repeated, in conclusion, that the loss in the economy of the plant is, under ordinary circumstances, much less considerable than the income: as a consequence the plant continues to gain in weight and to accumulate potential energy.

In the remaining lectures we shall consider the mechanisms of growth and of movement, and the physiology of reproduction. The next lecture will be devoted to the subject of Growth.

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LECTURE XV.

GROWTH.

WE have already learned, from our brief consideration of the subject in the last lecture, something about growth. We understand at least what we mean by growth. We use this word to express the permanent (*i.e.* irreversible) changes of form, usually accompanied by a permanent increase in bulk, which are established in the course of the development of plants and their organs. Each plant and each part of a plant has an inherent tendency to assume a certain ultimate form, but this ultimate form is only gradually assumed. All plants and all parts of plants begin their existence with a form which is different from that which they possess when mature, and the higher the morphological differentiation of a plant the greater is this difference, and the more numerous the stages which intervene between the primitive and the mature form.

I have been careful to say that change of form is *usually* connected with increase in bulk, for this connexion is by no means necessary. It is easy to imagine that change of form may be effected, not by the addition of material, but simply by the redistribution of material.

The general statements made above with regard to plants and their organs are true also of the individual cells of multicellular plants, and not only of cells but of all organised structures, cell-walls and starch-grains for instance. The form which a cell shall ultimately assume depends upon the organising properties of its protoplasm, though, as we

shall see, the expression of the organising activity may be more or less modified by external circumstances. The various degrees of histological differentiation presented by plants is simply the expression of a greater or smaller similarity in the organising properties of the protoplasm of the cells of which each plant consists. For instance, the greater thickness of the wall of one cell as compared with that of another, though they exist side by side and under the same conditions, is due to differences in the organising properties of the protoplasm in the two cases. Further, the differences in form exhibited by starch-grains are to be traced to a similar cause: the difference in form between the starch-grain of the Wheat and that of the Potato, for example, can only be accounted for by referring it to a difference in the organising properties of the amyloplasts in the two plants.

We may begin our more detailed study of growth by briefly enumerating the general conditions upon which it depends. With some of these we are already familiar. We know, for instance, that growth can only take place when the growing organ is adequately supplied with material in the form of what we have termed the plastic products of the metabolism of the plant. Growth is then ultimately dependent, so far as the necessary material is concerned, upon constructive metabolism. We know also that growth is associated with active destructive metabolism; that it is dependent, in the case of aërobiotic plants, upon the absorption of free oxygen, and, in the case of anaërobiotic plants, upon a supply of fermentable substance. Growth is then dependent, so far as the necessary energy is concerned, upon destructive metabolism. Again, it was shewn at length in the last lecture that growth can only go on within certain limits of temperature. Finally, there is one other essential condition, and that is an adequate supply of water to the growing organ: this is of importance in order that the cell or cells may be in a state of turgidity (p. 40), without which, as we shall see, growth is impossible.

It must not be supposed, however, that, provided that an organ is supplied with the necessary material, that the neces-

sary energy is being evolved, that the temperature is favourable, and that its cells are turgid, the organ will continue to grow indefinitely. Speaking generally we may say that the power of growing is possessed by an organ (and this is equally true of each individual cell of a multicellular organ) only during a particular period of its life: when this period is past, and during this period the organ has attained its limit of size and its permanent form, growth ceases, however favourable to continued growth the conditions may be.

Under certain circumstances, however, a mature organ, which has completed its period of growth, may again begin to grow. When, for instance, the general conditions under which an organ has been growing are suddenly altered, the disturbance may stimulate the organ to grow. Thus, it is commonly observed that when the haulms of Grasses are laid horizontally they will, in the course of a few days, assume an erect (vertical) position. This is due, as Sachs has shewn, to the fact that growth has recommenced in the nodes near the base of the haulm, and that it has taken place in such a way that the elongation of the lower surface of the nodes is greater than that of the upper surface. Again, injury to an organ may induce the growth of the cells in the neighbourhood of the seat of injury. Thus, cuts in stems, etc., are healed by the formation of a tissue termed *callus*, which is formed largely by the renewed growth of cells which had ceased to grow: further, injuries inflicted by insects often give rise to active local growth, of which the formation of *galls* is a conspicuous example, and this is true also in many cases when organs are attacked by parasitic Fungi. The most remarkable instances of an induction of growth are, however, to be found in connexion with reproduction. The egg or oosphere of plants is a cell which has ceased to grow, and if it remain unfertilised it will perish. But when it has been fertilised it grows actively and gives rise to the embryo. In very many cases the stimulating effect of fertilisation is not confined to the egg, but also induces growth in related organs: it is in consequence of such an induction of growth that the fruit of Phanerogams, for instance, is formed.

With these preliminary remarks we will pass on to consider the mechanics of growth, and we will begin by taking the case of a single cell.

I. *The Mechanics of Growth.*

All young cells (omitting from consideration those which do not possess a cell-wall) consist at first of a mass of protoplasm, including a nucleus, which is closely invested by a cell-wall, the whole being saturated with water. When the cell begins to increase in size, the protoplasm ceases to occupy the whole of the space enclosed by the cell-wall, that is to say that the bulk of the protoplasm does not increase as rapidly as the area of the cell-wall. Since the protoplasm remains in close connexion with the cell-wall at all points, the result of the disparity between the growth of the protoplasm and that of the cell-wall is that small cavities, termed vacuoles, make their appearance in the interior of the protoplasm, in which watery fluid, the cell-sap, collects. As the cell further increases in size, the vacuoles also become larger and usually coalesce so as to form a single large vacuole or sap-cavity which is lined at the surface by the peripheral protoplasm (primordial utricle), and which is traversed, for a time at least, by protoplasmic strands connecting the primordial utricle with a mass of protoplasm investing the more or less centrally placed nucleus. This condition of the cell is well shewn in Fig. 3 (p. 13).

These are very briefly the phenomena which may be observed in a growing cell: we have now to seek an explanation of them. The point upon which we shall first fix our attention is the growth in area of the cell-wall. It may be stated at once that the growth in area of the cell-wall is due to pressure exerted upon it by the cell-contents. In the early stage of the development of the cell, when it contains no vacuole, it is the protoplasm which exercises this pressure: in the later stages of its growth, it is the cell-sap which exercises it. We have already learned (p. 39) how a hydrostatic pressure comes to be set up in a cell, and there is evidence to

prove that the existence of this hydrostatic pressure, in other words, a turgid condition of the cell, is essential to its growth. It is a matter of common experience that plants will not grow unless they are supplied with water; on the contrary, under these conditions they wither. This point was made the subject of experiment by Sorauer. He grew a number of Barley-plants in soils containing different proportions of moisture, 10, 20, 40, or 60 per cent. of the amount requisite for the complete saturation of the soil, the other conditions being the same in all cases, and he found that within a certain limit—for, as we have already learned (p. 49), an excess of water is hurtful—the more moist the soil the more perfect was the development of the plant. We have here the proof of the importance of water in the process of growth. In the light of de Vries' experiments, we are able to explain Sorauer's results by attributing the imperfect growth of the plants in the relatively dry soils to the fact that in the absence of an adequate supply of water the turgidity of the growing cells could not be maintained. De Vries found, namely, that the growth of branches, peduncles, etc., was more or less diminished when they were placed in solutions of neutral salts (NaCl or KNO_3) of sufficient concentration to withdraw water from the growing cells and thus to diminish their turgidity, and that growth was entirely arrested when the solutions were sufficiently concentrated to cause complete plasmolysis in the cells (p. 43). The arrest of growth was not due to any injury done to the cells by the reagent employed, for de Vries observed that after thorough washing in water to remove the salt the organs resumed their growth.

It appears, however, that turgidity is not in all cases essential to the growth of cell-walls. Strasburger has pointed out that when pollen-tubes are being formed from pollen-grains the pollen-grains are not turgid. He attributes the growth in length of the pollen-tube to the pressure of the contained protoplasm. This is probably true, as mentioned above, of the growth of all cells in its first stage.

The distension of the cell-wall in consequence of the turgidity of the cell is not, however, growth, for the size of the cell can be diminished by diminishing the turgidity.

When we were discussing the osmotic properties of the cell (p. 39) we found that immersion in a 4 per cent. nitre-solution causes growing cells to become smaller, the reduction in size being due to the abstraction of water from the vacuole, in other words, to diminished turgidity. Increase in size of the cell due to growth cannot be affected in this way; it is permanent. But though the distension due to turgidity is not actual growth, yet it is only when thus distended that the cell-wall is capable of growth. The mechanism of the growth of the cell-wall is briefly this. Let us suppose a cell-wall to be of a certain size; it is then stretched somewhat by the turgidity of the cell: this temporary distension is gradually rendered permanent by growth, that is, by actual additions to the substance of the cell-wall; this increase in size is followed by further distensions, and these in turn are gradually rendered permanent by actual growth. A growing cell-wall is always on the stretch; at the same time a continuous addition to its substance is taking place which enables it constantly to increase in area, and this constitutes its growth.

We have now to deal with the question as to the mode in which the additions to the substance of the cell-wall, by means of which it grows in area, are made. This is a much-debated question, and there are two theories concerning it which especially demand our attention. The older one, due to Naegeli, is known as the *theory of intussusception* (p. 16). Starting from the fundamental idea of the micellar structure of the cell-wall (p. 32), Naegeli explains the growth of cell-walls as follows: when a growing cell is turgid the cell-wall is stretched and its constituent micellæ are so widely separated from each other as to admit of the intercalation of new micellæ of cellulose into the intervening watery areas; in this way the extended condition of the cell-wall is rendered permanent, and by a repetition of the process further growth takes place. The more recent view, of which Strasburger is the principal exponent, is entirely opposed to the preceding. In the first place he rejects the micellar theory, and he considers the existence of any mode of intussusceptive growth to be extremely improbable. He attributes the growth in area,

as well as the growth in thickness, of cell-walls to *apposition*. The distension of a cell-wall due to turgidity is rendered permanent, not by the intercalation of fresh particles of cellulose, but by the deposition of a layer of cellulose upon the internal surface of the one already existing. So long as the cell is turgid, this deposition of fresh layers of cellulose does not produce any considerable thickening of the cell-wall because, in consequence of the tension to which they are subjected, the layers are very thin; it is only when the cell has ceased to be turgid and has ceased to grow that the thickness of the cell-wall begins to increase materially (p. 291).

We will content ourselves with this brief statement of the two most important views as to the growth of cell-walls, for it would lead us too far were we to attempt to discuss the vast mass of facts and of observations upon which they are based. It is also impossible at this stage of the development of the subject to pronounce definitely for the one or for the other. Still, inasmuch as it has now been conclusively proved that the growth of starch-grains (p. 181) and the increase in thickness of cell-walls takes place by apposition, it is not improbable that the growth in area of cell-walls is effected in the same way.

In some cases the growth in area of the cell-wall is certainly not effected by intussusception, but by a modified form of apposition; for instance, the *intercalary* growth of the cell-walls in *Œdogonium*.

It has been already pointed out that the growth of the protoplasm in a cell is commonly small as compared with the growth of the cell-wall. We know so little about the structure of protoplasm that it is impossible at present to give any account of its mode of growth. It appears, however, that its growth is interstitial, that is, that growth goes on throughout its substance.

2. *Structure and Properties of Growing Organs.*

In our further study of growth we shall have to deal principally with growing organs which consist of a number of cells; it is important, therefore, that we should first of all form some idea of the structure and properties of such organs.

The members of plants which exhibit morphological differentiation, stem, leaf, and root, and the body of many Thallophytes, grow at first throughout their whole extent; but at a later period in their development the capacity for growth is possessed by certain parts only. As a rule the growth in length of a stem, a root, or a leaf, is confined to its apex. But this rule is not without exceptions, for it is not unfrequently the case that a zone of cells near the upper or lower ends of the internodes of stems or near the bases of leaves remains capable of growth; such zones are termed *intercalary zones of growth*. The growth in thickness too of stems and roots is confined to layers of cells at a greater or less depth from the surface, which may or may not be continuous so as to form complete zones as seen in transverse sections of the members.

In the growing apex of a member two regions are to be distinguished: (1) the apical region, or *punctum vegetations*, in which growth is relatively slow but cell-division active: (2) a region behind the apex in which growth is rapid, that is, in which the increase in size of the cells is active, but there is little or no cell-division, at least by the formation of transverse walls. Behind this, growth, at least in length, has ceased. An estimate of the relative lengths of these regions is afforded by Sachs' observations given in the following table. He marked out the terminal internode of the stem of a plant of *Phaseolus multiflorus* into twelve lengths, each of 3.5 mm., and he determined the amount of elongation of each of these lengths during a period of forty hours.

	<i>Increment.</i>		<i>Increment.</i>
Length 1 (apical) ...	2'0 mm.	Length 7 ...	1'8 mm.
" 2 ...	2'5 "	" 8 ...	1'0 "
" 3 ...	4'5 "	" 9 ...	1'0 "
" 4 ...	6'5 "	" 10 ...	0'5 "
" 5 ...	5'5 "	" 11 ...	0'5 "
" 6 ...	3'0 "	" 12 ...	0'5 "

We see that the maximum of growth took place in the fourth length. In view of the small difference in the rate of growth between the first and second lengths, and of the great difference between the second and third lengths, we may estimate the length of the *punctum vegetationis* in this case at 7 millimetres. The length of the second region is clearly much greater: we may estimate it at about 21 millimetres. The length of the whole growing region is therefore about 28 millimetres.

It must not be supposed, however, that the growing region of stems is confined to a single internode: it frequently extends over several internodes, the number being different in different plants, as the following table drawn up by Sachs will shew.

Plant	Length of growing region	Number of internodes
<i>Fritillaria imperialis</i>	7—9 c.m.	1
<i>Allium Porrum</i>	about 40 "	1
<i>Allium Cepa</i>	" 30 "	1
<i>Cephalaria procera</i>	" 35 "	3
<i>Valeriana Phu</i>	" 25 "	4
<i>Polygonum Sieboldi</i>	" 15 "	4—5
<i>Asparagus asper</i>	" 20 "	numerous

According to Askenasy there are growing simultaneously, in *Galium Mollugo* 8—10 internodes, in *Myriophyllum* 25—30, in *Elodea* 40—50, and in *Hippuris* there are so many that he doubts if any of them cease growing so long as the plant lives.

In roots Sachs found, as shewn in the following table, that the region of most rapid growth lies much nearer to the apex

than in stems, so that the growing region is altogether shorter.

The measurements were made upon a primary root of *Vicia Faba*: in this case the lengths were only of 1 mm., and the time 24 hours.

	<i>Increment.</i>		<i>Increment.</i>
Length 1 (apical) ...	1·5 mm.	Length 6 ...	1·3 mm.
" 2 ...	5·8 "	" 7 ...	0·5 "
" 3 ...	8·2 "	" 8 ...	0·3 "
" 4 ...	3·5 "	" 9 ...	0·2 "
" 5 ...	1·6 "	" 10 ...	0·1 "

In this case the length of the *punctum vegetationis* was not more than 1 millimetre, and that of the second region not more than 9 millimetres.

There is, however, no abrupt transition from the one region to the other. If we imagine a growing apex to be marked out into a great number of successive narrow transverse zones, beginning at the apex, each such zone will consist of cells growing with a certain degree of rapidity which is not the same as that of the zones on either side of it. Between the zones which exhibit respectively the greatest and the least rapidity of growth, there are a number of zones exhibiting various intermediate degrees of rapidity. These facts may be more clearly expressed by means of a formula. If the successive zones of a growing apex are indicated as $I \dots N \dots N+x$, the apical zone being I , the zone of most rapid growth being N , and the last zone of the growing region being $N+x$, the relation of their respective increments in the same time is as follows:

$$\begin{array}{ccccccc}
 \text{(apex) } I < II < III & \dots & < N^{\text{th}} > & N + I & \dots & > N + x. \\
 & & \text{maximum} & & & & \text{cessation.}
 \end{array}$$

In intercalary zones of growth the same two regions are to be distinguished, but in these cases the zone of cell-division lies between two zones of active growth. This relation is illustrated in the following table of some of Stebler's observations on the growth of the leaves of the Onion.

The basal portion of the lamina and the upper portion of the sheathing portion of the leaf were marked out into zones of 2·5 m.m. each,

zone I being the lowest and zone IX the uppermost : the figures give the increment in length of each zone for 24 hours.

		Day I	Day II	Day III	Day IV	
Sheath	{ Zone I	0.1 mm.	0.3 mm.	0.6 mm.	0.8 mm.	
	" II	0.1 "	0.4 "	1.0 "	2.2 "	
	" III	0.1 "	0.2 "	0.7 "	0.8 "	
	" IV	0.4 "	0.4 "	3.1 "	3.4 "	
	Lamina	" V	0.4 "	0.5 "	1.5 "	2.5 "
		" VI	0.2 "	0.3 "	1.0 "	1.7 "
		" VII	0.2 "	0.3 "	1.0 "	1.6 "
		" VIII	0.2 "	0.2 "	0.5 "	1.3 "
		" IX	0.1 "	0.1 "	0.1 "	0.2 "

Passing now to the properties of growing organs, the one which is of the greatest physiological importance is that of responding to the action of stimuli. Stimuli of the most various kinds, that of light, of gravitation, of electricity, of contact of foreign bodies, etc., produce modifications in the turgidity of the growing cells, which, when rendered permanent by growth, find their expression in curvatures and other alterations in the form and direction of growth of the organs, giving rise to the phenomena which are included under the terms heliotropism and geotropism, to the twining of tendrils, etc.; these phenomena we will study in subsequent lectures. In endeavouring to account for the ready response of growing organs to the action of these various stimuli, it is usually ascribed to an especial irritability of their protoplasm. But we must not overlook the greater mechanical facilities for such a response which young cells possess as compared with mature cells; we can easily understand that the form of a young cell with a relatively extensible cell-wall will be much more obviously affected by changes induced in its protoplasm, than that of an old cell in which the cell-wall is relatively inextensible.

A few words may be devoted to the purely physical properties of growing organs. It appears, from the observations of Sachs, that growing internodes are highly extensible but very imperfectly elastic. They are therefore very flexible: if they are strongly bent they retain a permanent curvature,

the concave side being shortened and the convex side lengthened; by repeated bending they may be moulded into almost any form. A familiar illustration of the flexibility of growing organs is afforded by the pendent position of many flower-buds on their peduncles or pedicels; the position is due to the fact that the flexible stalk is curved by the weight of the bud. Curvature of a growing organ can also be induced by concussion. If an erect growing shoot be struck laterally, a curvature, which persists for a time, is the result. Prillieux has pointed out that if the shoot be struck near the apex, its curvature is such that it is convex on the side upon which the blow fell: if, however, the shoot be struck near its base, the vibration travels upwards in the form of a wave, and the curvature of the apical growing portion is such that its concavity is on the side which was struck.

With regard to the distribution of extensibility in growing organs De Vries has shewn that, in growing stems, the maximum of extensibility and of flexibility exists somewhat behind the *punctum vegetationis*, that is, in the region of most active growth. As the tissues become mature their extensibility diminishes and their elasticity increases.

3. *Tensions in Growing Organs.*

We have learned that a state of tension, turgidity, as it is termed, is an essential condition of growth. All growing organs, therefore, exhibit this form of tension. But we have now to deal with tensions of another kind which are due, in the first place, to the fact that the cells do not all tend in the course of their growth to attain the same form, but to assume different forms. At the apex of a growing stem, for instance, some of the cells increase in all dimensions to form the kind of permanent tissue which is known as parenchyma, whereas others increase especially in length to form the kind of permanent tissue which is known as prosenchyma. Further, this histological differentiation is accompanied by differences in the chemical composition and in the physical properties of the cell-walls. The walls of the epidermal cells,

at least towards their free surface, become thickened and cuticularised; the cells forming the vascular tissue and the sclerenchyma-strands become thickened and lignified, and in some instances (vessels) they lose their protoplasmic contents. The result is that the epidermal, vascular, and sclerenchymatous tissues become more and more inextensible and rigid. The cell-walls of the parenchymatous ground-tissue—of which the pith constitutes the principal mass—have not, on the other hand, undergone these changes; they remain, for a time at least, thin and extensible. Inasmuch as these different tissues are firmly coherent; and since the epidermal, fibrous, and vascular tissues are relatively rigid, whereas the thin-walled parenchymatous tissue is relatively highly extensible and tends to expand in consequence of its turgidity; tensions are set up between them the nature of which we shall proceed to study.

It has been found that the tensions thus arising are distributed in two directions, longitudinally and transversely. The longitudinal tension in growing stem-structures (shoots, peduncles, petioles) can be readily demonstrated by splitting the organ from above downwards, by two longitudinal cuts at right angles to each other, into four segments: the segments diverge and bend concavely outwards. This curvature is due to the elongation of the pith and to the shortening of the external tissues. Whilst the organ was still entire, the turgid pith was prevented from elongating to its full extent by the rigidity of the other tissues; it was in a state of *active* or *positive* tension: the external tissues, and especially the epidermis, were stretched by the pith; they were in a state of *passive* or *negative* tension. This is made clear by the following measurements which are due to Sachs.

A thick longitudinal slice was cut out of a growing internode of *Silphium perfoliatum*: it was then laid flat, and the pith was divided by a longitudinal cut; the two halves diverged.

	Shortening of the concave outer (epidermal) side.	Lengthening of the convex inner (pith) side.
Right half	2·4 per cent.	9·3 per cent. of the length of the entire internode.
Left half	2·8 „	9·3 „ „

In other cases the various tissues were separated from each other and the variation of their length determined, as in the following instance. The length of the internode is taken as 100, and the variations in length are estimated as percentages, shortening being indicated by a minus sign, and lengthening by a plus sign. The plant in the case given was *Nicotiana Tabacum*.

Number of the internode, beginning at the youngest	Variation in length of the tissues		
	Cortex	Vascular tissue	Pith
I—IV	-5.9	-1.5	+2.9
V—VII	-3.1	-1.1	+3.5
VIII—IX	-3.5	-1.5	+0.9
X—XI	-0.5	-0.5	+2.4

The following general expression for the relative lengths of the tissues after isolation has been given by Sachs, where E, C, V, P, stand respectively for epidermis, cortex, vascular tissue, and pith :

$$E < C < V < P > V > C > E.$$

This expression also states the relative active tension (compression) of the layers, for the greater the compression the greater will be the elongation of a tissue on isolation. The expression for the passive tension (stretching) will be

$$E > C > V > P < V < C < E.$$

The most general statement of the distribution of the longitudinal tension in stem-structures is that, passing from the centre to the surface, each of the layers of tissue is stretched by the layers internal to it, and is compressed by the layers external to it.

In the case of roots the longitudinal tension is much less considerable. If the growing apex of a root be slit vertically, the two halves remain at first in contact : it is only after lying for some time in water, and in consequence of subsequent growth, that any curvature becomes perceptible. It is then of this kind, that the two halves remain in contact at the apex, but bend away from each other, so that their external

surfaces are convex, between the apex and the point up to which the cut reaches. This curvature is due to the more active growth of the cortical ground-tissue which lies between the vascular tissue and the epidermis, and which constitutes the principal mass of the parenchymatous ground-tissue of the root. It indicates the existence in the root of a longitudinal tension, though a very slight one, of this kind, that the cortical ground-tissue is in a state of active or positive tension, and that the vascular and the epidermal tissues are in a state of passive or negative tension.

The transverse tension in growing stem-structures can be readily demonstrated by taking a rather thick transverse section of the growing region and dividing it into two halves by a diametrical cut, when the two cut edges will become convex to each other: or again, by taking off a ring of cortical tissue and attempting to replace it, when it will be found impossible to make the two ends meet. The curvature, in the first case, is due to the expansion of the pith, and to the shortening of the external tissues: the increase in bulk, in the second case, is due to the expansion of the pith consequent upon the removal of the resisting cortical tissue. The transverse tension is due to the fact that the thin-walled turgid parenchymatous tissue, and especially the pith, tends to expand, not in length only, but in all directions. Moreover the epidermis tends to become narrow in consequence of being stretched by the longitudinal tension, and this contributes materially to increase the transverse tension. The general distribution of the transverse tension is much the same as that of the longitudinal tension.

In roots the transverse tension, like the longitudinal, is scarcely appreciable. If a transverse section of the growing region of a root be taken and divided in the manner described above, no curvature will be at first seen, but, if the halves be left in water, they will gradually become concave to each other, owing to the expansion of the cortical parenchymatous tissue.

In some instances (internodes of Grasses and *Equisetum*, peduncles of Dandelion, etc.) the growth in circumference of the organ is so great that the pith not only exercises no

transverse pressure upon the external tissues, but is stretched radially by them, and to such an extent that it cannot keep pace with their tangential growth, but ruptures, so that the organs become hollow.

Inasmuch as these tensions are the result of unequal turgidity and growth and of the progress of histological differentiation, we should expect to find that they are exhibited in different degrees by different regions in a growing organ. This has been determined experimentally by Kraus. He has found, with regard to the longitudinal tension, that in the youngest internode of a stem the pith does not alter in length on isolation; it was therefore not in a state of tension when in the internode; but the external tissues, vascular, cortical, and epidermal, shorten somewhat on isolation, and were therefore in a state of passive tension. In somewhat older internodes the pith is slightly compressed and the external tissues stretched, the tension being greater the more external the tissue; this stage corresponds to the numerical illustration given above. In still older internodes the only perceptible effect of the isolation of the tissues is the elongation of the pith. These observations are to be explained thus; that in the youngest internode the histological differentiation is rudimentary and the external tissues are very extensible and yield readily to the tension due to the expansion of the pith, whereas in the older internodes histological differentiation has proceeded so far that the vascular and epidermal tissues are well-developed and their cell-walls have become thickened and somewhat rigid, but they still yield to the expansion of the pith; in the still older internodes the vascular and epidermal tissues have become fully developed and are now so rigid that they do not yield at all to the turgid pith, but passively resist it. The transverse tension is distributed in the manner described above for the longitudinal tension, but, as already mentioned, the surface-growth of the organ may eventually be so great as to cause a radial stretching of the pith and even its rupture. The tensions are greatest in the second of the stages described above, when the external tissues offer a certain elastic resistance to the expansion of

the pith but are stretched by it; in the third stage the tensions are less considerable, and in still older internodes in which the pith-cells have ceased to be extensible and even to be turgid the tensions disappear altogether.

In many plants, those parts of the stems and roots which have ceased to grow in length, continue to grow in thickness by means of a zone of meristematic cells. The most common mode (Dicotyledons, Conifers) of this growth in thickness is that new cells are produced by division from this zone, which is termed the *cambium-layer*, and that these then grow to form, on the outside of the cambium-layer, bast or phloëm-tissue, and on the inside, wood or xylem-tissue. Constant additions are thus made to the vascular tissue on each side of the cambium-layer. The result is that the tissues external to the ring of vascular tissue, namely the older bast, the cortical, and the epidermal tissues, are subjected to a transverse pressure from within outwards, and that the tissues internal to the cambium-layer, namely, the older wood and the pith, are subjected to a transverse pressure from without inwards. And conversely, the tissues outside the cambium-layer exercise a pressure upon it from without inwards, and the tissues inside the cambium-layer exercise a pressure upon it from within outwards. A considerable tension is thus set up between the internal and the external tissues, the effect of which is to stretch the latter in the peripheral direction, that is, in a direction parallel to the surface of a transverse section of the organ, and to compress the former, though owing to the rigidity of the older wood the effect of the compression is slight. The relation between the various external layers of tissue is this, that each is stretched by the layer next inside it and compressed by the layer next outside it. This great and increasing pressure soon produces a visible effect upon the external tissues: they rupture, and longitudinal fissures appear on the surface. The rupture does not, however, produce open wounds, for in the meantime a formation of cork has been taking place beneath the epidermis. The cork, in its turn, is ruptured and shed in scales or in rings which are replaced by fresh formations.

4. *Influence of the Tensions upon the Growth of the Cells.*

We gather from what has already been said that the wall of a growing cell is subjected in all cases to a pressure from within, due to its own turgidity, and, in the case of a cell forming part of a tissue, to a pressure from without exerted upon it by the surrounding cells. It has been already mentioned that each cell tends in the course of its growth to assume a particular form, and we have now to determine in the first place the mode in which this tendency obtains expression, and secondly, the effect of the pressure of surrounding cells in modifying the form which the cell naturally tends to assume.

In discussing the former of these points, let us first consider the case of a cell, a unicellular plant for example, which is free, that is, not coherent with other cells. In this case only the internal pressure due to turgidity has to be taken into account. The form assumed under such circumstances by the cell in the course of its growth is determined by the distribution of extensibility in the cell-wall. If the cell-wall be uniformly extensible, then, since the hydrostatic pressure is the same at all points of its internal surface, the cell-wall will be uniformly stretched, and the general form of the cell will continue to be that which it originally possessed. If, however, the cell-wall be not uniformly extensible, but some areas are more extensible than others, then the more extensible areas will yield to the internal pressure, and the result will be the formation of outgrowths and a complete change in the form of the cell.

The inequalities of extensibility in the wall of a growing cell can only be ascribed to differences of structure in different parts. These differences of structure may depend upon differences in thickness due to an unequal deposition of cellulose on the internal surface of the wall, or upon an alteration in the molecular structure of the wall effected by the protoplasm, the result of which is to cause

certain areas of the cell-wall to become less dense, more capable of imbibition (p. 15), and then also more extensible, than the rest. No adequate explanation can at present be given of the nature of this action of the protoplasm, but there can be no doubt that it actually takes place. As an illustration of its importance in relation to change of form, Strasburger mentions that when a lateral branch is to be developed upon a somewhat old cell of *Cladophora*, an area of the cell-wall, at the point where the branch is subsequently borne, swells up by imbibition, becomes more extensible than the rest of the wall, and, under the pressure of turgidity, is forced outwards so as to form a protuberance. The further growth of this protuberance is effected by the same means: the wall remains extensible at the apex, and thus the protuberance elongates until the limit of growth is reached. It is then, in any case, by the protoplasm that the distribution of extensibility in the growing cell-wall is determined, and it is therefore upon the protoplasm that the ultimate form of the cell depends.

We will now pass to the second of the two points raised above, namely, the effect of the tension of the tissues upon the form ultimately assumed by the cells of which they consist. It is obvious that when a number of cells are closely coherent, as in a growing point, the pressure which they mutually exert must to some extent modify the natural growth of the individual cells, and must therefore considerably affect the ultimate form of the cells. Examples of this are constantly presenting themselves in the study of the histology of plants. The most striking of these are produced by the transverse tension, especially that which is set up in consequence of the secondary growth in thickness of stems and roots. Still the longitudinal tension is not without its effect in this respect, though it is not so readily demonstrable. There can be no doubt, for instance, that the elongated form of the cells of the fibrous and vascular tissues is due in great part to the stretching to which they were subjected, as described above, by the turgid pith whilst they were still growing: and conversely, the resistance of the peripheral tissues

causes the cells of the pith to be shorter and broader than they otherwise would be.

A good illustration of the effect of the transverse tension which exists in growing stems independently of a secondary growth in thickness, is afforded by the development of *tyloses*. It had long been observed by histologists that the cavities of the vessels of the wood of the stems and roots of various plants are filled with delicate parenchymatous tissue, but the mode of origin of this tissue was not clearly understood until Reess made his researches upon the subject. It is formed in this way. When a vessel having large bordered pits in its wall abuts upon a parenchymatous cell, the delicate membrane which separates the lumen of the vessel from the cavity of the cell gradually grows into the lumen of the vessel so as to form a considerable protuberance (Fig. 40), the tylose,

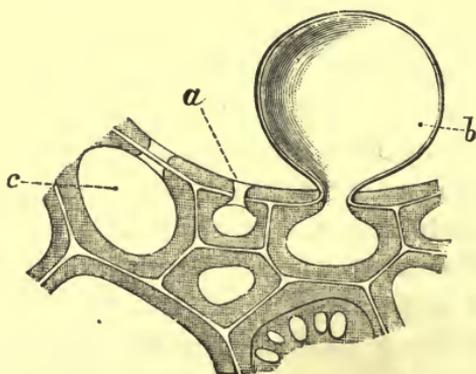


FIG. 40 (after Weiss). Portion of a vessel (a) of *Vitis vinifera* with adjoining wood-cells (c), one of which has grown into the lumen of the vessel to form a tylose (b).

which may even undergo cell-division. This takes place at several points in the wall of the vessel, and thus its lumen becomes filled with parenchymatous tissue. The physiological explanation of the phenomenon is this. The turgid parenchymatous cells are compressed longitudinally by the resistance offered by the fibrous and vascular tissues to their elongation: the effect of this is that the parenchymatous cells tend to expand laterally, and they press with great force against the lateral walls of the fibres and vessels. The pres-

sure upon the wall between a parenchymatous and a vascular cell is, whilst the vascular cell is young and turgid, the same on both sides, but, as the vascular cell becomes gradually differentiated so as to form a segment of a vessel, it loses its protoplasmic contents, and with them its capacity for becoming turgid: the wall is now subject to pressure from the side of the parenchymatous cell only, and those portions of it which have remained thin and extensible, the pit-membranes, yield to the pressure and grow out into tyloses in the manner described above. The fact that the parenchymatous cells begin to grow at those points at which the pressure upon them is removed, proves that their growth is hindered by the pressure to which they are subjected by the other tissues, and this must have much to do with determining their ultimate size and form.

The effect of the transverse tension due to the secondary growth in thickness of stems and roots manifests itself very clearly and in various ways. For instance, it is characteristic of the cortical tissues of these organs that their cells, as seen in transverse section, are elongated peripherally. This elongation is the expression of the stretching of the cells under the radial pressure exerted upon them by the growing vascular tissue. In some cases this peripheral stretching may be carried so far that the two walls of the cells meet and the cavities are completely obliterated: Strasburger mentions the older sieve-tubes of *Pinus* as affording instances of this. Another illustration of the effect of this tension in modifying the form of cells is afforded by the difference in size, as seen in transverse section, between the vessels and cells of the wood produced in the spring and those produced in the autumn, the difference to which is due the marking out of the wood into the "annual rings" which is so conspicuous in the wood of dicotyledonous and coniferous shrubs and trees. The difference in size is due to the fact that the transverse tension is greater in the autumn than in the spring. During the winter the cortical tissue becomes dry and cracks, so that when the formation of new wood from the cambium-layer begins in the spring the transverse tension is relatively small

and the cells formed are relatively large: but as the summer goes on the tension increases, owing to the continued formation of wood and bast by the cambium, and the size of the newly formed cells diminishes. De Vries has proved the correctness of this explanation by artificially increasing the tension in branches in the spring by means of a tightly wrapped ligature of twine, and observing that the cells formed under the ligature were smaller than those formed beyond the limits of the ligature. Knight's experiments supply evidence of the same kind. He fixed young apple-trees so that the lower part of the stem could not be moved by the wind, leaving the upper part free to move. He found that the upper free part increased in diameter much more rapidly than the lower fixed part. The explanation of this difference is that, owing to the swaying caused by the wind, the cortical tissues of the upper free portion were stretched, and therefore the pressure exercised by them upon the growing cells in the cambium-region was smaller than that in the lower fixed portion of the stem.

The existence of this considerable transverse tension and its effect upon the development of the tissues has long been recognised in horticulture. It is a common practice to split the cortex of young trees in the summer with a view to promoting the formation of woody tissue. The consequence of this is that more water can be conveyed upward to the growing parts, and an increased formation of buds and leaves is brought about.

A further illustration of the effect of this transverse tension upon the development of the tissues is afforded by excentric stems and roots, in which, namely, the annual rings of wood and the cortex are thicker at some parts than at others. This is due to local differences of tension; where the tension is the smallest the growth in thickness is the most rapid, and conversely. The differences of tension are due to a loosening of the cortex at certain parts which may be brought about by various causes. Thus Knight observed in the case of young apple-trees which were so secured that they could be swayed by the wind only in a plane lying

north and south, that in the course of a year the north and south diameter of the stem exceeded the east and west diameter in the proportion of thirteen to eleven. The greater growth in the thickness along the north and south diameter is the consequence of the stretching and loosening of the cortex on the north and south sides of the stem by the action of the wind. Again, Detlefsen has observed that the development of lateral branches on stems and roots produces excentricity which is likewise the expression of local diminution of the transverse tension. The diminished tension is the result of the growth of the lateral branches which tend to loosen the cortex and hence to diminish the tension. There is thus a region extending for some distance downwards from any of the larger lateral branches of the stem and upwards from any of those of the root in which the tension is diminished; accordingly growth in thickness is more active here, and the annual rings of the stem or of the root come to be excentric.

We may perhaps include among the phenomena which we are now considering some of the cases of torsion, those, namely, which appear to be due to internal causes. The surface of many organs, especially internodes and leaves, present striæ which twist round the long axis of the organ. They are very apparent, for instance, in the internodes of *Chara*. These striæ of cortical tissue are, as Sachs points out, necessarily longer than the organ on which they are present, and this suggests that they are due to a longer duration of the growth of the cortical as compared with the internal tissues, a conclusion which is supported by the fact that the striæ make their appearance towards the end of the period of growth in length of the organ. The increase in length of the external tissues is resisted by the internal tissues. If the line of action of this resistance were parallel to the long axis of the organ, the external tissues would not become twisted, but would remain in a state of positive tension: this can be, however, but rarely the case; hence the result of the tension between the external and the internal tissues is that the former become twisted. This explanation is supported by

Kraus' observations on the occurrence of torsion in etiolated internodes, a peculiarity to which Sachs first drew attention. Kraus finds that the peripheral cortical cells, towards the end of their growth, pass from the parenchymatous to the prosenchymatous form; this is accompanied by considerable elongation, and it is at this time that torsion can be noticed on the surface. Observations leading to the same conclusions had been previously made by Braun on the development of prosenchymatous wood-cells from the cambium.

In connexion with these cases of torsion, we may notice a curious phenomenon exhibited by roots which de Vries has recently brought to light. It had been observed long ago that the surface of the older parts of many roots (Red Clover, Beet, *Dipsacus Fullonum*, Artichoke) is marked by transverse or oblique wrinkles. De Vries finds that these wrinkles are due to a change in form of the parenchymatous cells of the root. When growth in length has ceased, these cells tend to increase in breadth, and in so doing become shorter: this causes the wrinkles in the cortical tissue, and also curvatures of the vascular tissue.

5. *The Grand Period of Growth in Length.*

Now that we have acquired some notion of the structure and properties of growing organs and of the mutual relations of the cells composing them when they are multicellular, we may go on to consider in greater detail the process of growth itself. It has been already mentioned (p. 333) that the growth of a cell is, generally speaking, limited to a particular period of its life. But the rate of growth is not uniform throughout this period. At first the cell grows slowly, then more and more rapidly until a maximum rapidity is reached, and then the rapidity diminishes until growth ceases altogether. This cycle is termed the *Grand Period of Growth*. It is due entirely to causes inherent in the growing cell, and though its regularity may be temporarily interfered with by variations in external conditions, yet it will on the whole assert itself in opposition to them.

The grand period is exhibited as well by multicellular organs as by single cells, and we shall best illustrate it by reference to the former. We have seen (p. 338) that a growing apex may be regarded as consisting of successive zones of cells: those nearest the apex consist of young cells which are growing but slowly; others, further from the apex, consist of older cells which are growing rapidly; others again, still further from the apex, consist of nearly mature cells which are ceasing to grow. This mode of regarding the growing apex gives us an idea of the distribution of the activity of growth *in space*. If, however, we regard these zones, not as a series of successive zones, but as representing successive stages in the growth of a single zone, we gain a conception of the distribution of the activity of growth *in time*, that is, of the Grand Period. As a matter of fact any one zone does, in the course of its growth, occupy the positions of these successive zones and exhibits the corresponding rates of growth. At first it lies near the apex in the *punctum vegetationis*, and then its growth is slow: by the formation of new cells in front of it, it is gradually removed further and further from the apex, and its growth becomes more and more rapid until the maximum rapidity is attained; as its distance from the apex continues to increase, the rapidity of its growth rapidly diminishes, and ultimately it ceases to grow.

The following determinations of the grand period of growth of zones of growing organs were made by Sachs.

1. Zone 1 mm. in length, marked just behind the *punctum vegetationis* of a primary root of *Vicia Faba*.

<i>Time.</i>	<i>Increment.</i>
1st day (24 hours)	1·8 mm.
2nd "	37 "
3rd "	17·5 "
4th "	16·5 "
5th "	17·0 "
6th "	14·5 "
7th "	7·0 "
8th "	0·0 "

2. Zone 3.5 mm. in length, at the upper end of the first internode of *Phaseolus multiflorus*.

<i>Time.</i>	<i>Increment.</i>
1st day (24 hours)	1'2 mm.
2nd „	1'5 „
3rd „	2'5 „
4th „	5'5 „
5th „	7'0 „
6th „	9'0 „
7th „	14'0 „
8th „	10'0 „
9th „	7'0 „
10th „	2'0 „

The grand period of an entire internode of the flowering stem of *Fritillaria imperialis*: the figures represent the increments in periods of 24 hours (Sachs).

March 20	2'0	March 30	6'3
„ 21	5'2	„ 31	4'7
„ 22	6'1	April 1	5'8
„ 23	6'8	„ 2	4'4
„ 24	9'3	„ 3	3'8
„ 25	13'4	„ 4	2'0
„ 26	12'2	„ 5	1'2
„ 27	8'5	„ 6	0'7
„ 28	10'6	„ 7	0'0
„ 29	10'3		

Inasmuch as a growing organ, a root or an internode for instance, consists of a number of zones growing simultaneously, the increase in length of the organ in a given time will be the sum of the increments of the growing zones, the rate of its growth at a given time will be the mean of the rates of growth of the zones, and its grand period will begin at the commencement of that of the first zone and will extend to the end of that of the last.

The following table of observations made by Sachs upon an internode of *Phaseolus multiflorus* illustrates the relations mentioned above. The internode was marked out into 12 zones each 3.5 mm. long: the figures give the daily increment in millimetres.

It will be seen that the figures refer only to the latter part of the grand period of the internode.

Zones	Day I	II	III	IV	V	VI	VII	VIII	IX	X	Total elongation of each zone and of whole internode
Uppermost (youngest)	1	1.5	2.5	5.5	7.0	9.0	14.0	10.0	7.0	2.0	59.7
	2	1.5	6.0	9.0	9.5	9.5	3.5	1.0			41.5
	3	2.7	6.5	6.0	2.0						20.2
	4	3.9	3.0	1.0							10.4
	5	3.3	0.5								4.8
	6	1.8									2.3
	7	1.1	0.5								1.3
	8	0.6	0.2								0.9
	9	0.6	0.3								0.6
	10	0.3									0.3
	11	0.3									0.3
	12	0.3									0.3
Daily elongation of whole internode)	17.6	10.5	18.5	21.5	18.5	18.5	17.5	11.0	7.0	2.0	142.6

Again, since a stem consists of a number of internodes several of which may be growing simultaneously, the growth of the stem as a whole will stand in the same relation to the growth of its constituent internodes, as the growth of the internodes does to that of their constituent zones.

Another point worthy of note is that the duration of growth and the mean rate of growth is not necessarily the same for all internodes. It has been observed in many cases that the internodes first formed in a growing-season are shorter than those formed somewhat later, and that those which are formed towards the end of the season are again short. These differences in length are the expression of differences in the energy of growth of the internodes; the longer the internode, the greater its energy of growth: and since the length of the internode is the product of the mean rate of growth multiplied by the units of time, differences in the energy of growth find their expression either in greater or less rapidity of growth, or in longer or shorter grand periods.

The grand period of growth may be conveniently represented by curves constructed with units of time as abscissæ and units of increment in length as ordinates. If the curve for any organ be constructed from measurements made at long intervals, say of 24 hours, the outline of the curve will be tolerably even: but if it be constructed from measurements made at short intervals, the outline of the curve will be found to be very irregular, and the irregularity will be the greater the shorter the intervals at which the measurements are made. These irregularities are to be ascribed, to some extent, to variations in the external conditions, to variations of temperature, in intensity of illumination, etc.; these we shall subsequently consider in detail under the head of the Daily Periodicity of Growth. But many of them cannot be thus accounted for, and these must be regarded as due to variations in the rate of growth which are dependent upon conditions inherent in the organ. Sachs was the first to draw attention to these irregularities in the curve of the grand period, and he termed them "stossweise Aenderungen."

In illustration of these irregular spontaneous variations the following instances may be mentioned.

Baranetzky, in his researches on the growth in length of stems, kept various plants for some days in darkness at as nearly as possible a constant temperature, and made hourly

measurements. He found that in the course of their growth irregular periods (indicated by the occurrence of maxima) occurred: thus in plants of *Gesneria tubiflora* the period usually extended over 2—4, and sometimes over 6—8 hours, and in some etiolated plants of *Brassica Rapa* he detected a fairly regular daily period in the growth of the stems, the maximum occurring once in every 24 hours at approximately the same time for each particular plant.

Drude studied the growth of the leaves of *Victoria regia*. In consequence of the great rapidity of growth he was able to make an observation every five minutes; hence his results exhibit very clearly the frequency and the extent of the spontaneous irregular variations in the rate of growth.

The following are examples of Drude's observations: they begin at 11 p.m. on Aug. 4 and extend to 1 a.m. on August 5: the temperature both of the water and of the air varied scarcely at all during the time, and the plant was exposed to candle-light: the measurements refer to the growth of the petiole only, and are in millimetres.

	11 p.m.—12	12—1 a.m.
Total growth per hour	99·4	127·9
1st five minutes	7·1	8·6
2nd "	8·6	7·7
3rd "	8·8	8·6
4th "	9·0	7·2
5th "	8·0	7·0
6th "	9·1	9·3
7th "	7·9	6·8
8th "	9·3	10·0
9th "	7·9	12·4
10th "	8·0	15·0
11th "	7·4	17·4
12th "	8·3	17·9

In our consideration of growth of length, we have hitherto tacitly assumed that all the cells which constitute any given transverse zone of a growing organ are growing with the same rapidity at any given moment. But this is by no means always the case. In organs which grow rapidly the rate of

growth of the cells lying at the same level is commonly not uniform. These variations in the rate of growth are, like those which we have already considered, spontaneous: they take place when the external conditions are maintained as constant as possible, for example, when temperature does not vary and the plant is kept in darkness.

The effect of these variations upon the direction of growth of an organ will be made clear by the following considerations. As the result of its growth, every organ takes up a certain definite position. A straight line running through the axis of the organ from its base to its apex will indicate the direction in which its growth in length has taken place. If, during the whole period of the growth of an organ the growth of each transverse zone is uniform throughout its whole extent, a line drawn through the axis of the growing portion will at all times coincide with the prolongation of the line drawn through the axis of the portion which has ceased to grow. But if, in one or more zones, the growth of one portion be greater for any time than that of the remainder, the line drawn through the axis of the growing portion will not at that time coincide with the prolongation of the line drawn through the axis of the portion which has ceased to grow, but will at some point form an angle with it. This deviation of the two lines constitutes the *Nutation* of the organ, and the extent of the nutation is measured by the size of the angle at the point of intersection of the two lines. Let us, to illustrate these statements, take the case of an erect growing stem. A line drawn through the axis of that portion of the stem which has ceased to grow, is vertical. If all the transverse zones of the growing portion are growing at a uniform rate throughout their whole extent, the line drawn through the axis of the growing portion will also be vertical. But if certain portions of one or more zones lying together at one side are growing more rapidly than the remaining portions, the apex of the stem will be tilted out of the vertical away from the side on which growth is most active, and hence the lines drawn respectively through the axes of the parts of the stem which have and have not ceased

to grow will form an angle at a point in the region in which the unequal growth is taking place.

Coming now to the actual phenomena of nutation, we find that it presents itself in different forms, the form being dependent upon the peculiar organisation of the plant which we may attempt to explain in the following manner. The simplest form of nutation is that in which the axis of the growing portion travels in one plane from one side to the other of the prolongation of the axis of the portion which has ceased to grow, forming an angle with it first on this side and then on that. It is this form of nutation which is usually termed *Simple Nutation*, or merely *Nutation*. It is produced by the alternate and more rapid growth of two opposite longitudinal halves of the growing region of the organ, the two longitudinal halves occupying permanently the same relative positions. A more complex form of nutation is that which is known as *Revolving Nutation*. In this, the axis of the growing portion does not oscillate from side to side of the prolongation of the axis of the portion which has ceased to grow, but describes an orbit about it. This, like simple nutation, is produced by the more rapid growth of one side of the organ as compared with that of the side opposite to it, but the differences in the rapidity of growth are not confined in this case to two particular sides. A wave of more rapid growth travels, as it were, round the growing organ from segment to segment. Let us take illustrative cases. A growing organ exhibits simple nutation in any one plane, say a plane running east and west; this is due to the alternate more rapid growth of the west and east sides of the organ, and the differences in the rate of growth are exhibited only by these two sides. In an organ which exhibits revolving nutation, the nutation is not confined to any one plane, but takes place from east to west, from north to south, and in all intermediate planes as well; all sides take on in succession a period of most rapid growth.

According to Baranetzky revolving nutation is not spontaneous but is induced by the action of gravity. Stems which are withdrawn from

the action of gravity exhibit only some form of simple or undulating (see *infra*) nutation.

We will now discuss the form of the orbit described by the apex of a growing organ which exhibits revolving nutation. The form of the orbit depends upon two factors: first, upon the form of the outline (as seen in transverse section) of the growing organ: secondly, upon the relative rapidity and duration of the more active growth attained in succession by the various segments. If the increased rapidity of growth attained by each segment, and the time of duration of this more rapid growth, be the same for all, it is clear that the form of the orbit will be determined by the form of the transverse section of the region in which the unequal growth is taking place: for instance, if, as is very commonly the case, the transverse section of the organ is approximately circular, then the form of the orbit will be approximately circular. But if one or more of the segments attain a greater rapidity of growth than is attained by the others, or if the duration of the period of more rapid growth is longer in some segments than in others, then the form of the orbit will not correspond to the outline of a transverse section of the organ, but will deviate more or less from it. These factors cooperate to produce the different forms of the orbit which vary from the circular, in which all diameters are equal, to forms in which the longest diameter is very much greater than the shortest, to forms, that is, which approximate to a straight line. We see then that we have all intermediate forms of orbit, from the straight line in simple nutation, to the circular which is the most perfect expression of revolving nutation. It is because of the existence of all these intermediate forms that Darwin has ceased to distinguish between "simple" and "revolving" nutation, but includes all these phenomena under the one term *Circumnutation*.

The length of the diameter of the orbit is determined by the length of the portion of the growing organ which intervenes between the apex and the region of nutation, and upon the curvature of the growing portion. For instance, Darwin

observed in the case of a Hop-plant, that the length of the circumnutating portion of the stem was about 15 inches, and the curvature was such that the diameter of the orbit was 19 inches: in the case of a plant of *Ceropegia Gardnerii* the circumnutating stem, 31 inches long, was nearly horizontal, so that the diameter of the orbit was about 5 feet.

We have dealt, so far, with those phenomena of nutation which would be best observed by looking down from above upon a nutating apex, that is, with the horizontal motion, and we have therefore spoken as if the orbit lay accurately in one plane. We must remember, however, that while the apex of a growing organ is describing its orbit it is also elongating, that it has also a vertical motion; its path is then such that the orbit does not lie exactly in one plane. The path described by the apex of a nutating organ will of course depend upon the form of its nutation. The apex of an organ exhibiting simple nutation will trace a zig-zag course about the prolongation of the axis of the portion which has ceased to grow, whereas that of an organ exhibiting revolving nutation will trace a spiral of some form. In the latter case the direction of the spiral is not always the same: in some plants (Hop, *Scyphanthus elegans*, *Tamus communis*, *Lonicera brachypoda*, etc.) the direction of nutation is that of the sun, or of the hands of a watch, in others (*Akebia quinata*, *Wistaria chinensis*, *Phaseolus vulgaris*, *Ceropegia Gardnerii*, various species of Convolvulaceæ, *Aristolochia gigas*) the direction of nutation is contrary to that of the sun or of the hands of a watch.

The rate at which the orbit is described varies widely in different plants, as the following observations made by Darwin will shew:

Plant.	Time for one complete revolution.			
	Longest.		Shortest.	
	H.	M.	H.	M.
<i>Tamus communis</i>	3	10	2	30
Hop	2	20	2	0
<i>Akebia quinata</i>	4	0	1	45
<i>Wistaria chinensis</i>	3	21	2	5
<i>Ceropegia Gardnerii</i>	7	55	5	15
<i>Adhatoda cydonifolia</i>	48		26	30

and further, the rate is not uniform for any given plant as the above table shews. The variations in the rate of revolution of any one plant are doubtless to be attributed to some extent to variations in external conditions; but it appears from Darwin's observations that the rate of revolution is generally slower at the commencement of circumnutation than it is subsequently.

The following diagram will serve to illustrate circumnutation. The small upper circle divided into segments represents an ideal transverse

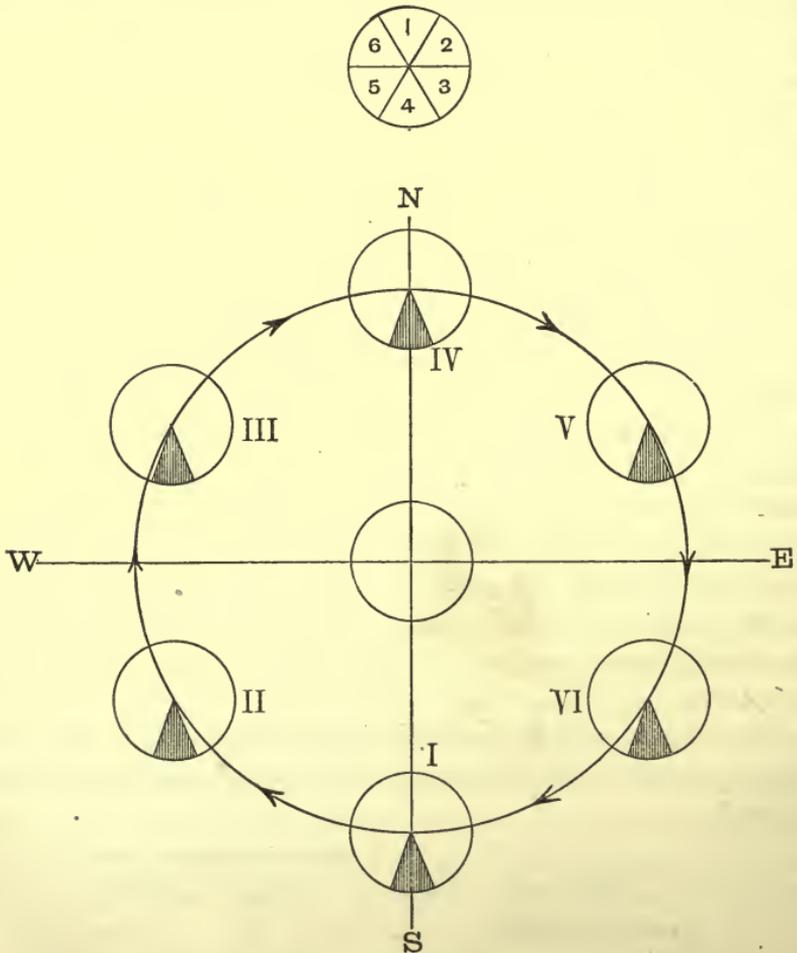


FIG. 41.

section of the region of nutation of a stem exhibiting circumnutation. The large circle below represents the orbit of circumnutation as seen from above, and the small circles upon it represent different positions of

the apex of the stem in its orbit: the shaded segment in each of the small circles serves to indicate the position throughout the orbit of one and the same side of the stem: the small circle in the centre of the orbit represents the position of the apex when the axis of the growing portion coincides with the prolongation of the axis of the portion which has ceased to grow. Let us assume, to begin with, that the rate of growth is uniform in all the segments of the transverse section of the growing region; the position of the apex of the stem at this time is indicated by the small circle about the centre of the orbit. But let us suppose that the growth in length is not uniform and that a portion of the growing region, segment 1 for instance, is the seat of the most rapid growth; then, as explained above, segment 4, which is opposite to segment 1, will be the portion which is growing in length at the slowest rate: the effect of this unequal growth is that the north side of the organ becomes convex and the south side concave, and in consequence of this curvature the apex is removed from its first position to a position which we may call I. The wave of rapid growth then travels from segment 1 to segment 2, and the apex travels from position I to position II; each pair of opposite segments exhibit in succession a kind of polarity, such that when one of the segments is growing the most rapidly, the one diametrically opposite to it is growing the least rapidly: at length segment 1 again becomes the seat of the most rapid growth and the apex again comes to lie in position I.

It will be observed that the shaded segment faces towards the same side, the south, in all positions of the orbit. This illustrates the fact that circumnutation is not accompanied by any twisting of the organ about its own axis. In this case the direction of nutation is that of the sun or of the hands of a watch, and the orbit has been assumed to be a circle.

The nutation of a growing organ is the more conspicuous the greater its activity of growth: the nutation of stems, for instance, is more marked than that of roots. With regard to stems it must be remembered that since several internodes may be growing at the same time, they may be also nutating at the same time. Darwin observed in the plants with which he experimented that two, and sometimes three, internodes exhibited circumnutation simultaneously. But it by no means follows that they nutate synchronously; on the contrary, they do not; for, as we have seen, the rate of nutation varies with the age of the organ. In a case of this kind the movement of the apex is the resultant effect of the nutation of the internodes which are still growing.

We have now considered spontaneous irregularities of growth as expressed in nutation, but we have by no means exhausted the subject. Other phenomena belonging to the same category remain to be considered. It has long been observed that in bilaterally symmetrical organs the growth of one surface of the organ is, for a considerable time, more active than that of the other. This is most marked in those bilateral organs which are also *dorsiventral*, that is, organs in which the two surfaces have a different structure and are endowed with different properties. Thus, in ordinary foliage-leaves, which are characteristically dorsiventral organs, the growth of the dorsal (usually the lower) surface of the leaf exceeds at first and for a considerable time that of the ventral (upper), so that the leaf is more or less folded up upon itself. It is in consequence of this that the young leaves, when they are developed near together at the apex of a shoot, close up to form a bud; and it is also to this that the circinate vernation of many leaves, those of Ferns for example, and the coiling of the young tendrils of the Cucurbitaceæ, is due. It is only at a relatively late period that the growth of the other surface becomes the more active. De Vries has introduced a convenient terminology for expressing these relations. When the dorsal surface is the one which is growing the more actively, the organ is said to be in a state of *hyponasty*; when the ventral, the organ is said to be in a state of *epinasty*.

These phenomena are clearly allied to the nutations which we have already studied. The cause is in both cases the same, namely, the unequal rate of growth of opposite sides of an organ. The difference is this, that whereas in nutation the relations of the two opposite sides are frequently reversed in the course of the growth of the organ, so that the period of a complete cycle is short, in hyponastic and epinastic organs the reversal of the relations between the two sides takes place only once (foliage-leaves) or at most two or three times (stamens for instance) in the course of the growth of the organ, so that the period of a complete cycle is very long. Hyponasty and epinasty are simply words used to describe a very slow form of nutation.

The form of experiment adopted by de Vries for demonstrating hyponasty and epinasty was as follows. Petioles and midribs of well-developed but still growing leaves, freed from their laminæ, and bilateral shoots which had been previously growing more or less horizontally, were fixed vertically with their basal ends in wet sand and were kept in the dark. The position with relation to the vertical taken up by the apex after some time afforded an indication of the mode of growth of the organ. The most common result was that the apices had deviated from the vertical towards the lower surface of the organ in consequence of this surface having become concave; in some cases the opposite was observed, that is, the apices curved towards the normally upper surface. By this means he ascertained that nearly all leaves and parts of leaves (in this stage of development), the lateral branches of inflorescences, and many horizontal shoots, were epinastic, and that some few midribs and many horizontal shoots were hyponastic.

Other spontaneous irregularities of growth allied to epinasty and hyponasty are exhibited by organs which are not bilaterally but radially symmetrical, and which subsequently exhibit circumnutation. In seedlings in which the cotyledons are epigeal, the hypocotyledonary portion of the stem (hypocotyl), as described by Darwin, is strongly arched when it escapes from the seed-coats. This curvature is due to the more rapid growth of one longitudinal half of the hypocotyl as compared with that of the other. The hypocotyl gradually becomes straight in consequence of the increasing rapidity of growth of the side which was originally concave. We cannot properly use the terms "hyponasty" and "epinasty" in these cases, for the hypocotyl is not bilateral. But we may conventionally regard the surface which is at first concave as the anterior or ventral surface, and term its period of rapid growth epinasty: similarly, we may regard the surface which is at first convex as the posterior or dorsal surface, and term its period of rapid growth hyponasty. On this convention we may say that the original curvature of the hypocotyl is due to hyponasty, and its subsequent straightening to epinasty.

Similar phenomena are exhibited by the epicotyledonary portion of the stem (epicotyl) of seedlings. This is also arched as it breaks through the ground, and the curvature is due, as in the hypocotyl, to the fact that the posterior side

has been growing more rapidly than the anterior. Like the hypocotyl, the epicotyl subsequently becomes straight, but not so directly. In the first place, the plumule nutates. The nutation exhibits itself in the first instance as a simple oscillation in one plane, the effect of which is to cause variations in the angle between the pendent plumule and the straight portion of the epicotyl. Thus Wortmann observed in seedlings of *Phaseolus multiflorus* that the plumule hung down parallel to the straight erect portion of the epicotyl so that the angle between them (the angle of nutation) was 180° : in consequence of the temporary more rapid growth of the concave side the angle was then diminished to 90° or less, increasing again to 180° in consequence of the subsequent more rapid growth of the convex side. This simple nutation in one plane is clearly manifested only so long as the epicotyl is prevented from nutating in other planes by the cotyledons. When it escapes from between the cotyledons the alternate more rapid growth of the two longitudinal halves manifests itself in a swaying movement of the pendent plumule from one side to the other so that it describes a semicircle. In addition to this movement of nutation, Wiesner has observed that at an early stage the anterior side of the epicotyl begins to grow more rapidly near its base than the corresponding portion of the posterior side (epinasty), so that in this region the anterior side becomes convex. The whole epicotyl then somewhat resembles an elongated letter S in form, the two convex portions being the regions of the more active unilateral growth separated by an indifferent zone, as Wiesner terms it, in which the growth of the two sides is equal. It happens not unfrequently that there are more than two curvatures in one internode, and they may exist simultaneously in several internodes, so that the form of the whole organ is more complicated. This exhibition of irregularity of growth Wiesner terms *undulating nutation*. In the course of the subsequent growth of the epicotyl, the lower curvature first disappears in consequence of hyponasty, and then the upper in consequence of epinasty, so that it becomes straight.

Wiesner gives the following account of the growth in length of the epicotyl of *Phaseolus multiflorus* from its first development to its maturity. As it exists in the seed it is short (about 1 mm.) and straight. When it first begins to grow in length, its growth is uniform but slow, and longitudinal cell-division is very active. It then begins to grow more rapidly and becomes curved by hyponasty; at this stage cell-division is less active. As growth proceeds it becomes more rapid, and, in consequence of epinasty in its lower part, the epicotyl exhibits undulating nutation, cell-division still going on. Finally the epicotyl becomes straight and cell-division ceases: at this stage the rapidity of growth in length is the greatest, but it gradually diminishes until growth ceases altogether.

It might be suggested that the nutations of hypocotyls and epicotyls are induced by the action of gravity, that is, that they are not spontaneous; but the investigations of Sachs, Wortmann, and Vöchting, have shewn that the nutations are not dependent upon gravitation, for they are exhibited by seedlings which are made to revolve slowly round a horizontal axis, so that the action of gravity is uniform on all sides.

Finally, with regard to the cause of the grand period. We have already (p. 292) laid stress on the dependence of growth upon destructive metabolism, and it has also been pointed out (p. 196) that in growing organs destructive metabolism, as estimated by respiration, is very active. The grand period of growth is probably to be regarded as the expression of a corresponding grand period of destructive metabolism in the growing organ. Mayer has in fact found that the grand curve of growth in seedlings runs nearly parallel with the curve of the absorption of oxygen by them.

The influence of external conditions upon growing organs will be considered in the next two or three lectures.

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LECTURE XVI.

IRRITABILITY.

IT was pointed out in the first lecture (p. 7) that, amongst other fundamental properties, the protoplasm of plants is endowed with that of *Irritability*, a certain sensitiveness, that is, to the influence of external agents, and we have since learned (p. 301) to regard movement as one manifestation of this irritability.

In dealing now more fully with the influence of external agents in inducing or preventing movement, or in modifying either the rapidity or the direction of any movement which the organ may be already performing, we must clearly distinguish their influence as merely normal conditions, upon the proper combination of which the possibility of any manifestation of irritability depends, and their direct action upon the protoplasm in inducing or arresting movement; the former we will speak of as the *tonic* influence of external conditions, the latter as the *stimulating* action of external agents.

In endeavouring to make clear the difference between tonic influence and stimulating action we must, in the first place, form some idea of the internal conditions of movement. We have seen (p. 302) that a movement can only take place when there is present in the protoplasm of the organ a supply of readily decomposable material by the decomposition of which the necessary energy is evolved. Without entering at present upon a detailed discussion of the mechanism of movements, we may go on to state that this

evolution of energy is accompanied by a change in form of the protoplasm, and that the performance of a movement by an organ is the external expression of a change in form of the protoplasm of some or all of its cells. We can, in fact, only obtain satisfactory evidence of the existence of irritability in organs which are so constructed that they can respond by movements to changes in the form of the protoplasm of their cells. Such are growing organs, and organs, the motile organs *par excellence*, which retain, after they have ceased to grow, such a structure that movement is possible to them. But we must be careful not to assume that irritability is restricted to growing and to motile organs. For all we know to the contrary, it is possessed by the protoplasm of all plant-organs, and, if in any case the action of a stimulus is not followed by a responsive movement, we must, before we assume the absence of irritability, assure ourselves that the structure of the organ is such that a movement is a mechanical possibility (p. 341).

Movement, then, depends essentially upon the irritability and motility of the protoplasm, and it is upon these properties that external conditions exert their tonic influence and thus affect movement. Under the most favourable external conditions the evolution of energy and the concomitant change in form of the protoplasm take place most actively, and movement follows; but any variation in these conditions will induce retardation or arrest of movement, the retarding effect being attributable either to a diminished evolution of energy, or to a diminished motility of the protoplasm. To take a single illustration. We have seen (p. 293) that growth takes place with greatest rapidity at a certain optimum temperature, and that at temperatures either above or below this temperature the rapidity of growth is perceptibly less, and that at extreme temperatures growth is altogether arrested.

We pass now to consider the stimulating action of external agents. Movements, we have seen, are either spontaneous or induced. With regard to the former, we have ascribed them (p. 301) to the action of internal stimuli, but we may perhaps account for them more simply and generally by referring

them to the spontaneous decomposition of the decomposable substance, without assuming the intervention of internal stimuli. In any case they are the expression of what we have termed the *automatism* of the organism (p. 7). With regard to the stimulating effect of an external agent, we may, taking the above view of the intimate cause of spontaneous movement as a basis, account for it thus, that it precipitates the spontaneous decomposition of the decomposable substance which the irritable protoplasm contains, and thus determines an evolution of energy which, provided that the anatomical structure of the organ permits, finds its external expression in a movement. This mode of regarding the action of an external stimulus enables us to understand how it is that the energy evolved in consequence of its action is incommensurately greater than the energy of the stimulus. The relation may be illustrated by comparing the force exerted in pulling the trigger of a rifle with the momentum of the travelling bullet.

In some cases the effect of a stimulus appears to be that it arrests movement. It will be shewn in detail later in the course that spontaneous movement is arrested by stimulation, but it is nevertheless true that stimulation induces movement. The immediate effect of stimulation in such a case is to induce a change of form in the protoplasm of the cell or cells, with the further effect that the recovery of irritability is much prolonged, the more so the stronger the stimulus has been. It is for this reason that when an organ exhibiting spontaneous movements is stimulated, its movements will cease for some time.

There is this general peculiarity to be noted in the relation of motile organs to changes in the tonic conditions, or to the stimulating action of external agents, namely, that the effect induced is not immediately manifested. For instance, if, under a certain combination of external conditions an organ is growing with a certain rapidity, and the external conditions be so changed as to involve a slower or a faster rate of growth, the change in the rate of growth will not coincide in point of time with the change in the external conditions, but the

previous rate of growth will be maintained for a longer or shorter time before the organ accommodates itself to the new conditions. The same is true of stimulation: a movement is not immediately produced by the action of a stimulus, but there intervenes between the action and the response a longer or shorter "latent period," which is of course extremely short when compared with the corresponding period in the response to a change in the tonic conditions.

The degree of general irritability is by no means uniform among plants. We shall hereafter meet with the greatest possible differences in this respect, some plant-organs being scarcely at all sensitive to the action of any external agent, whereas others are highly sensitive to all. Again, a plant-organ is not necessarily equally sensitive to the action of different agents; we may perhaps most readily form a satisfactory conception of this by ascribing to the organ a "specific irritability" with regard to each agent, this specific irritability being in some cases relatively considerable and in others relatively slight.

With regard to the distribution of irritability in a plant-organ, the sensitiveness to the action of a stimulus may be possessed equally by all parts, or it may be localised in some particular part, or, again, it may be possessed in unequal degrees by different parts. It is not necessarily the case that the irritable region of the organ is also that part of it by which the responsive movement is performed, but the irritable and motile regions may be more or less widely separated. When this is the case there must evidently be some means of communication between them, so that the effect produced in the irritable region by the action of the stimulus may be transmitted to the motile region. This communication is set up most probably by means of the delicate filaments which, as mentioned in a previous lecture (p. 23), have been found in many cases to connect the protoplasm-bodies of adjacent cells. We will return to this subject and discuss it more fully in a subsequent lecture.

It will be convenient to classify the movements of plant-organs in the manner suggested above, into, namely, the

movements of growing organs, and the movements of mature motile organs. It must not, however, be supposed that this classification is anything more than a matter of convenience. There is no fundamental difference between the movements of growing and of mature organs; on the contrary, they are essentially similar. But there is this distinction, that whereas the position assumed by a growing organ in consequence of a movement may be rendered permanent and irreversible by growth, the position assumed by a mature motile organ in consequence of a movement is never thus rendered permanent but may be changed and reassumed an indefinite number of times.

I. *The Irritability of Growing Organs.*

We may regard growth as a slow movement spontaneously performed by the growing organ. The effect of the action of an external agent upon a growing organ is to change either the rate or the direction of this movement. Confining ourselves for the present to the consideration of changes in the rate of growth, we will, before discussing the influence of external conditions in inducing them, enumerate the variations which spontaneously occur. In the last lecture we found that the rate of growth of organs presents spontaneous irregular variations (*stossweise Aenderungen*, p. 358), as well as the spontaneous regular variations which constitute the grand period. These spontaneous variations in rapidity may be ascribed to variations in the evolution of energy upon which growth depends (p. 292), or to variations in the conditions upon which, as we have seen (pp. 40, 335), the turgidity which is essential to the growth of cells depends; for instance, to variations in the osmotic properties of the cell-sap, in the physical properties of the primordial utricle, or, finally, in those of the cell-wall. We found, further, that the rate of growth is usually not uniform in all parts of the transverse growing zones, so that the growth in length of an organ rarely, if ever, takes place in a straight line, but that its apex nutates. This nutation we found to be due to spontaneous

variations in the relative rate of growth of opposite sides of the organ, or, to express it in a single word, to spontaneous *heterauxesis*. This heterauxesis may be accounted for in the same way as the irregularities in the rate of growth in length of the organ as a whole. If the evolution of energy be equally active in all the cells of any given transverse zone of a growing organ, and if the mechanical conditions be the same in all, they will all grow at the same uniform rate, and the organ will not exhibit nutation, but its apex will travel upward in a straight line. When, however, these conditions are not fulfilled, heterauxesis takes place and the organ nutates.

We will defer for the present a discussion of the intimate causes of spontaneous heterauxesis and will pass on to the consideration of the influence of external conditions in inducing variations in the rate of growth. We have already learned incidentally that certain external conditions have an important influence upon growth. We have learned, for instance (p. 292), that aërobiotic plants do not grow in the absence of free oxygen, nor anaërobiotic plants in the absence of an adequate supply of fermentable material. We have ascertained further that growth will only go on within certain limits of temperature (p. 293), and finally, that one of the essential conditions of growth of an organ is the supply of enough water to maintain the growing cell or cells in a state of turgidity (p. 335).

TEMPERATURE.

It was pointed out in a previous lecture (p. 293), that for each plant there is a minimum temperature at which growth is just possible, an optimum temperature at which it is most active, and a maximum temperature at which it is arrested. There remain to be noted one or two points in the relations between growth and temperature which we shall find of importance hereafter when we come to consider the effect of the simultaneous variation of several external conditions, and seek to analyse the complex result.

The first point is this: that in estimating the effect of a rise of temperature upon the rate of growth, it must be borne in mind that the accelerating effect is to be calculated, not with reference to the zero-point of the thermometer, but from the ascertained zero-point or minimum temperature for growth of the plant. Secondly, the acceleration of growth due to a rise of temperature between the minimum and the optimum is not proportional to the number of degrees, but is greater for each degree as the temperature approaches the optimum. This is illustrated by the figures given in a previous lecture (p. 293).

Temperature influences growth in this way, that for any given degree of temperature, between the minimum and the maximum, there is a corresponding rate of growth. But in producing this effect, temperature does not act as a stimulus: temperature, as such, exercises not a stimulating influence, but a tonic effect, which is due to the fact that the manifestation of irritability is dependent upon temperature. Growth, for instance, is more active at the optimum than at either the minimum or the maximum temperature because at that temperature the necessary evolution of energy is taking place with sufficient activity (p. 295), and the protoplasm is probably in its most motile state. The arrest of growth at a temperature below the minimum is probably to be ascribed to an insufficient evolution of energy, whereas the arrest of growth at a temperature above the maximum cannot be ascribed to this cause, for at such a temperature the evolution of energy, as estimated by the activity of destructive metabolism (p. 295), is very considerable. The arrest of growth in the latter case can only be accounted for by ascribing it to an arrest of the motility of the protoplasm. The relation between temperature and the manifestation of irritability (*thermotonus*) will be frequently illustrated hereafter.

Variations of temperature have, however, in some cases, a *stimulating* effect. From his researches on the growth of seedlings, Köppen came to the conclusion that frequent and considerable variations of temperature cause a retardation of growth, that is, that the growth in length of an organ in a given

time is smaller when the temperature is made to vary frequently between two points, than when it is constant at the mean between these two points. But Pedersen has found that this is not the case, but that when the higher temperature was not allowed to exceed the optimum by many degrees, variations of temperature produced no perceptible effect upon the growth of the roots with which he experimented. Pfeffer has investigated the matter with regard to leaves, and has found that these, too, are unaffected in their growth by variations of temperature. But in his researches on the opening and closing of flowers, Pfeffer found that in some cases the perianth-leaves were very highly sensitive to a variation of temperature. The flowers of *Crocus vernus* and of *Tulipa Gesneriana* opened under the influence of a rise of temperature and closed under the influence of a fall. This only took place, however, within certain limits of temperature. In *Crocus vernus*, for example, a rise of temperature produced no opening-movement until a certain minimum temperature, about 9° C., had been reached; at a relatively high temperature, about 27° C., the opening ceased, and on a further rise, at 28.6° C., closing began but was usually incomplete: at 36.7° C. all movement ceased: a fall of temperature produced in all cases a closing-movement.

Pfeffer clearly established, in the first instance, that the opening and closing of flowers is a phenomenon of growth, and moreover of heterauxesis, the movement being due in either case to the unequal growth of the two surfaces of the dorsiventral perianth-leaf. This heterauxesis may be induced entirely by the variations of temperature, for when a flower is kept in darkness and at a constant temperature, it does not open or close. The relation between the two surfaces, during opening or closing, is this, that only the one side grows perceptibly; thus, in opening, the upper or inner surface grows, whereas the lower does not grow at all or only very little, and conversely, in closing, the lower or outer surface grows and the upper scarcely grows at all. The dependence of these movements upon the stimulating action of variations of temperature has been clearly brought out by

Pfeffer. From his measurements it is evident that each variation, whether it be a rise or a fall of temperature, is followed by a temporary acceleration of the mean rate of growth of the perianth-leaf as a whole; after a time the rate of growth adapts itself to the tonic influence of the temperature, whether it be higher or lower, to which the flower has been exposed.

All the explanation which can be given of these facts, without venturing on speculation, is this; that the perianth-leaves of these plants are so constituted that they respond to the stimulating effect of a rise of temperature within certain limits by an accelerated growth of the upper surface, by what we may term induced epinasty, and to all falls of temperature, as well as to all rises above the upper limit, by an accelerated growth of the lower surface, by induced hyponasty. Unlike the great majority of plant-organs, these perianth-leaves are endowed with a specific irritability to variations of temperature, as is clearly proved by the fact that any variation of temperature is followed by an acceleration of their mean rate of growth. That this acceleration should express itself in the form of heterauxesis we may probably attribute to the dorso-ventrality (p. 366) of the organs, but we are quite unable to account for the fact that the acceleration due to a rise of temperature should particularly and constantly affect the upper surface, and that due to a fall of temperature should similarly affect the lower surface.

LIGHT.

In entering upon the consideration of the influence of light upon the rate of growth, we will begin by enquiring into the *tonic* influence of light, that is, into its relation to the irritability and motility of the protoplasm of growing organs, and we will then go on to study the *stimulating* action of variations in the intensity of light, and, finally, the combined tonic effect of light and of temperature.

The Tonic Influence of Light. Phototonus. The response of a growing organ to the action of a stimulus, by an alteration in either the rate or direction of its growth depends, as we have already learned, upon two conditions, namely, that the protoplasm should be irritable and motile, and that the mechanical structure permits of the movement (p. 341). In some cases, organs, notably dorsiventral leaves, cease to exhibit irritability, and in fact cease to grow altogether, when they are kept for some days in continuous darkness. On being exposed for some short time to light they regain their irritability, as is clearly shewn by the fact that they then respond by variations in their rate of growth to variations in the intensity of the light to which they are exposed. Similarly, exposure to light of great intensity induces a loss of irritability and leads to the arrest of growth. Wiesner has found, for example, that the heliotropic effect of light diminishes when the intensity of the light to which the organ is exposed exceeds a certain optimum which varies with the plant, and disappears altogether at a certain maximum intensity, which may be either somewhat higher or lower than that at which growth is arrested. The peculiar condition induced by exposure to light of a certain intensity, in which protoplasm is capable of exhibiting irritability, has been called by Sachs *Phototonus*.

We may conveniently consider here the general question of the effect of continuous darkness and of subsequent exposure to light upon the development of plant-organs. One of the most striking features presented by plants which have been grown in darkness is the smallness of the leaves. This is not a universal rule, by any means, though it applies in the vast majority of cases when the leaves are dorsiventral. The radial or bilateral leaves characteristic of many Monocotyledons become excessively elongated in darkness, just as shoots do, but their breadth is diminished. And even among dorsiventral leaves exceptions occur; the leaves of the Beet, for example, attain a considerable size in darkness. From Sachs' observations it appears that leaves which, when they unfold under normal conditions, become fully exposed to light

at a comparatively early stage in their development, are those which are most affected in their growth by continuous darkness; whereas those, such as sheathing leaves, which are naturally protected more or less from exposure to light by others investing them, attain a relatively more perfect expansion.

The radial or bilateral leaves, we have said, resemble internodes in that they become excessively elongated in darkness, and the question naturally arises why do dorsiventral leaves behave otherwise? It seems that growth in breadth is in all cases hindered or prevented by darkness. Not only do dorsiventral leaves afford examples of this, but stems also: for example, the broad leaf-like internodes of Cactaceæ such as *Opuntia* are developed in darkness as slender cylindrical or prismatic structures.

Several explanations of the remarkable effect of the absence of light in diminishing or preventing the expansion of leaf-blades have been offered, and it will not be uninteresting to consider them.

G. Kraus endeavoured to explain it by his well-known "self-nutrition" theory; he ascribed it to the fact that, in darkness, leaves are incapable of performing one of their most important functions, namely, the construction of organic substance. This explanation has, however, been shewn to be quite inadequate by the observations of Batalin, of Rauwenhoff, of Godlewski, and of myself.^(Chenopods) As a matter of fact, leaves continue to grow when they are placed for a time in darkness, in blue light, or in an atmosphere which contains no carbon dioxide, under conditions, that is, which render impossible the normal formation of organic substance in them.

Batalin suggested as a possible cause of the smallness of leaves grown in darkness, that the process of cell-division is arrested under these circumstances. But this suggestion is shewn to be valueless by the fact that radial or bilateral leaves grow excessively in darkness, and that even some dorsiventral leaves grow considerably. Further, Prantl ascertained that the average number of cells in a leaf of the embryo of *Phaseolus*, whilst still in the seed, was 343, whereas that in

the etiolated leaf of a seedling varied from 1375—2571, and in the normal leaf from 1429—2273. These figures clearly prove that cell-multiplication by division takes place in leaves in darkness. The arrest of growth is not due to a diminished formation of cells in the leaf, but to an interference with the growth of the cells formed. The arrest of growth may have, however, the effect of diminishing the activity of cell-division, for the division of cells is dependent upon their growth.

Other observers, such as Rzentkowsky, Mer, and C. Kraus, have correlated the smallness of leaves in darkness with the excessive elongation of the internodes of shoots, and regard the latter as the cause of the former. In support of this view those cases may be adduced in which, as in the Beet, the leaves are fairly well-developed in darkness whilst the stem exhibits no excessive elongation, or those, such as *Allium*, *Iris*, and other Monocotyledons, in which the leaves become excessively elongated in darkness whilst the stem does not. But the converse of this is not true, namely, that excessively elongated stems always bear very small leaves. For instance, according to Rauwenhoff, the shoot of *Fritillaria imperialis* becomes excessively elongated in darkness, whereas there is no corresponding difference in size between the leaves of an etiolated and of a normal plant. Again, it has been shewn by Sénéquier, G. Kraus, and Godlewski, that if a leaf-blade be kept in darkness whilst the rest of the plant is exposed to light the blade remains small, though it is true, as Sachs' observations prove, that the leaf-blade may attain a greater size under these conditions than it does when the whole plant is kept in darkness. It may be indeed admitted that the excessive consumption of plastic material in the rapid growth of the stem, tends, when the store is limited, to affect prejudicially the growth of the leaves. Godlewski has in fact found, in the case of seedlings of the Radish, that the excessive elongation of the hypocotyl tends to diminish the development of the cotyledons. But, taking all the facts into consideration, the excessive elongation of the internodes of etiolated plants cannot be accepted as the cause of the smallness of the leaves,

though it must be taken into account in endeavouring to explain the fact.

Finally, Prantl ascribes the smallness of the leaves to an unhealthy condition induced by the continuous darkness; he regards it, in fact, as a pathological phenomenon. But this is no explanation. The smallness of the dorsiventral leaves is not more of a pathological phenomenon than the excessive elongation of the internodes; if the one is a pathological phenomenon, then so is the other. And why should radial or bilateral leaves become excessively elongated in darkness? The question still remains why unhealthiness should express itself, in the one case, in arrested growth, and in the other, in excessively active growth.

We shall best obtain, not perhaps a full explanation, but a suggestive insight into the nature of this phenomenon by a consideration of the resumption of growth under the influence of light. Exposure to light, as mentioned above, restores to leaves which have been long kept in darkness the condition of phototonus; it enables them to grow and to respond to the stimulating action of light; this is probably also true with regard to their power of responding to other stimulating agents. We may attribute, then, the effect of prolonged absence of light, or of exposure to too intense light, like the effect of exposure to extreme temperatures, to a destruction of either the irritability or the motility of the protoplasm of the growing cells; probably the latter is the more important factor in producing the result. We cannot, however, in any way account for the difference of behaviour in this respect between stems and leaves.

Before leaving the subject we may briefly notice the facts which have been observed with regard to the behaviour of young etiolated leaves on their exposure to light. Detmer found that on exposing young etiolated seedlings of *Phaseolus* and *Cucurbita* for short periods to light of a certain intensity, they resumed their growth and exhibited distinct epinasty. He explains this by assuming that light induced a more rapid growth of the upper surface, and he speaks of this induced epinasty as photo-epinasty. It must be remembered, how-

ever, that all young dorsiventral leaves are epinastic at a certain stage in their development (p. 366). The natural unstrained explanation seems to be that the leaves were in the epinastic stage of development, and that when they resumed growth under the tonic influence of light they exhibited epinasty. It is quite possible that, if exposed to light at the appropriate stage of their development, leaves would similarly exhibit a "photo-hyponasty."

We will conclude our consideration of the relation of leaves to the tonic influence of light with a brief comparative account of their structure when normal and etiolated. In normal leaves, as a rule, the tissue underlying the morphologically superior (dorsal) surface of the leaf consists of closely-packed elongated mesophyll-cells so placed that their long axes are at right angles to the surface; these cells, of which there may be several layers, constitute the palisade-parenchyma (see Fig. 13, p. 70). The tissue near the morphologically lower (ventral) surface consists of irregular loosely arranged mesophyll-cells, with large intercellular spaces, constituting the spongy parenchyma. The epidermis of the lower surface is much more abundantly supplied with stomata than that of the upper. The difference of structure between the two surfaces is induced by light. Stahl has shewn that the development of the palisade-parenchyma is always more marked in leaves which have been fully exposed to the sun than in those which have grown in the shade. It is only when the leaf, as is commonly the case, lies more or less nearly horizontally, that the palisade-parenchyma is developed exclusively towards the upper surface; when, as is sometimes the case, the leaf-blade lies in a vertical plane, the palisade-parenchyma is almost equally developed in relation with both surfaces, for both are then exposed to nearly the same illumination. In etiolated leaves the differentiation of palisade-parenchyma and spongy parenchyma does not take place.

Growth in continuous darkness leads to various other important modifications in the general habit and structure of a plant. In illustration of this let us consider two Potato-

shoots which have grown from tubers, the one under normal conditions, the other in darkness. We are first struck with the difference in colour between the two shoots: the one which has grown in darkness, the etiolated shoot, has a white stem, and leaves which are at first pinkish, owing to the presence of colouring-matters in the sap of the cells, and subsequently pale yellow, whilst the other, the normal shoot, is green, leaves and stem alike. The former is destitute of chlorophyll, the latter possesses it (p. 262). The next point of difference is in the length and thickness of the internodes of the stems, those of the etiolated plant being much longer and more slender than those of the normal plant. Further, the angle made with the main stem by the lateral branches and by the petioles of the leaves with the main stem is smaller in the etiolated than in the normal shoot. Finally, the smallness of the leaves of the etiolated shoot, as compared with those of the normal shoot, attracts our attention, but, as we have already fully discussed that subject, we will now confine our attention to the internodes.

Shoots, then, differ from most leaves in that continuous darkness does not arrest their growth. But excessive elongation of the internodes is not always exhibited by shoots which have grown in permanent darkness. It is exhibited by the majority of shoots which are adapted for growth in length under the normal alternation of day and night. Some shoots of this kind seem, however, as Sachs has pointed out, to attain their maximum of elongation under normal conditions, and these do not become excessively elongated when they grow in permanent darkness. As instances of such "normally etiolated" shoots, as he calls them, Sachs mentions those of *Dioscorea Batatas* and of the Hop. Other shoots, again, which have no natural tendency to elongate when growing under normal conditions, do not do so in darkness. This was found by Sachs to be the case in the Beetroot and in *Cactus speciosus*; the etiolated shoots of the latter plant had in fact shorter internodes than those of normal shoots. Shoots which are not adapted for growth in length under the normal alternation of day

and night do not become excessively elongated in permanent darkness. Sachs has observed, for instance, that this is the case in the hypocotyls of seedlings having hypogean cotyledons.

An idea of the relative elongation of etiolated and of normal internodes will be best afforded by comparative measurements. The following are from Sachs.

	<i>Normal.</i>	<i>Etiolated.</i>
Hypocotyl of <i>Polygonum Fagopyrum</i>	2—3	35—40 centim.
” ” <i>Cucurbita Pepo</i>	3—4	40—50 ”
Epicotyl ” <i>Phaseolus multiflorus</i>	32	93 millim.

The excessive elongation of an internode is by no means always accompanied by a diminished thickness. Sachs, G. Kraus, and others, have observed numerous instances in which the internodes of etiolated were quite as thick as those of normal shoots. Kraus indeed mentions one case (*Lupinus termis*) in which the etiolated hypocotyl was more than twice as thick as a normal hypocotyl.

We will now endeavour to ascertain the cause of the usual excessive elongation of etiolated internodes, and we will enquire first into the structure of these organs. It has long been known that, as a rule those histological elements, such as epidermal, collenchymatous, and sclerenchymatous cells, which, in a normal internode, have thick walls, commonly have thin walls in an etiolated internode. Further, the number of the fibrovascular bundles, and the number of the cells constituting them, is commonly smaller in the latter than in the former. The practical importance of this difference in structure has been demonstrated by Koch, who has shewn that the “laying” of Cereal crops is due to the imperfect development of the tissues of the stem, and that this is the result of an insufficient exposure to light in consequence of the plants being too close together (see p. 137).

The accompanying figures, due to Koch, illustrate to some extent the histological differences between an internode of a plant grown in the light and that of one grown in darkness. In this particular case *A* is a transverse section of an internode of a Rye-plant grown fully exposed

to light; *B* is a section of the corresponding internode of a "laid" plant imperfectly exposed to light.

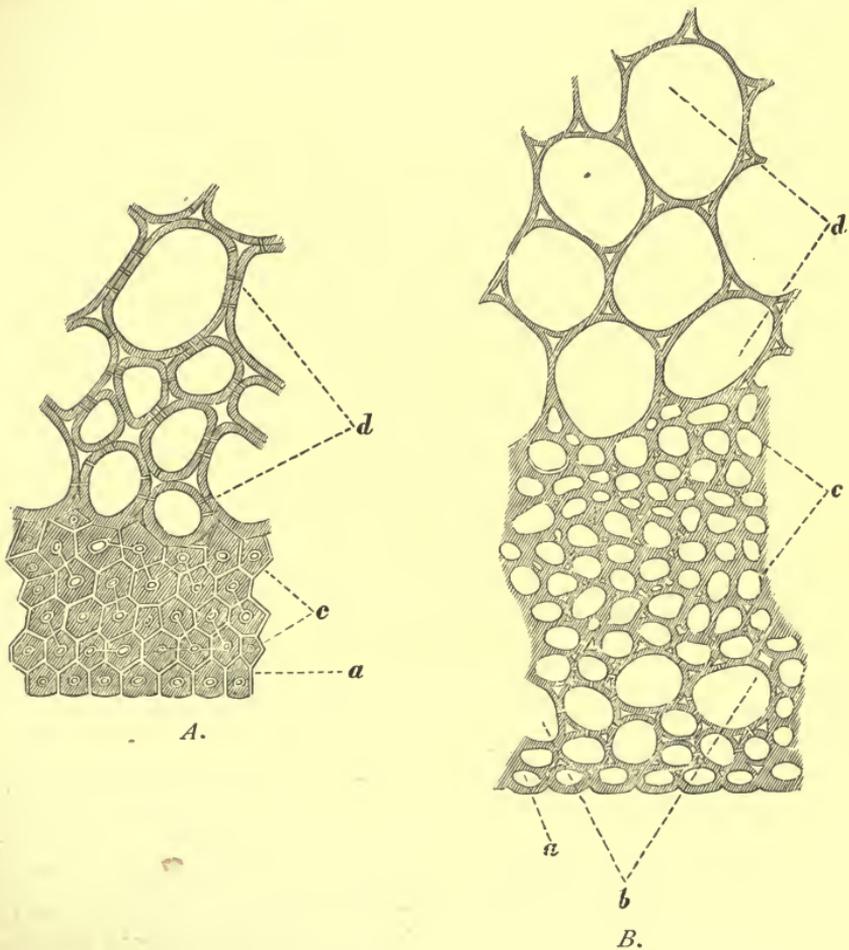


FIG. 42 (after Koch). *a*, epidermis; *b*, cortical parenchyma; *c*, sclerenchyma; *d*, vascular tissue.

It has been found, further, by Kraus, Koch, and Rauwenhoff, that the epidermal and parenchymatous cells of excessively elongated etiolated internodes are much longer than those of the corresponding normal internodes, and that they are also rather more numerous.

The following table, taken from Rauwenhoff's work, illustrates the relative development of the tissues and the length of the cells in normal and etiolated internodes. The plant used was *Polygonum cuspidatum*.

The numbers represent divisions of the eye-piece micrometer.

<i>Transverse section.</i>			<i>Normal.</i>	<i>Etiolated.</i>
Radial diameter of an entire vascular bundle			95	55
”	”	the hard bast	16	8
”	”	” soft ” (incl. cambium)	9	12
”	”	” xylem	55	22
”	”	” medullary sheath	20	13
”	”	” medullary cells	15·2	51
<i>Longitudinal section.</i>				
Mean length of the epidermal cells			5·5	13·5
”	”	” cortical ”	12·2	32·4
”	”	” hard bast fibres	90	89
”	”	” wood ”	88	88
”	”	” medullary cells	29·5	62

The conclusion arrived at by observations of this kind by Kraus and by Rauwenhoff is this, that the excessive elongation of etiolated internodes is due to an exaggerated growth of the parenchymatous cells, a conclusion which the facts seem fully to justify. But this is not a final explanation, for the exaggerated growth of the parenchymatous cells has yet to be accounted for.

Kraus attributes this exaggerated growth principally to the thinness of the walls of the epidermal, collenchymatous, and sclerenchymatous cells, in consequence of which they remain extensible and offer but little resistance to the elongation of the parenchymatous cells. He considers that an etiolated internode remains in that condition which, as mentioned in a previous lecture (p. 346), is characteristic of very young normal internodes. In such an internode, it will be remembered, the parenchymatous tissue (pith) does not elongate on isolation, but the other tissues shorten. If this be so, then, in the etiolated as in the young normal internode, the longitudinal tissue-tension must be small, and Kraus adduces observations which shew that this is, sometimes at least, actually the case. Again, if this be so, then internodes which, when grown under normal conditions, exhibit longitudinal tissue-tension in a high degree, should be especially remarkable for excessive elongation when grown in continuous darkness. Kraus mentions the long narrow leaves of various Monocotyledons, such as the Onion, the Hyacinth, the Crocus,

etc., as instances of organs which fulfil these conditions, and he also brings forward, as evidence of a negative character, his observation that the internodes of *Cucurbita* exhibit normally only a very slight longitudinal tension and that they do not become excessively elongated in darkness, an observation which has also been made by Rauwenhoff in the case of *Ipomœa*. But it does not appear that the longitudinal tissue-tension is always small in etiolated internodes, for Rauwenhoff has observed an evident tension in etiolated internodes of *Phaseolus*, *Fuchsia*, *Rosa*, and *Polygonum*, and Sachs mentions that he has often observed a considerable tension in etiolated internodes. It would rather appear that, in etiolated, as in normal internodes, the longitudinal tissue-tension varies at different stages of growth, though perhaps not precisely in the same way in the two cases. It is, in fact, impossible to understand the fact brought out by Rauwenhoff that the fibres of etiolated internodes are not excessively elongated, if the longitudinal tissue-tension remains small during the whole period of growth.

With regard to the thinness, in etiolated internodes, of the walls of cells which have thick walls in normal internodes, it must be pointed out that neither the different tissues, nor different stems, behave alike in this respect. All observers agree in stating that the epidermal and collenchymatous cells have relatively thin walls in etiolated internodes, but their statements differ with regard to the fibrous and vascular cells. Kraus and Rauwenhoff have observed that the walls of these cells are thin in etiolated internodes, whereas other observers, notably Batalin, have not found this to be so. It may be concluded that the thinness of the walls is more conspicuous and constant in the case of epidermal and of collenchymatous cells than in that of fibrous and of vascular cells. Kraus attributes the thinness of the walls to the fact that the leaves of internodes growing in darkness are unable to manufacture the necessary plastic material for the due development of the tissues. It may be admitted that if this material is not forthcoming the development of the tissues will be imperfect. But it must be remembered that such differences in structure

are exhibited by shoots which grow from rhizomes and tubers, and which are therefore abundantly supplied with plastic material. It might be suggested that the thinness of the walls is due to the excessive growth in length of the cells. This explanation may be of some value as regards epidermal and collenchymatous cells (see p. 337), but it does not seem to be applicable to sclerenchymatous cells, for Rauwenhoff observed, as mentioned above, that the hard-bast fibres of an etiolated internode of *Polygonum cuspidatum* were not excessively elongated, and yet he found that their walls were thin. It appears that light has some direct influence upon the thickening of cell-walls, but it is not possible at present to explain the nature of this influence.

It cannot be denied that the thinness of the walls of these cells which normally have thick walls is favourable to the elongation of the parenchymatous cells of an etiolated internode, but the most important factor in their excessive elongation is their own more active growth quite apart from these mechanical conditions. Kraus admits that the proper elongation of these cells is of importance, but he maintains that their elongation is due, not to a true growth of their walls by the addition of solid substance, but merely to the taking up of water into them. In support of this view he states that the pith and cortex of growing internodes increase in weight in consequence of an increase of the water which their cells contain rather than in consequence of an addition of solid substance. This view is, however, incorrect. Karsten had already pointed out that etiolated seedlings of *Phaseolus multiflorus* contain as much cellulose as normal seedlings of the same age, and Godlewski has since found by comparative analyses of the hypocotyls of normal (grown in light but not supplied with CO₂) and of etiolated seedlings of *Raphanus* that the total dry weight of organic substance is approximately the same in both. It is true that he finds that the hypocotyls of the etiolated seedlings contain proportionately more water than those of the normal seedlings, but the fact remains that the amount of organic substance built up into tissue is about the same in both cases. The

parenchymatous cells, then, of etiolated internodes do not merely expand, but actually grow. The excess of water in etiolated as compared with normal internodes is doubtless attributable to the fact, to which attention has been already drawn (p. 268), that the cell-sap of the former is richer in organic acids than that of the latter. In view of the osmotic activity of these substances (p. 41), it may be inferred that the turgidity of the cells is greater in etiolated than in normal internodes. From observations made in his laboratory, by means of the method of plasmolysis, on normal and etiolated internodes, which shew that the amount of shortening is about the same in both, Pfeffer concludes that the turgidity is the same in both. It must, however, be borne in mind that the shortening exhibited by an organ on plasmolysis is simply the expression of that amount of elongation of the cells due to the hydrostatic pressure of their contents, which has not yet been rendered permanent by actual growth. It is quite possible to imagine that the elongation of highly turgid cells might be so rapidly followed up and rendered permanent by growth that an internode would shorten scarcely at all on plasmolysis. What Pfeffer's observations tend to prove is that the elongation of the cells in etiolated internodes is rendered permanent by growth more rapidly than in normal internodes. The final conclusion to be drawn is this, that, since there is reason to believe that the turgidity of the cells of etiolated internodes is greater than that of normal internodes, and since the shortening of the former on plasmolysis is not greater than that of the latter, the increase in surface of the cell-walls by actual growth is more active in the former than in the latter.

It is, then, to the active growth of their parenchymatous cells that the excessive elongation of etiolated internodes is to be ascribed. We will now enquire into the causes of this more active growth in darkness. Various explanations have been offered. It has been suggested, namely, that under these conditions the normal correlation of nutrition between the different organs may be interfered with. For example, Famintzin observed, in the case of Cress-seedlings,

that the average length of the hypocotyl and primary root taken together was about the same whether the plant had grown in light or in darkness, a result which was confirmed with regard to other plants by Lasareff, the hypocotyl being longer and the root shorter in the etiolated than in the normal plant. Again, C. Kraus accounts for the usual smallness of the leaves of etiolated shoots by regarding it as a consequence of the excessive elongation of the internodes. As a matter of fact, this is not the case, as Godlewski has shewn. But assuming it for a moment, we must admit that the converse also will be true, that active growth of the leaves will restrain the excessive growth of the internodes in darkness. Godlewski has found, however, that the excessive growth of the hypocotyl of the Radish in darkness is only very slightly diminished when the cotyledons are enabled to grow by exposure to light. Naturally when there is only a limited supply of plastic material the growth of any one organ will eventually be affected by the demands made upon the store by the other growing organs. But this does not at all touch the real point at issue, that, namely, whilst there is an adequate supply of plastic material, the growth of some organs should be promoted by the absence of light, and that of others hindered. Another explanation of the excessive elongation of etiolated internodes is that offered by Rauwenhoff, who concludes that it is due to the influence to gravity which, as we shall learn more fully hereafter, tends to cause stems to grow erect. It is difficult to reconcile this view with the fact that an excessive elongation of the internodes in darkness takes place when the plant is hung upside down, so that its normal relation to gravity is reversed, and also when the growing plant is made to rotate slowly about a horizontal axis in darkness so that the effect of gravity is eliminated.

The only satisfactory explanation that can be given is that when a shoot grows in the light, the light exercises a tonic influence upon the growing cells such that their growth is retarded, whereas in darkness, in the absence of this tonic influence, their growth is more rapid. We will postpone a fuller consideration of this matter for a short time.

Before we leave this subject it may be incidentally mentioned that organs other than internodes become excessively elongated when grown in darkness. Excessive elongation is exhibited by the stalks, which belong to the category of shoots in the more extended sense in which Sachs uses the term, which bear the fructification of various Fungi. Brefeld mentions, for instance, that whereas the subaërial hypha which bears the sporangium of *Pilobolus microsporus* usually attains a length of about half an inch, when grown in darkness it attains a length of from eight to ten inches, and under these circumstances no sporangium is produced: and again, that the stipe of *Coprinus stercorearius*, which is usually only an inch or so long, may attain in darkness a length of two feet, the pileus remaining rudimentary.

From the facts with which we have just become acquainted we learn that the absence of light is, as a rule, favourable to the growth in length of shoots, and from this purely negative evidence we may conclude that light tends to retard growth in length. But there is abundant positive evidence forthcoming to establish this point. Sachs has observed, for instance, that if a potato be allowed to sprout, exposed as fully as possible to light, the shoots attain only a very inconsiderable length. In one case shoots thus exposed for nearly eight weeks were only a little more than one centimetre long, whereas etiolated shoots of the same age were 15—20 centimetres long. The shoots of the Potato are normally developed under ground, so that they pass through the first stage of their growth in more or less complete darkness; they appear to be adapted for growth in darkness during this stage, so that when they are exposed to light the effect of its retarding influence is shewn in the conspicuous manner described above.

The retarding influence of light upon growth in length has also been determined directly by comparative measurements. Strehl found the relative elongation during a period of eighteen days, of the roots and hypocotyls of seedlings of *Lupinus albus*, some of which were grown in darkness and an equal number (34) under the normal alternation of day and night, to be as follows:

Root		Hypocotyl		Root + Hypocotyl	
Normal	Etiolated	Normal	Etiolated	Normal	Etiolated
169.0	185.8	41.2	51.9	201.2	237.7

The numbers represent millimetres.

Von Wolkoff made similar observations on the roots of seedlings of *Pisum sativum*.

Twelve seedlings were measured in each case, and the period of growth was 5 days. The measurements are in millimetres.

	In the dark.	Under normal conditions.
Total elongation	923	715

The effect of light in retarding the rate of growth in length makes itself evident even after a short exposure. This is strikingly shewn by the results of some experiments which I made with the exact sporangiferous hyphæ of *Phycomyces nitens*. These delicate filaments are upgrowths of the much-branched tubular cell which constitutes the mycelium of this plant. The plant was grown in darkness and was exposed at intervals to light.

The following are the measurements made at intervals of an hour upon a hypha.

Time	Hourly growth	Temperature
8—9 a.m.	2.70	22.9° C.
10 "	2.70	24.3
11 "	2.30*	26.0
12 noon	2.90	25.0
1 p.m.	2.70*	25.8
2 "	3.20	25.3
3 "	3.50	25.2
4 "	2.90*	25.0
5 "	3.20	25.1
6 "	2.80	25.3

* Exposed to light.

The figures correspond to $\frac{1}{10}$ s of a millimetre.

This table is rendered more intelligible by the following diagram, in which the thick line is the course of growth, the thin line that of the temperature, and the unshaded spaces the periods of exposure to light. The figures on the left side represent $\frac{1}{10}$ s of a millimetre, those on the right degrees of temperature, and those on the top hours.

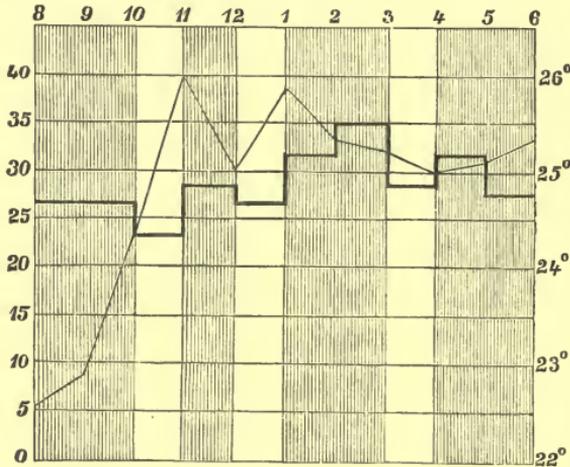


FIG. 43. Diagram illustrating the retarding influence of light upon the growth of a sub-aërial hypha of *Phycomyces*.

The growth of leaves also, when they are in a phototonic condition, is retarded by exposure to light; this is clear from Prantl's observations and from my own.

The following table illustrates my observations. The plant used was *Secale cereale*. The plant was kept in darkness and exposed at intervals to light.

Time	Hourly growth	Temperature
7—8 a.m.	1'10	22'4 ⁰ C.
9 "	1'20	22'4
10 "	1'50	23'5
11 } *	1'50	24'0
12 } *	1'40	
1 p.m.	1'30	26'4
2 "	1'50	25'8
3 "	1'70	25'0
4 "	1'70	25'3
5 "	1'80	24'6
6 "	1'60	24'2
7 "	1'50	24'0

* Exposed to light.

Since, as we see, light retards growth, it can be easily conceived that its retarding effect will vary with its intensity. Illustrations of this are afforded by variations in the size of leaves grown under different conditions of illumination. Leaves grown fully exposed to sunlight are smaller than those grown in bright diffused light, and those grown in weak light are small, not much larger, in fact, than those grown in darkness. The most striking illustration is afforded by Wiesner's observation, to which allusion has already been made, that exposure to very intense light arrests growth altogether. The general relation of the intensity of light to the rate of growth of shoots is then this, that at a certain maximum intensity growth is prevented, and that, as the intensity diminishes, the rate of growth gradually increases, attaining a maximum rapidity in darkness.

The effect of light in retarding growth is not immediately perceptible on exposure, at least in the case of organs of complex structure; nor does its effect immediately cease when the organ is replaced into darkness. This is shewn in the table of my observations on the leaf of *Secale cereale* (Rye). During the period of exposure to light (11-12) the rate of growth was somewhat retarded, and the retardation was probably greater than it appears to have been, for the rate of growth was increasing. But the full effect was exhibited in the succeeding hour (12-1) when, in spite of the natural acceleration and of a rise of temperature, the rate of growth further diminished, and it clearly persisted during the next hour. We shall have occasion to consider the "persistent influence" of light more fully when we are discussing the conditions of the daily period of growth.

We may now enquire whether or not all the rays of the spectrum are alike capable of inducing a retardation of growth in length. It may at once be stated that this is not the case. The observations of Sachs, of Kraus, and of Rauwenhoff, shew that when plants are grown in the rays of low refrangibility (yellow, orange, red) they present, though not quite in the same degree, the abnormalities of form which are characteristic of etiolation, that is, their internodes become excessively

elongated and their leaves remain small, and Rauwenhoff has found that the structure of internodes grown in light of low refrangibility is similar to that of etiolated internodes. On the other hand, plants grown exposed to the rays of high refrangibility (violet, indigo, blue) resemble those which have grown in white light. It appears, therefore, that it is the rays of high refrangibility which exercise the retarding influence upon the rate of growth.

The relative effect of exposure to the rays of high and of low refrangibility is clearly shewn in the following tables of observations made by me upon the sporangiferous hyphæ of *Phycomyces nitens*. The figures are $\frac{1}{10}$ s of a millimetre; the time of exposure to light was an hour in each case.

A. Blue light.

Time	Hourly growth	Temperature
8—9 a.m.	2'20	20'0 ⁰ C.
10 "	3'00	24'9
11 "	2'20	26'9
12 noon	2'70	26'6
1 p.m.	2'90	27'8
2 "	3'90	27'1
3 "	3'90	27'6
4 "	3'90	26'5
5 "	4'40	26'1

* Exposed to light.

B. Yellow light.

Time	Hourly growth	Temperature
8—9 a.m.	1'40	21'0 ⁰ C.
10 "	1'70	21'5
11 "	2'20	21'7
12 noon	2'70	22'8
1 p.m.	3'10	23'5
2 "	3'30	23'0
3 "	3'00	22'6
4 "	3'30	22'5

* Exposed to yellow light.

** Exposed to daylight.

In conclusion we may endeavour to form some idea as to the mode of action of light in retarding growth. The effect of the tonic action of light in diminishing the rate of growth is probably to be ascribed to an interference with the motility of the protoplasm of the growing cells, for we know that when the light is of medium intensity, irritability, as indicated by heliotropic curvature for instance, is well-marked, while the rate of growth is considerably lower than it is in darkness. We may regard, then, the tonic action of light, manifested in its retarding effect upon the rate of growth, as an inhibitory action, and as being due to the induction of a certain degree of rigidity in the protoplasm, the rigidity being slight at low intensity and gradually increasing with the intensity, until, under the influence of very intense light, it is complete. A detailed discussion of this point will be given hereafter when we come to the general explanation of all the various phenomena of this kind.

It will be advantageous to give some account of the methods by which the measurement of growing organs has been made. It has been made in some cases by simply using the rule ; in others, by observing the elongation of the organ by means of some form of telescope, with reference to a fixed scale either in the telescope or applied to the organ : in other cases, again, by means of pointers connected with the organ and playing over a graduated arc. The most convenient form of instrument is the self-registering auxanometer, first devised by Sachs, in which the point traces its rise and fall upon a piece of smoked paper fastened on to a rotating drum. Appended is a figure of Baranetzky's improved form of self-registering auxanometer. It consists of a table bearing the rotating drum, and carrying on each side a stand, which will slide up and down as required, for the plants ; in the figure only one plant is in position. A thread is attached by one end to the top of the stem of the plant, and has a weight at the other end to keep it tense. It passes over a pulley, and on the same axle as this pulley there is a large grooved wheel : over this wheel and the other above it there passes an endless cord to which the indicator is attached, the point of the indicator being in contact with the revolving drum. An elongation of the stem will cause the weight at the end of the thread to sink, and will cause the pulley to turn : this movement will be communicated to the grooved wheel on the same axle, and will cause a movement of the indicator which will be traced on the drum. The drum may be made to rotate

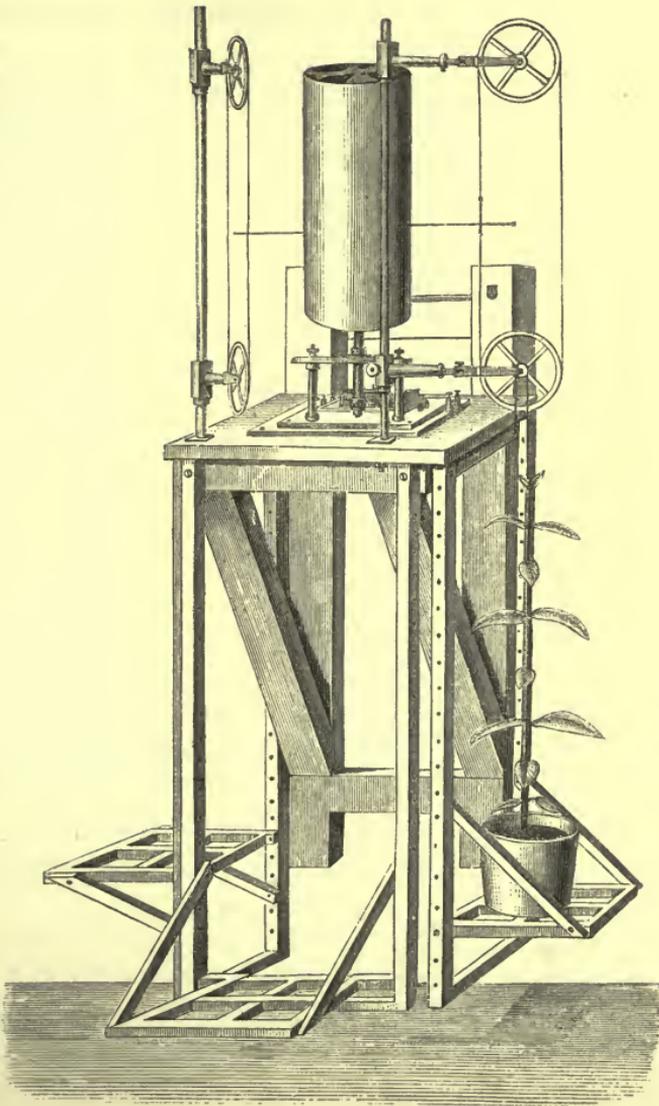


FIG. 44. Baranetzky's self-registering auxanometer.

either uniformly, by clockwork, or in jerks, by means of an electric current: the instrument in the figure is arranged for the latter mode of rotation.

The Stimulating Action of Light. The effect of variations in the intensity of light, as such, upon the rate of growth is a subject which has not as yet been adequately investigated. The only facts bearing upon it are those ascertained by Pfeffer in his investigation of the opening and closing of flowers. He found, namely, that exposure to light of a certain intensity caused the flowers to open, and to darkness to close. Exposure to direct sunlight caused some flowers (*Oxalis valdiviana*, *Calendula*, *Leontodon*, *Venidium*, and other Composites) to close, so that possibly there may be an optimum intensity for inducing opening. An increase of intensity, within certain limits induces, then, opening, and a diminution closing. It is probable, though he made no measurements, that exposure to light or removal from light, causes, like variations of temperature (see *ante*, p. 379), a temporary acceleration of the mean rate of growth. We cannot explain, here, any more than we could with regard to variations of temperature, how it is that the induced variations in the rate of growth should be manifested by the accelerated growth of the upper or the lower surface according to circumstances. These remarks are probably also applicable to the rising and falling of the young growing leaves of certain plants (*Chenopodium album*, *Polygonum aviculare*, *Stellaria*, *Linum*, *Impatiens*, *Polygonum Convolvulus*), observed by Batalin, and to that of cotyledons observed by Darwin.

The Daily Period of Growth in Length. The tonic influence of light upon growth can in no case be more clearly observed than by the study of the growth of plant-organs in its relation to the normal alternation of exposure to light and darkness which takes place in each day of twenty-four hours. The alternation of day and night causes, as might be expected, daily variations in the rate of growth in length; these are tolerably uniform for each period of twenty-four hours, and constitute what is known as the daily period of growth in length.

The daily period of growth in length was first thoroughly studied by Sachs, and we may take some of his results to illustrate our present consideration of the subject.

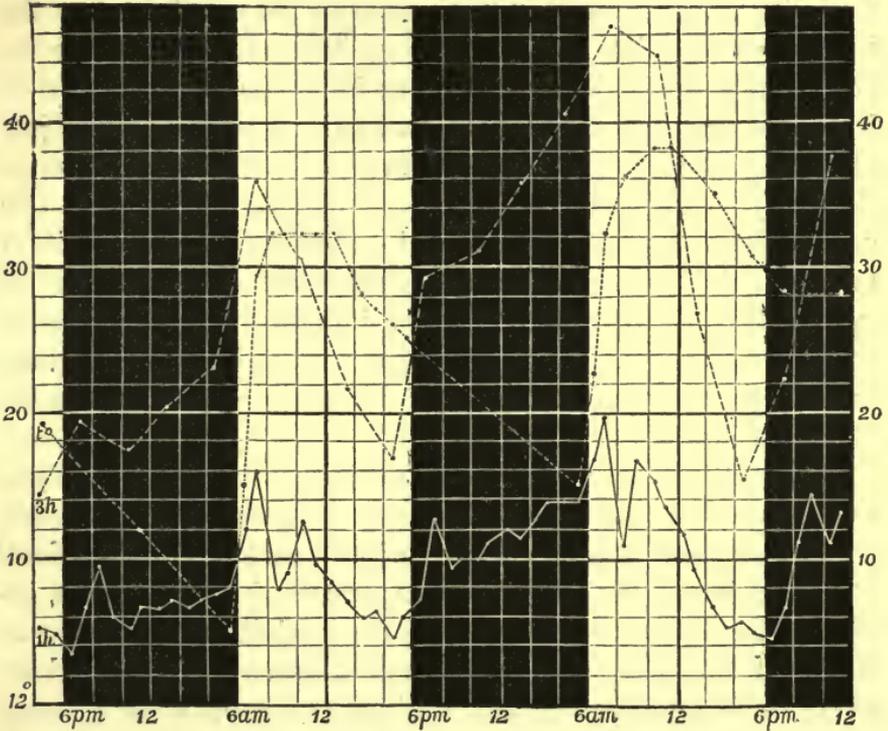


FIG. 45 (after Sachs). Curves of the daily period of growth in length of the stem of *Dahlia variabilis*. $1h$ is the curve constructed from hourly observations, and $3h$ is the curve constructed from observations made every three hours; t° is the curve of temperature. The abscissæ represent periods of two hours, and the divisions of the ordinates represent units of increment in length. With regard to the temperature, the base-line indicates 12° R., and five of the divisions of the ordinates correspond to 1° R. The shaded spaces represent periods of darkness.

A general inspection of the curves, particularly of the curve constructed from observations made every three hours, shews, as might be expected, that the rate of growth increases during the night, and diminishes during the day. It will be noticed that the effect of exposure to light or to darkness does not manifest itself suddenly, but that in the one case the curve gradually falls and that, in the other, it gradually rises.

It will also be observed that the maxima are not attained during the periods of darkness, but shortly after the exposure of the plant to light, and, further, that the occurrence of the minima does not coincide in point of time with the greatest intensity of light, but that they occur in the evening when the intensity of the light is diminishing. These facts illustrate the statements made above that the influence of light makes itself only gradually apparent, and that it persists for a time after the growing organ has been more or less completely withdrawn from exposure to light. A comparison of the two curves shews that the one (3 h) is more even than the other (1 h). This is due to the fact that when measurements of growing organs are made at short intervals, the spontaneous irregular variations (see p. 358) of the rate of growth become much more apparent than when the measurements are made at longer intervals.

It must, however, be remarked that the alternation of light and darkness is accompanied by other changes in the external conditions, and that it affects various processes of the plant. If we observe the curve of temperature in Fig. 45, for instance, we see that it rises during the periods of exposure to light, and falls during the periods of darkness. We know that at a high temperature the rapidity of growth is greater, whereas at a low temperature it is less; hence, the different prevailing temperatures constitute an important factor in determining the form of the curve of growth. Again, a high temperature and exposure to light promotes transpiration, and we know that very active transpiration tends to retard growth. The curves in the figure are therefore not merely simply the expression of the action of light upon growth, but they are the resultant expression of this action, of the influence of various temperatures, and possibly of the influence of variations in the activity of transpiration. The fall of the curve of growth during a period of exposure to light is not so rapid as it might be, because the retarding effect of light is to some extent counteracted by the accelerating influence of the higher temperature; but, on the other hand, the retarding effect of light may be assisted by the increased

transpiration. Similarly, the rise of the curve of growth during a period of darkness is not so rapid as it might be, because the accompanying low temperature exercises a slight retarding influence ; but, on the other hand, the acceleration may be promoted by the diminution of transpiration.

A similar daily periodicity has been observed by Prantl in the growth both in breadth and length of the leaves of dicotyledonous plants, by Stebler in the growth in length of the leaves of monocotyledonous plants, and by Strehl in the growth in length of roots.

The daily periodicity of growth induced in a plant by exposure to the normal alternation of day and night does not necessarily cease when the plant is kept in continuous darkness, but may persist for a longer or shorter time. Baranetzky has observed this in various species of *Gesneria*, in *Helianthus annuus* and *tuberosus*, and in *Brassica Rapa*. But the duration of this persistence varies in different plants. Baranetzky could observe the daily period in *Gesneria tubiflora* for only two or three days, whereas he could detect it in *Helianthus tuberosus* after fourteen days in continuous darkness. The occurrence of the minima and maxima becomes eventually irregular, and is then the expression of the irregular spontaneous variations of growth (see p. 358). Entirely etiolated plants, plants, that is, which have been grown from the beginning in darkness and have not been exposed to the alternation of day and night, do not exhibit a daily periodicity of growth, but only the irregular spontaneous variations. It was indeed mentioned in a previous lecture (p. 359) that Baranetzky observed a fairly regular daily period in the growth of the stem of an entirely etiolated plant of *Brassica Rapa*. He is inclined to regard this as due to heredity, but it is at least equally probable that it is a mere coincidence, that the spontaneous variation happened in this case to occupy a period of twenty-four hours.

Some interesting examples of daily periodicity of growth are afforded by the opening and closing of the flowers, and by the rising and falling of the leaves, of certain plants. With regard to the opening and closing of flowers, we know already that opening is induced by exposure to light, and

in some cases by a rise of temperature, and that closing is induced by withdrawal of light, and in some cases by a fall of temperature (pages 378 and 400). We can thus readily understand how it is that many flowers open in the morning, when the intensity of light is increasing and the temperature rising, and close in the evening when the intensity of light is diminishing and the temperature falling. The daily period is the response of the growing perianth-leaves to the variations in external conditions which accompany the alternation of day and night.

This induced daily periodicity is impressed more or less deeply upon the organisation of the flower, as is shewn by the fact that the exhibition of it does not at once cease when the flower is kept under nearly constant external conditions, in darkness and at an approximately uniform temperature. Pfeffer observed, for instance, that flowers of the Daisy, when placed one evening in darkness, opened the next morning, though later than usual, and attempted feebly to close in the evening; on the second day slight opening-and-closing movements were made. The degree in which it has been impressed can also be estimated by comparing the effect of sudden disturbances of the external conditions. For example, Pfeffer found that the flowers of *Ficaria* and of *Anemone* open much more quickly than they close when subjected, of course in darkness, to the influence of a rise and then of an equal fall of temperature in the morning when their natural tendency was to open. In *Crocus* and *Tulipa*, a rise of temperature causes the flowers to open in the afternoon when they are closing. In other cases (*Ficaria*, *Galanthus*), a rise of temperature in the afternoon when the flowers are closing, induces only a partial opening. In others again (*Nymphæa alba*, *Oxalis rosea* and *valdiviana*, *Mesembryanthemum tricolor* and *echinatum*, *Compositæ*) the flowers cannot be made to open in the evening by a rise of temperature which acts rapidly when they are subjected to it, of course in darkness, in the morning-hours. Similarly with regard to the action of light, the effect of withdrawal from light is much less marked in the morning-hours than in the evening-hours. The effect,

then, of variations of external conditions is more or less marked in proportion as it coincides with or opposes the course of the daily period.

A few remarks may be added with regard to the rising and falling of growing foliage-leaves (see p. 400). It has long been known that the young growing leaves of various plants take up different positions by day and by night. Batalin, who has the most recently studied this subject, mentions the following cases: leaves which rise at night, *Chenopodium*, *Polygonum aviculare*, *Stellaria*, *Linum*: leaves which fall at night, various species of *Impatiens*, *Polygonum Convolvulus*, *Sida Napæa*. Batalin has shewn that these movements, like the opening and closing of flowers are undoubtedly phenomena of growth, and probably their daily periodicity is induced in the same way in both these cases.

Daily periodicity of the Tensions of the Tissues. In a previous lecture (p. 342) attention was drawn to the existence of tissue-tensions in growing organs, and the mechanical conditions upon which these tensions depend were discussed. We will now study them in their relations to external conditions, and we shall find they afford information which will materially contribute to an understanding of the mode in which variations in the external conditions give rise to corresponding variations in the rate of growth.

In the course of his researches, to which allusion was then frequently made, Kraus ascertained that the tissue-tensions are considerably affected by variations in the external conditions. He observed that the tensions, both longitudinal and transverse, exhibit a daily periodicity in shoots which are exposed to the normal alternation of day and night, such that the tensions diminish from dawn throughout the day as the intensity of light increases, and begin to increase in the early afternoon as the intensity of the light diminishes. This periodicity is dependent upon previous exposure to the alternation of day and night, for if a shoot be kept in continuous darkness, the daily period gradually disappears, and is replaced by irregular variations. The daily period can only be observed when the temperature is sufficiently high; thus,

in the shoots of plants growing in the open air, it can only be observed during the summer but not in the winter. It does not appear, however, that variations of temperature contribute largely to the production of the daily periodicity, for Kraus found that only very considerable variations of temperature, far greater than those which usually occur in any one period of twenty-four hours during the summer months, materially affect the intensity of the tensions. For instance, a very marked increase in the tensions is produced when a shoot which has been kept at a temperature of $7-8^{\circ}$ C. is exposed to a temperature of $15^{\circ}-20^{\circ}$ C. So long as the temperature varies within certain normal limits, say between 10° C., and 30° C., the variations do not appear to affect the daily period.

Millardet has observed a similar daily periodicity of the tensions in *Mimosa pudica*, the Sensitive Plant. His observations confirm the statements of Kraus with regard to the relation of the daily period to variations in the external conditions in all respects except with regard to the influence of temperature. Millardet found, namely, that a rise of temperature from 18° to 32° C. materially increased the tension, and that a fall from 30° to 19° C. materially diminished it.

Kraus ascribes the daily periodicity of the tensions to variations in the turgidity of the parenchymatous tissues, particularly of the pith. When a shoot is insufficiently supplied with water, it is the pith which is most affected, as is shewn by the fact that it becomes shorter, under these circumstances, than any of the other tissues. This explanation is confirmed by results obtained in his subsequent investigations on the same subject but in rather a different direction. He has found, namely, that not only shoots, but all plant-organs, whether growing or not, exhibit a daily period of variation in bulk, provided always that the temperature is not too low. The course of the daily period is this, that the organs diminish in bulk (as estimated by their diameters) from early morning until afternoon, when the minimum is reached, and then increase in bulk until towards dawn, when the maximum is attained.

These variations in bulk depend largely upon the variations

in the total quantity of the water which the organ contains, and this again depends upon the relative gain of water by absorption and loss by transpiration, assuming that the organ forms part of a plant growing under normal conditions. As regards absorption, we learned in a previous lecture (p. 95) that the root-pressure exhibits a daily periodicity such that the maximum is generally attained in the afternoon, and the minimum about twelve hours later. On comparing the daily period of root-pressure with that of variation in bulk, we find that the two in no wise correspond; the maximum of the former falls at about the time of the minimum of the latter. As regards transpiration, we have learned in a previous lecture (p. 109) that this process is carried on more actively in light than in darkness, and that a relatively high temperature is favourable to it: it seems therefore possible that the diminution in bulk during the day may be due to the loss of water by transpiration. Kraus has found, as a matter of fact, that the removal of the leaves in the day-time arrests the normal diminution in bulk of the stem. The daily variation in the total quantity is due, then, to the excess of the loss over the supply by day, and the excess of the supply over the loss by night.

Inasmuch as these variations in bulk are thus dependent upon variations in the quantity of water which the organs contain, and in view of the general similarity between the course of the daily period of variation in bulk and that of the daily period of the tensions, it would seem natural to regard the one as the cause of the other. The change in the diameter of a branch, for instance, is due, according to Kraus, either chiefly to the swelling by imbibition of the walls of the wood-cells, or chiefly to the expansion of the parenchymatous tissues. In whichever of these ways the increase in bulk takes place, it is clear that it must increase the tissue-tensions in the organ; similarly a decrease in bulk involves a diminution of the tissue-tensions.

But these variations in bulk are not wholly due to variations in the total quantity of water which the organ contains, but they depend also upon the distribution of the water. Perhaps the most interesting of Kraus' observations

is that pieces of stout branches, sawn off and cemented at both ends, exhibit the daily periodicity of variation in bulk, and further that the diameter of such pieces increases when they are withdrawn from the influence of light, the temperature being constant, and also when they are subjected to a rise of temperature in darkness. In these cases the increase in diameter is entirely due to the cortical parenchyma, the bulk of the wood either remaining unaltered or decreasing. The expansion of the cortical parenchyma, cannot be due to an increase in the total quantity of water, for none enters the piece of branch during the experiment. It is due entirely to a redistribution of the water present. This factor doubtless enters largely into the production of the variations in diameter of rooted plants. The wood appears to act as a reservoir (see p. 99) of water upon which the cortical parenchyma can draw in expansion, and to which it can return the excess of water on contraction.

These facts are of great importance, for they afford an illustration of the sensitiveness of the protoplasm of cells which belong neither to growing, in length at least, or to motile organs, and also in that they throw light upon the mechanism of growth and of movement. A full discussion of them is reserved for the present, but as much may be now said concerning them, that they confirm what has been said as to the effect of temperature in increasing the motility of the protoplasm, and of light in decreasing it. The significance of these facts is this, that as the motility of the protoplasm of the parenchymatous cells increases under the influence of a higher temperature, the vacuoles increase in size and the cells take up more water ; and conversely, that as the motility of the protoplasm diminishes under the influence of light, the parenchymatous cells give up water. When this takes place in a growing organ, the growth of the cells must obviously be correspondingly affected, and, as a matter of fact, the daily period of variation in bulk and that of growth are closely similar. The daily variation in bulk of the cells is then the cause of the daily periodicity of tensions, and, in growing organs, of the daily periodicity of growth in length.

GRAVITATION.

In view of the influence which different temperatures and different intensities of light exercise upon the rate of growth in length, the question naturally suggests itself, inasmuch as growing organs respond by curvatures to alterations in their relation to the line of action of gravity, whether or not their rate of growth would be affected by reversing their normal relations to the line of action of gravity, or by neutralising the action of gravity, or, finally, by exposing them to the action of a centrifugal force, which has the same action upon them as gravity, either greater or less than that of gravity. Elfving has endeavoured to give an answer to this by his experiments on organs which normally grow vertically, either upwards or downwards. He found, in the first place, that the sporangiferous hyphæ of *Phycomyces nitens* grow rather less rapidly in the inverted than in the normal erect position. He concludes that this retardation is due to the alteration of the relation of the axis of the organ to the line of action of gravity, and he considers it to be probable that the effect would be the same in the case of all organs which normally grow upwards. This conclusion is supported by the observations of Vöchting, who has noted that the pendent branches of so-called "weeping trees" grow in length less rapidly than their erect branches. This point cannot, however, be regarded as having been fully investigated, for the corresponding observations have not yet been made upon organs which normally grow downwards, but we may perhaps compare the action of gravity upon the rate of growth of an organ in its normal condition to the effect of the optimum temperature upon the rate of growth, and the effect of a reversal of the normal relation of the organ to the line of action of gravity to the effect of a temperature either higher or lower than the optimum. In the second place, Elfving has found, by further experiments with *Phycomyces*, that the rate of growth of the hyphæ is the same whether they grow in their normal position, or whether the action of gravity upon them is neutralised by causing them to rotate slowly round a hori-

zontal axis by means of a machine, termed a Clinostat, which will be described hereafter. Similar results were obtained by Schwarz in the case of roots. Finally, Elfving found, by experiments with peas pinned to a disc of cork which was made to rotate rapidly, that a considerable centrifugal force, acting along the axis of growth of the roots of seedlings in the direction from the base to the apex, did not cause any material alteration in the rate of their growth as compared with that of roots growing under normal conditions. This result, again, has been confirmed by Schwarz.

ELECTRICITY.

The effect upon its rate of growth in length of the passage of constant currents through a growing organ was made the subject of investigation by Elfving. He found that when a current runs through the long axis of a root, its growth is retarded, and more markedly when the direction of the current is opposed to that of the growth in length of the root. These results have been confirmed by Müller-Hettlingen. The influence of the current appears to be of a tonic nature.

PRESSURE AND TRACTION.

The effects of pressure and traction upon the rate of growth of organs, though for the most part they can hardly be regarded as phenomena of irritability, but as purely mechanical, may be conveniently considered here. In a former lecture (p. 348) we discussed the effect of the tensions of the tissues upon growing cells, and we then learned that pressure limits the growth of the cells in the direction in which it is applied. Generally speaking, the effect of pressure upon a growing organ is the same as that produced upon growing cells by the resistance of the older tissues; pressure retards the growth of that portion of the organ to which it is applied. Sachs gives a number of illustrative cases of this: if the root of a seedling be grown so that it comes into permanent contact with some solid body, it gradually curves round it, in consequence of the growth in length of that

surface of the root which is in contact with the solid body being less rapid than that of the opposite free surface; similarly, the aërial roots of Aroids and Orchids become closely applied to solid bodies, and delicate filaments, such as the hyphæ of Fungi and pollen-tubes behave in precisely the same manner. The softer and the more yielding the tissue of the organ, the more easily will it be thus affected by pressure; for instance, the pileus of Agarics growing in woods often grows over and more or less completely encloses leaves, pieces of stick, etc., the slight weight of these objects sufficing to arrest the growth of that portion of the pileus upon which they were lying. Another illustration is afforded by the effect of the mutual pressure of organs arising close together in modifying their individual form and relative arrangement. Schwendener has drawn attention to this in the case of leaves, and has been able to arrive at a simple mechanical explanation of the phenomena of phyllotaxy.

But external pressure has, in many cases, another and quite opposite effect upon growth. In these cases it promotes the growth of the organ, it acts as a stimulus to it. For example, von Mohl has shewn that the haustoria of *Cuscuta* and *Cassytha* are only formed when there is continuous contact with a solid body; and similarly, as Darwin and Pfeffer have found, the adhesive discs on the tendrils of the Virginian Creeper are only formed under the same circumstances. In some plants these discs are formed independently of such contact: this has been observed in *Ampelopsis Veitchii* (M^cNab), in *Haplolophium* (F. Müller), and in *Zanonia macrocarpia* (Treub): but it appears that the size of the discs is very much increased by contact. Again, Darwin has pointed out that tendrils and the petioles of leaf-climbers become much thicker, when they have come into contact with a support, than they were before, and Treub has drawn attention to the occurrence of precisely the same thing in the hooks of certain hook-climbers.

The accompanying figures of sections of a free and of an attached petiole of *Solanum jasminoides* give some idea of the effect of pressure in stimulating to growth.

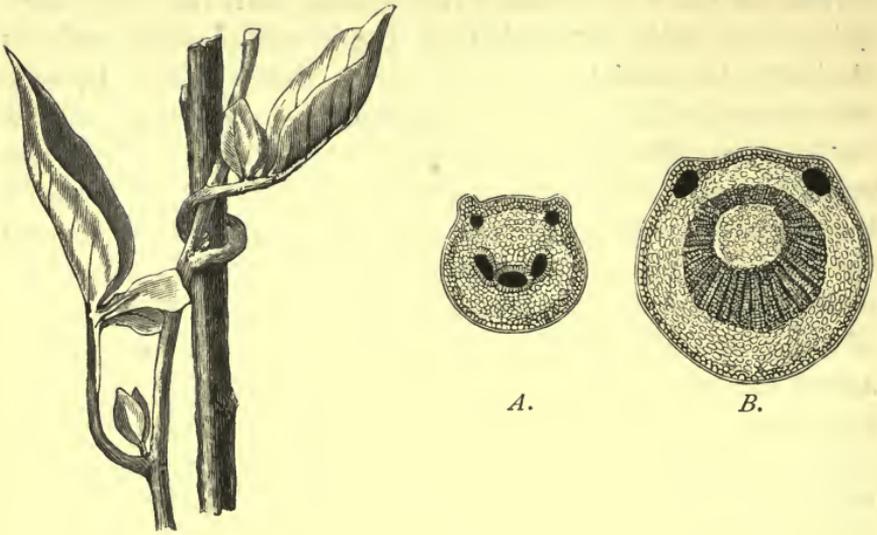


FIG. 46 (after Darwin). Petiole of *Solanum jasminoides* clasp a stick. *A*, transverse section of free petiole; *B*, transverse section of a petiole some weeks after it had clasp a stick.

Treub has observed the increased growth in the thickness of the hooks in consequence of contact in the following plants: *Uncaria* (Rubiaceæ), *Ancistrocladus* (Dipterocarpeæ), *Artabotrys* (Anonaceæ), *Luvunga* (Aurantiaceæ), *Olax* (Olacineæ), *Hugonia* (Linaceæ), and *Strychnos* (Loganiaceæ). The following figure exhibits the difference in thickness between a hook which has and one which has not come into contact with a support.

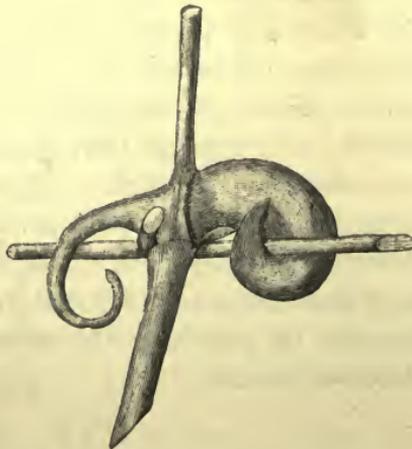


FIG. 47 (after Treub). Hooks of *Uncaria ovalifolia*.

With regard to traction, we learned, in our consideration of the tensions of the tissues (p. 349) that it promotes the growth of the cell in the direction in which it is applied, as is well shewn in the case of the epidermal and hypodermal cells of etiolated plants. That long-continued traction in one particular direction promotes growth in length of organs in that direction is illustrated by the well-known fact that the stems of trailing plants which grow in streams are longer when the current is swift than when it is sluggish. The effect of traction is apparently only distinctly manifested when the traction is long-continued, consequently it cannot be detected in comparatively brief experiments. Thus in Schwarz's experiments upon the influence of centrifugal force upon the rate of growth in length, to which allusion was made above, the traction, though it must have been considerable in view of the rapidity of rotation (in some cases 156 revolutions per minute, when the centrifugal force was twenty times as great as that of gravity), exercised no perceptible influence upon the growth in length of the roots during the experiment. A singular effect of traction was observed by Baranetzky in his researches on the growth in length of stems (see p. 398). He found, namely, that when a stem of a plant on the auxanometer was stretched somewhat by the weight passing over the pulley (see Fig. 44), its rate of growth was retarded. The significance of this fact is not clear, but it would appear that in this case the traction has a stimulating, as opposed to a simply mechanical, effect.

With this we conclude our account of the influence of external conditions in modifying the rate of growth of organs. In the next lecture we will consider their influence in causing alterations in the direction of growth.

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LECTURE XVII.

IRRITABILITY OF GROWING ORGANS (*continued*).

IN the last lecture we considered the irritability of growing organs as exhibited in their response, by alterations in the *rate* of their growth, more particularly of their growth in length, to the action of various external influences. In the present lecture we will further pursue the study of this subject by considering the response, by alterations in the *direction* of their growth, which growing organs give to the action of external agents.

Before, however, we can enter upon the consideration of changes in the direction of growth due to the action of external stimuli, we must ascertain as far as possible what internal influences there may be which contribute to determine the direction of growth of an organ. We learned, in a previous lecture (p. 360), that the growth in length of an organ rarely, if ever, takes place in a straight line, in consequence of spontaneous heterauxesis, but that its apex nutates. The changes in the direction of growth which constitute nutation are, however, only temporary; as growth ceases, the axis of an organ becomes approximately straight. In endeavouring to account for this fact, we must remember that, in nature, plant-organs are exposed to the action of light, of gravity, and of other agents which tend to modify the direction of their growth. We must not assume, simply because we see that a stem or a branch is straight, that it has an inherent tendency to grow in a straight line, for its straight-

ness may be largely due to the action of light, gravity, etc. In order to determine whether or not there is any inherent tendency in a plant-organ to grow straight, it must be grown under such conditions that neither light, nor gravitation, nor any other external agent, can exercise any directive influence upon it.

The directive influence of an external agent can be eliminated in either of two ways; by removing the agent altogether, or by arranging that all sides of the plant-organ shall be equally exposed to its influence. Thus, the action of light can be got rid of by placing the plant in darkness, or by causing it to revolve so that each side of the organ is exposed for equal periods of time to light falling upon it in any given direction. Similarly the effect of the action of gravity is eliminated by causing the organ to rotate slowly round a horizontal axis, so that each side of the organ makes any given angle with the line of action of gravity for equal periods of time.

The instrument for slow rotation of this kind is known as the "Clinostat," and we owe its introduction into experimental physiology to Sachs. Annexed is a figure of a convenient form of clinostat.

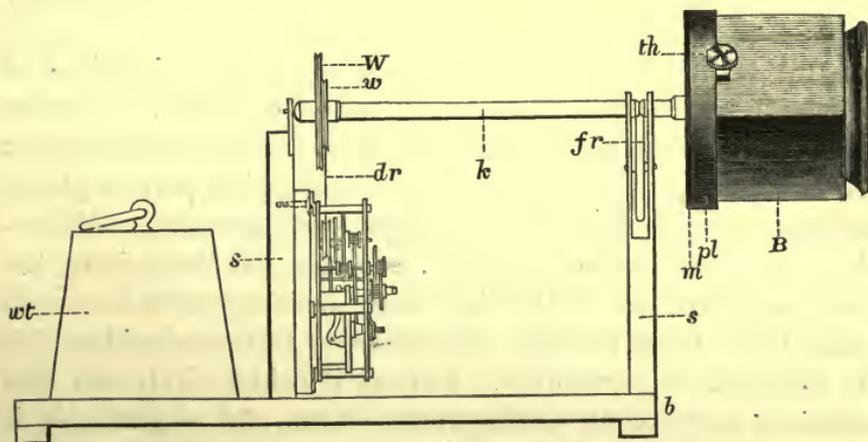


FIG. 48 (after F. Darwin). The Clinostat.

It consists of a stand, *b*, bearing two upright supports, *s*, *s*, on which the spindle, *k*, rests. The spindle bears near one end the two driving-wheels, *W* and *w*, over either of which the driving-cord, *dr*, connected with the clock-work below, may be led. The spindle rests towards its other end on friction-wheels, *fr*, and is screwed on to a metal plate which plays freely between the metal plate *m* and the disc of wood, *pl*, to which the box *B* (containing in this case a flower-pot) may be fixed by means of

the screw *th*. The weight, *wt*, counterbalances the box and anything it may contain.

In order to ensure the necessary uniformity of rotation it is necessary that the centre of gravity of the box, *B*, and its contents should lie in the axis of rotation. The centering is effected by altering the position of the above-named movable brass plate, which lies in a chamber between *m* and *pl*, and which can be fixed in any requisite position.

A great number of experiments, with the solution of this problem as their object, have been made by Vöchting. He has found, in the case of peduncles, branches, primary shoots and roots, that when these organs are withdrawn as far as possible from the action of all external directive influences, their axes of growth are nearly straight. In certain cases he observed that organs which had been purposely induced to curve, straightened themselves out during the course of the experiment. The only at all satisfactory account is that offered by Vöchting, that growing organs possess a tendency, which he calls *Rectipetality*, to grow in a straight line, and so far as anything is known about it at present, this tendency appears to be inherent in them.

But we have yet more to learn about the directions of growth spontaneously assumed by growing organs. In order to pursue this subject we must revert to the fact mentioned in the first lecture (p. 9) that, with the exception only of plants of the lowest organisation, the plant-body presents a distinction of a base and of an apex, and that the line joining the base and the apex is the line along which growth in length takes place (also p. 360). We will now further elucidate this by reference to examples. Let us consider, first, the filamentous body of an Oedogonium. One end of the body is attached, the other is free; the former is the base and the latter the apex; the line joining the two is the axis of growth. The growth in length of the body is not, however, localised in this case at either the base or the apex, but it elongates by the growth of all its constituent cells; its growth is intercalary. In a plant-body of somewhat higher organisation, such as that of a *Fucus*, we find, as in Oedogonium, the distinction of a base and an apex. We find, however, in a body of this kind,

that all the cells are not capable of growth, but that certain cells only can grow, and that these, stating the matter, in its simplest form, are confined to the apex, constituting what we know as a *punctum vegetationis* (p. 338). In a typical embryonic Vascular Plant we find that the body presents a higher degree of complexity, in that a *punctum vegetationis* is present at each end of its axis of growth. In this case the body consists of two well-defined members, each having its free apex and *punctum vegetationis*, their common base being the plane along which they are welded together. If, as is quite permissible, we compare the body of a *Fucus* to a cone standing on its base, the *punctum vegetationis* being at the apex, we must compare the body of the Vascular Plant to two cones with their bases in contact. These two members, as we shall learn hereafter, possess different kinds and degrees of irritability, and on this account we call them by different names; the one we call the *primary shoot*, the other the *primary root*.

If, now, we observe the course of growth in these various plant-bodies, we find in *Oedogonium* and in *Fucus*, that the axis of growth is approximately a straight line. Similarly, the axes of growth of both the primary shoot and the primary root of the embryonic Vascular Plant are approximately straight lines; their axes of growth form, in fact, one continuous straight line; but the growth in length of primary shoot and primary root takes place in opposite directions along this straight line. This opposition in the direction of growth of primary shoot and primary root is a point of great importance in the subject with which we are now engaged.

We may now proceed to enquire somewhat into the causation of these phenomena, in order to ascertain how far they are the expression of tendencies inherent in the plants.

The body of an *Oedogonium* is developed from a zoospore which is ovoid in form and moves by means of a cirlet of cilia surrounding the more pointed end which is hyaline and uncoloured. As the zoospore swims, the pointed end is directed forwards, and when it comes to rest the zoospore

attaches itself by this end, which accordingly becomes the base of the new plant. The egg or oospore from which the body of *Fucus* is developed does not present this distinction of two ends, this polarity as we may term it, and, inasmuch as it is spherical, it is not easy to ascertain whether or not it is always one particular area of the surface of the egg which becomes attached and constitutes the base of the young plant. However this may be, it is certain that that portion of its surface which becomes attached always becomes the base, and the diametrically opposite surface always becomes the apex, of the young plant. In the case of the Vascular Plant, we find, as I have elsewhere pointed out, that, in the development of the embryo, primary stem and primary root, when these members are present, are always developed from diametrically opposite segments of the egg or oospore. Taking all these facts into consideration, it may be fairly concluded that the distinction of base and apex and, in Vascular Plants, the opposite direction of growth of primary stem and primary root are not induced by any external influences but are inherent in the plant. In the case of *Oedogonium*, where the reproductive cell itself already presents evident polarity, the polarity is impressed upon it by the parent plant.

In contrasting just now the general morphology of a *Fucus* with that of a Vascular Plant, we compared the body of the former to a cone standing on its base, and that of the latter to two cones joined by their bases, the apex of the cone being in all these cases a *punctum vegetationis*. We will now somewhat increase the complexity of our conception of the plant-body. We will imagine that the single case which corresponds to the main body of *Fucus*, and the two cones constituting that of the Vascular Plant, bear other cones upon their flanks, these lateral cones being attached by their bases and having their apices free. These cones may be taken to represent lateral branches, which, like the parent-member, present a distinction of base and apex, and each of which possesses a growing-point at its apex. We obtain in this way a simple idea of the composition of a plant-body in which branching takes place.

The mode of branching, the angle which the branches make with the primary shoot or root, if it persists, and with each other, is a very characteristic feature in the habit of a plant. We naturally assume that light and gravity must exercise a considerable influence in determining the form of branching of a plant, but we are now principally concerned with the question as to whether or not there is any inherent tendency which constitutes to determine the form of branching which any particular plant presents.

In the course of his observations upon the "Mobility of Plants," Dutrochet was led to consider the relation of branches to the axes bearing them, and he came to the conclusion, on grounds which we shall become acquainted with hereafter when we are considering the relation between the direction of growth of shoots and roots to the plane of the substratum bearing them, that the relation between axis and branches is of such a kind that the angle between them, in so far as it is not modified by external influences, is uniformly a right angle. It does not appear, however, at least as far as roots are concerned, that the angle in question is necessarily a right angle. In his researches upon the growth of the roots of seedlings, Sachs established the following facts concerning this angle, the *proper angle* as he terms it: the lateral roots which arise near the apex of the primary root make an acute angle with the acroscopic portion of it: those which arise near the base of the primary root are nearly horizontal, so that their proper angle is approximately a right angle: those, finally, which arise at the junction of the root with the hypocotyl, or from the hypocotyl itself, form an obtuse angle with the primary root and an acute angle with the hypocotyl, so that in this case the proper angle is greater than a right angle. The directive influence of the parent-axis upon the branch is not, then, as Dutrochet thought, simply an instance of the relation existing between an organ and its substratum, but it is a manifestation of correlation of growth. The existence of such a correlation of growth between axis and branch is placed beyond doubt by the fact, which has been frequently observed in certain species of *Pinus* and *Abies*, that if the

growing apex of the primary shoot be destroyed, one of the adjacent lateral branches will curve upwards and will take on, at the same time, the properties of a primary member. Sachs has observed that the same thing happens in the case of roots.

We see, then, that the direction of growth of organs is to some extent determined by their own proper rectipetality, and by the relation existing between them as members of one plant, between primary shoot and primary root, and between lateral branch and parent-axis.

We have yet to enquire into the relation of organs possessing different physiological properties to the action of external stimuli as affecting the direction of their growth. Some light will be thrown on the matter by a consideration of those spontaneous changes in the direction of growth with which we became acquainted in a previous lecture (p. 360) under the term Nutation. We then found that heterauxesis manifests itself in a characteristic way. The stems of some plants, for instance, exhibit circumnutation in its most typical form (see diagram, p. 364); others exhibit simple nutation, and others, again, exhibit that form of heterauxesis which we have become acquainted with under the terms "epinasty" and "hyponasty" (p. 366). The form of heterauxesis which an organ exhibits affords us an insight into its nature. In the case of an organ exhibiting revolving nutation, each side is in turn the one which is growing with the greatest rapidity; this we may take to be an indication of what may be termed *radial nature*. In a case of simple nutation, the heterauxesis is exhibited alternately by the two opposite sides of the organ; this we may take to be an indication of *bilateral nature*. Finally, organs exhibiting epinasty and hyponasty are also physiologically bilateral.

It may be conveniently mentioned here, that, in many cases, the symmetry of form of an organ corresponds with its physiological nature. Thus all organs which are physiologically radial present also a radial symmetry of form. But the converse does not hold, that is, not all organs possessing a radial symmetry of form are radial from the physiological

point of view. In support of this it may be repeated that radially symmetrical organs, like primary shoots (see p. 367), very frequently exhibit simple nutation, and also hyponasty and epinasty; further evidence of the bilateral nature of some radially symmetrical organs will be brought forward when we are considering the effect of the action of external influences. Again, organs which have a bilateral symmetry of form physiologically are bilateral; but physiological bilaterality is not confined to organs with bilateral symmetry, for, as we have just seen, bilateral nature is manifested by some radially symmetrical organs.

With regard to bilateral symmetry, there are two cases to be clearly distinguished; that, namely, in which the two flattened surfaces are the flanks of the organ, and that in which they are respectively superior and inferior. Striking examples of these two kinds of bilateral symmetry are to be found amongst leaves: the flattened leaves of some species of *Iris* exhibit bilateral symmetry of the former kind, in that their plane of extension is the antero-posterior plane; but the bilateral symmetry of the great majority of leaves is of the latter kind, for they are extended in the transverse plane, and thus present an upper and a lower surface, whence they are said to be *dorsiventral* (p. 366). The difference in external symmetry is connected with differences in internal structure and in properties. In the case of the simply bilateral or *isobilateral* organs, the internal structure of the two sides is symmetrical, whereas, in the case of the dorsiventrally bilateral organs, the internal structure differs in the neighbourhood of the two surfaces. Again, simple nutation is characteristic of isobilateral organs, whereas epinasty and hyponasty are characteristic of dorsiventral organs.

We may now pass to consider, in the most general way, the relation of plant-organs of different physiological properties to the action of external influences. We can judge of the nature of their response from the positions which they take up in the course of their growth under normal conditions. The positions which the organs take up under these circumstances are most various: thus, most primary roots are directed vertically

downwards and most primary shoots vertically upwards, whilst lateral branches, both of roots and shoots, are usually inclined to the vertical. We see at once that the response of different organs to the action of external influences is by no means the same, but that each responds in a manner peculiar to itself. The organs, to use Sachs' apt expression, are *anisotropic*, that is to say, they are endowed with different kinds of irritability and in different degrees. On this basis, we can at once classify all organs into two great groups; those, namely, which grow more or less nearly vertically, either upwards or downwards, and those which grow inclined at a greater or a smaller angle to the vertical. The organs of the former group are termed, in accordance with Sachs' proposed nomenclature, *orthotropic*, those of the latter *plagiotropic*. To the former group belong the great majority of organs which are physiologically radial, as well as isobilateral organs such as the Iris-leaves; to the latter belong all organs which are dorsiventrally organised. If we now enquire into the causes which determine the position of a plant-organ, we find that it must depend upon its peculiar irritability, and upon a certain balance between the responses given by the organ to the various directive influences which act upon it. The orthotropism of radial and of isobilateral organs, and the plagiotropism of dorsiventral organs depends in each case upon the peculiar irritability associated with their nature, and upon a certain relation between the responses which they give to the action of light, of gravity, etc.

We may, before leaving the subject, briefly enquire into the causation of these different kinds of physiological nature. In some cases they can only be accounted for by regarding them as inherent in the constitution of the organ. This appears to be the case, for example, with regard to the radial and isobilateral organs, and also with regard to certain dorsiventral organs, such as most leaves, and lateral branches, particularly those of forest-trees in which, according to Sachs and to Frank, the dorsiventrality is entirely due to internal causes. In other cases dorsiventrality is induced under the influence of external conditions, more particularly of light.

A few instances of this, illustrating the different degrees in which dorsiventrality can be impressed upon the plant, will be of interest. We will begin with an instance of what we may call a slightly dorsiventral organ. Sachs has observed that the young primary shoot of *Tropæolum majus* is at first orthotropic, and that the exposure of one side of the older internodes to intense light for a time, causes a considerable curvature so that the shoot becomes plagiotropic. It has also become physiologically dorsiventral, the illuminated side being the upper surface, but this is not strongly marked either in its external form or internal structure: it is radially symmetrical and the spiral phyllotaxis remains, but the ventral (inferior) surface has a tendency to form roots which the dorsal (superior) surface has not. Nor has the dorsiventrality penetrated deeply into the constitution of the shoot, for the exposure of any side of it, so long as it is still growing, for a time to intense light suffices to cause that side to become the dorsal (superior) surface and the opposite side the ventral (inferior) surface. A similar case, but one in which the dorsiventral nature is more marked, is described by Sachs in the Ivy. The primary shoot of the seedling is, like that of *Tropæolum*, at first orthotropic, and radial, but exposure to light on one side causes it to curve so that it is almost horizontal, the illuminated side being, in this position, the uppermost. It is then plagiotropic and exhibits evident dorsiventrality; the leaves, instead of being spirally arranged as they are in the orthotropic shoot, come to be arranged in two lateral rows, and the inferior (ventral) surface produces rootlets. The dorsiventrality penetrates more deeply into the constitution of the Ivy-shoot than it does in the case of the *Tropæolum*-shoot, but it is still capable of alteration: Sachs found, namely, that when a dorsiventral Ivy-shoot was exposed to light on one side for three or four weeks, the illuminated side became the dorsal, and the opposite side the ventral surface, that dorsiventrality was induced in a fresh plane. In the thalloid shoot of *Marchantia* we have a remarkable case of the induction of dorsiventrality, and of permanent dorsiventrality. We will trace the

development of the thalloid shoot—which, for the sake of brevity we will term the thallus—from one of the gemmæ of the plant. The gemma is a small discoid lenticular mass of parenchymatous cells, with two diametrically opposite depressions in its lateral margins. It is bilaterally symmetrical, and is not dorsiventral; but whichever of the two surfaces happens to come into contact with the soil when the gemma is sown becomes and remains the ventral surface, whereas the upper surface becomes and remains the dorsal. The internal structure, at first homogeneous throughout (see Fig. 49) undergoes

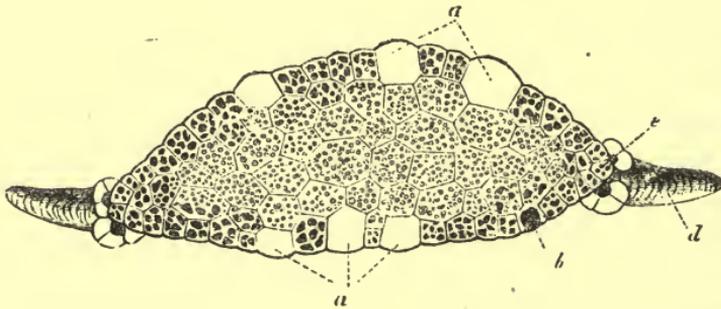


FIG. 49 (after Pfeffer). Gemma of *Marchantia* as seen in transverse section, the plane of section being across from one lateral depression (growing-point) to the other. *a*, cells capable of developing root-hairs; *e*, growing-point; *d*, the margin of the gemma projecting on the further side of the depression.

considerable modification as the gemma develops into the thallus, presenting, towards the upper surface the characteristic air-chambers; the lower surface bears a large number of root-hairs. The thallus is then distinctly dorsiventral. The induction of dorsiventrality may probably be partly due, as Pfeffer suggested, to the action of gravity and to the effect of contact with the substratum, but is chiefly due, as Zimmermann has clearly shewn, to the influence of light. It is, under all circumstances, the shaded side of the gemma which becomes the ventral surface of the thallus, and conversely it is, under all circumstances, the illuminated side of the gemma which becomes the dorsal surface of the thallus. When once induced, the dorsiventrality of the *Marchantia*-thallus appears to be irreversible. In comparing *Marchantia* with *Tropæolum*

Sachs well says that "Marchantia behaves to intense light like hard steel to a magnet; the steel, under the influence of the magnet itself becomes a magnet with fixed poles; Tro-pæolum, on the other hand, behaves to intense light like soft iron to a magnet; the soft iron assumes a definite but temporary polarity which disappears when the influence of the magnet is withdrawn."

The cases of induced dorsiventrality which have been described all refer to primary shoots. We will now briefly consider the case of lateral branches. We can easily understand how dorsiventrality could be induced in them, for they are developed in an oblique position to begin with. It appears that such an induction does, as a matter of fact, take place in the Coniferæ which differ in this respect from dicotyledonous forest-trees, the lateral branches of which, as already mentioned, (p. 424), are inherently dorsiventral. Frank found, namely, and his observation has been confirmed by de Vries, that in whatever position the lateral branch of any one of the many Conifers observed was allowed to develop from the bud, the upper surface became the dorsal surface and the lower the ventral. Light seems to take some part in inducing the dorsiventrality, though it is induced in branches grown in the dark, so that probably gravitation is the principal inducing agent in these cases.

Having now obtained the requisite preliminary information as to the internal influences which contribute to determine the direction of growth of plant-organs, and as to their properties, we may go on to consider the effect of external stimuli in modifying the direction of growth.

Radiant Energy. In our consideration of the influence of light upon the rate of growth, it was tacitly assumed that all sides of the growing organ were symmetrically exposed to light. We have now to deal with phenomena, included under the general term *Heliotropism*, a term which we owe to Frank, which are exhibited when the growing organ is not symmetrically illuminated on all sides. It will be convenient to discuss separately the phenomena exhibited by organs of different physiological properties.

It is a matter of common observation that when plants are grown in a window, that is, under conditions in which light falls laterally upon them, their stems curve towards the light, and their leaves place themselves so that the rays of light entering by the window fall as nearly as possible perpendicularly upon their upper surfaces. Confining our attention to the radial organ, the stem, we see that it curves in such a way as to direct its apex towards the source of light, that light, in fact, induces heterauxesis. Organs which behave in this way are said to be *positively heliotropic*, or, to use Darwin's terminology, simply *heliotropic*. It may be stated that, as a general rule, radial shoots and leaves—using the word shoot in the wide sense in which Sachs employs it—are positively heliotropic. As examples we may mention primary shoots, including the delicate stems of *Chara* and *Nitella* (Hofmeister), many peduncles, the multicellular stipes of some Fungi such as species of *Coprinus* (Hofmeister), and *Claviceps purpurea* (Duchartre), the sporangiferous hyphæ of unicellular Fungi such as *Mucor* and *Pilobolus* (Hofmeister, Sorokin), the filaments of unicellular Algæ such as *Vaucheria*. Among leaves, examples are afforded by the long radial leaves of various Monocotyledons, such as those of the Onion. Positive heliotropism has also been observed, as an exceptional case, by Hofmeister in old roots of *Ranunculus aquatilis*, and by Wiesner in the roots of the Onion (*Allium sativum*), but it is not well marked, and is only exhibited when the light is intense.

But the heterauxesis of a growing organ when light falls laterally upon it is not in all cases such that its apex comes to be directed towards the source of light. In some cases the organ curves in the opposite direction, so that its apex is directed away from the source of light. Organs which exhibit this kind of curvature are said to be *negatively heliotropic*, or, to use Darwin's terminology, *apheliotropic*. Negative heliotropism has been frequently observed in roots; in most aerial roots, for instance (Wiesner); in many ordinary roots (Wiesner); the root-hairs of *Marchantia*. Schmitz states that the mycelial filaments of *Rhizomorpha* (*Agaricus melleus*) are

negatively heliotropic, but Brefeld has been unable to confirm this observation. With regard to shoots, the hypocotyl of *Viscum* (Mistletoe) is negatively heliotropic (Dutrochet, Wiesner). It may be also mentioned here, as a matter of historical interest, that the discovery of negative heliotropism was made by Knight in his observations on the tendrils of *Vitis* and *Ampelopsis*. The consideration of their heliotropic properties will be deferred until we come to treat of dorsiventral organs (p. 443).

It is stated that some organs exhibit at one time positive, and at another negative, heliotropism. Thus, according to Sachs, the internodes of *Tropæolum majus* when young are positively heliotropic, whereas when they are older they are negatively heliotropic, and this is true also of the hypocotyl of the Ivy. Wiesner has observed an apparent change in heliotropic properties in the stems of *Galium versum* and *Mollugo*, and in radial shoots of *Cornus mas* and *sanguinea*. The same has been observed in the peduncles of *Erodium cicutarium* and in those of *Taraxacum officinale* by Vöchting. In all these cases the organs exhibit positive heliotropism when exposed to feeble light, and negative heliotropism when exposed to strong light. But it is a question if we have really to do here with a reversal of heliotropic properties. We know already (*supra*, p. 425) that exposure to intense unilateral illumination causes a change in the nature of the primary shoots of *Tropæolum* and of the Ivy; from being radial they become dorsiventral. It is highly probable that in all these cases the apparent reversal of heliotropic properties is simply the expression of such a change of nature. We will further consider this subject when we are dealing with the influence of light upon dorsiventral organs.

But there are cases of a reversal of heliotropic properties which is apparently not due to a variation in the intensity of the light, though no precise statement is made on this point in the account of the observations, but is dependent upon the biological conditions of the organs. Hofmeister states that the floral peduncle of *Linaria Cymbalaria* is positively heliotropic, but that when the fruit has replaced the flower

the peduncle is negatively heliotropic, and Wiesner, that the peduncle of *Helianthemum vulgare* is negatively heliotropic after fertilisation has taken place.

It will be readily understood that, in the course of its growth, a heliotropic organ may take up a definite position with reference to the direction of the incident rays of light, a position which we will term the *fixed light-position*. The most striking examples of this are afforded by inflorescences, particularly those which are capitulate or umbellate. In most cases when these inflorescences stand in the open, so that they are fully exposed to light, they stand erect, and when they are shaded on one side, as when they grow in a hedge, they curve so that the upper surface of the inflorescence is exposed to the brightest incident light. Wiesner mentions, as examples of this, *Chrysanthemum Leucanthemum*, *Achillea millefolia*, *Anthriscus vulgaris*, *Aegopodium Podagraria*, etc. In other cases the fixed light-position is a different one. The flowers, or more correctly the inflorescences, of the Sunflower (*Helianthus annuus*), even when the plant is growing quite in the open, direct their superior surfaces, not upwards, but to some quarter of the compass, usually to the south-east. This peculiarity cannot as yet be fully accounted for, though it doubtless depends upon some special form of heliotropic irritability. A clue to the explanation of it is afforded by investigations which have been made upon the assumption of their various fixed light-positions by dorsiventral organs, a subject which we shall fully discuss hereafter (p. 447).

Some radial organs do not, however, assume a fixed light position, but follow the daily course of the sun to a greater or less extent. It is usually accepted as a fact that this is the case in the Sunflower, but Wiesner has found that it is not so. Under normal conditions the inflorescences of the Sunflower assume a fixed light-position as described above; it is only when the peduncles are partially etiolated that any daily movement can be detected. Such a movement does, however, occur in various degrees in different plants. Thus, in *Sonchus arvensis*, according to Wiesner, the flowers are directed early in the morning towards the east, and they travel

until they point to the south-east; they remain in this position until the evening, and then curve so that their superior surfaces are directed upwards. The explanation of this is simple. The rays of the rising sun cause a positively heliotropic curvature of the peduncle, so that the flower points towards the east, and for a time the peduncle continues to curve so that the flower follows the sun. When the light becomes intense, the growth, and consequently the curvature, of the peduncle is arrested, and the flower is fixed in the position which it then occupies, a position usually such that it points to the south east. In the evening the peduncle straightens itself under the influence of gravity, so that the flower is directed vertically upwards. A more striking case is afforded by *Tragopogon orientale*. In this plant the growth of the peduncle is not arrested by the intense light, so that the positively heliotropic curvature continues all day, and the flower follows the sun, though the movement is less active in the afternoon than in the morning. In the evening the peduncle begins to straighten itself under the influence of gravity. Wiesner mentions as other instances of more or less well-marked movement, *Leontodon hastilis*, *Papaver Rhæas*, *Ranunculus arvensis*.

In many cases, finally, the ultimate position which the organs assume appears to be independent of the influence of light. Wiesner mentions as examples the inflorescences of *Verbascum*, of *Dipsacus*, *Gentiana*, and others. Even when light falls laterally upon them they continue to grow erect. This can only be accounted for by regarding the organs as being almost destitute of heliotropic irritability.

These are the general facts which have been ascertained as to the heliotropism of radial organs. In entering upon a closer study of them, we will, in the first place, direct our attention more especially to the influence of light in producing them. There are three principal points for us to consider: first, the relation of the direction of the incident rays to the curvature; secondly, the relation of the intensity of the light to the curvature; thirdly, the relative activity of rays of different wave-length in producing the curvature.

The importance of the direction of the incident rays as determining the curvature was first suggested by Sachs, and was subsequently more fully established by Müller-Thurgau. Müller found that the heliotropic effect becomes more marked as the angle of incidence increases from 0° to 90° . The curvature is, in fact, the expression of an attempt on the part of the growing organ to place its axis of growth parallel to the direction of the incident rays. This statement is equally true of both positively and negatively heliotropic organs, though the apex of the organ is directed in the one case towards the source of light, and in the other away from it.

With regard to the relation of the intensity of light to the heliotropic effect, it has long been a matter of common observation that when the two sides of a positively heliotropic organ are exposed to light of different intensity, the organ curves towards the stronger light. But it is erroneous to assume, as is commonly done, that the curvature is merely the effect of the difference in the intensity of illumination of the two sides of the organ. In the case of the delicate hyphæ of Fungi, for instance, the difference in the illumination of the two sides must be very slight, and yet curvature is effected. The curvature is, as we have seen, dependent upon the direction of the incident rays. But the curvature is affected by the intensity of these rays. It is to Wiesner that we owe a detailed investigation of this subject. He has found that variations in the intensity of the light produce distinct effects upon the curvature of the organ exposed to its action, and he has been led, by careful observation of these effects, to the following generalisations. There is for the organs of every plant an optimum intensity of light which induces the maximum of heliotropic effect; any increase or diminution of this intensity is followed by a diminution of the heliotropic effect. It was difficult to determine the lower limit of the action of light, that is, the intensity at which a heliotropic effect can only just be perceived, at least in the case of very sensitive organs (especially the stem of *Vicia sativa*), for they continue to react to light of very low intensity. With regard to the upper limit, Wiesner found that the degree of intensity at

which the heliotropic effect ceased to be exhibited was, in very sensitive organs, higher, and in less sensitive lower, than that which, as mentioned in the previous lecture (pp. 380, 396) sufficed to arrest growth altogether.

Wiesner obtained his results by placing the plants at known distances from an artificial source of light of known intensity, and by determining the time at which the first trace of curvature could be detected.

In the following table his determinations of the upper and lower limits and the optima of intensity of light are given. The unit of intensity is that of the normal flame at a distance of one metre.

	Upper limit	Optimum	Lower limit
<i>Vicia sativa</i> —epicotyl	204	0'44	below 0'008
<i>Lepidium sativum</i> —hypocotyl	816	0'25—0'11	„ 0'008
<i>Pisum sativum</i> —epicotyl	210	0'11	„ 0'008
<i>Vicia Faba</i> „	123	0'16	„ 0'012
<i>Phaseolus multiflorus</i> „	123	0'11	„ 0'008
<i>Helianthus annuus</i> —hypocotyl	330	0'16	„ 0'027
<i>Salix alba</i> —etiolated shoots	above 400	6'25	„ 1'560

Passing, now, to the relative heliotropic effect of rays of different wave-length, it has been ascertained by experiments with light that had passed through absorbent media (coloured liquids or glasses) that the heliotropic effect of the rays of high refrangibility is much greater than that of the rays of low refrangibility (Payer, Dutrochet, Zantedeschi, Sachs). Experiments made with the spectrum (Poggioli, Gardner, Guillemin, Wiesner) shew that all the visible rays, excepting the yellow, and, according to Wiesner, the invisible ultra-red and ultra-violet rays, produce heliotropic effects. Wiesner gives the following account of the relative heliotropic effect of the different rays. Sensitive organs, such as the stem of etiolated Vetch-seedlings, curve most strongly at the junction of the ultra-violet and violet rays; from this point the heliotropic effect diminishes until, in the yellow, it disappears; it begins to manifest itself again in the orange, and increases until it reaches a small secondary maximum in the ultra-red. The

heliotropic effect of the different rays is the same whether the curvature be positive or negative.

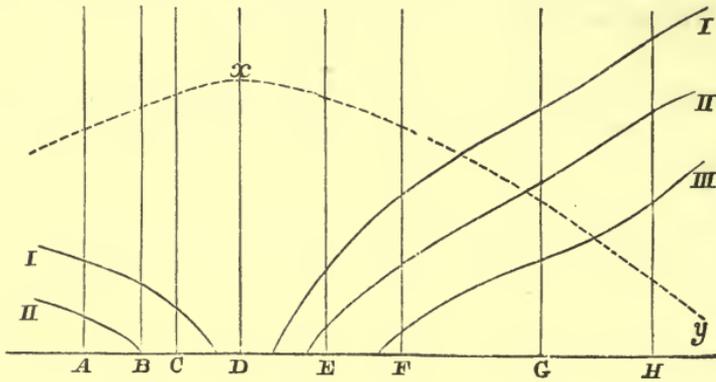


FIG. 50 (after Wiesner). Curve illustrating heliotropic effect of rays of different refrangibility. The letters A—H on the base line indicate the positions of the most conspicuous lines of the solar spectrum. The curves I, II, III represent the curvatures, under the influence of the different rays, of the Vetch, the Cress, and the Willow respectively. The curve $x y$ represents the relative effect of the different rays in retarding growth; it is greatest at y and least at x .

The effect of the dark heat-rays in affecting the direction of growth has been made the subject of special investigation by Wortmann. He has found, in agreement with the statements made above, that they are capable of exerting a very considerable influence in producing curvature. The phenomena thus produced may be conveniently designated by the term *Thermotropism*, suggested by van Tieghem. It appears, from Wortmann's experiments, as might be expected, that the reaction of organs to the action of the dark rays exhibits the same varieties as those with which we have become acquainted with in the case of the luminous rays; some curve away from the source of radiant heat, others towards it. For instance, when sporangiferous hyphæ of *Phycomyces* and shoots of Cress-seedlings were exposed to radiant heat, by placing them, either in the normal position or rotating on a clinostat, in an appropriate position with regard to a hot smoked tin-plate, they in all cases curved away from the source of heat, that is they shewed themselves to be negatively

thermotropic. Maize-seedlings, on the contrary, curved towards the source of heat, and thus proved themselves to be positively thermotropic. Similar results have been obtained by Barthélemy. In his experiments with Hyacinths, he found the roots to be positively, and the leaves to be negatively, thermotropic.

It was mentioned in the previous lecture (p. 374), that the effect of the action of an external agent upon an irritable organ is not at once exhibited, but that there intervenes between the commencement of the action and the first manifestation of a response, a latent period: and also that the effect of the action persists for a time after the action has ceased. This is very evident in the action of light in producing heliotropic heterauxesis. Wiesner has shewn, namely, that an organ exposed for a time to unilateral illumination, during which it exhibits no indication of curvature, will, on being placed in darkness, undergo heliotropic curvature. For instance, the epicotyls of some seedlings of *Phaseolus multiflorus* were exposed for one hour to unilateral illumination; during that time they exhibited no trace of curvature. They were then placed in darkness, and at the end of two hours they had undergone a well-marked positively heliotropic curvature. The exposure had induced in them the heliotropism which was subsequently manifested by curvature. This Wiesner speaks of as *photomechanical induction*. From his further investigation of this subject, Wiesner came to the conclusion that when photomechanical induction has once taken place, any further exposure to light is entirely without effect upon either the rapidity or the extent of curvature. In some cases (Cress, Vetch) Wiesner ascertained the length of exposure necessary for photomechanical induction; in both these plants, which are very sensitive, it amounted to one-third of the latent period, the latent period being 25 minutes for the Cress and 35 for the Vetch. The latent period and the persistent effect can, in fact, only be determined, or even perceived at all, in plants which respond rapidly to the stimulus of light.

We will now direct our attention to the heliotropic organ,

and enquire into the causes and nature of the curvature. It must be premised that not all radial organs are heliotropic. In addition to the peduncles already mentioned, the twining internodes of climbing plants, and the stem of the Mistletoe, are examples of shoots which are only slightly if at all heliotropic. Among roots, it appears that earth-roots are in most cases not at all heliotropic, and this is also true, though exceptionally, of some aërial roots. The degree of heliotropic irritability is also very different; in some cases it is such that, under appropriate conditions, the heliotropic curvature is performed in spite of the opposing effect of other influences, such as gravity, etc., whereas in other cases a curvature can only be detected when the action of all other directive influences is as far as possible prevented. The differences in heliotropic irritability are clearly illustrated by the fact, to which allusion has been made more than once in this and in the previous lecture, that the heliotropic effect is exhibited by highly sensitive organs at an intensity of light which is greater than that requisite to arrest growth, whereas in less sensitive organs the heliotropic effect ceases to be manifest at an intensity of light which is less than that requisite to arrest growth. Another means of estimating heliotropic irritability is afforded by the measurement of the angle made by the axis of an organ with the direction of the incident rays when the organ has ceased to curve heliotropically, the intensity of the light and the other conditions being constant. The more heliotropically irritable the organ, the more nearly will its axis come to coincide with the direction of the incident rays.

We may with advantage pause here for a moment to consider the fact, implied by the statement just made, that heliotropic curvature of an organ may take place without growth in length. We are, it is true, considering the various manifestations of irritability by growing organs, and yet we here include one exhibited by organs which cannot, strictly speaking, be said to be growing. Under ordinary conditions, heliotropic curvature, as we shall soon see more fully, is accompanied by growth in length; it is a phenomenon of growth in length, and is dependent upon the fulfilment of all

the conditions which are essential to growth in length. Under the exceptional conditions of illumination in the case before us, growth in length is rendered impossible; but the organ is nevertheless essentially a growing organ, for it is endowed with all the properties which, as we learned in a previous lecture (p. 341), are characteristic of growing organs. Amongst these properties, that of irritability was found to be conspicuous, and it is manifested in this case by a curvature which is not accompanied by growth in length.

We may now conveniently enquire as to what part of the growing organ is the seat of the heliotropic curvature, or, in other words, to ascertain the distribution of the heliotropic curvature throughout the growing region. Müller-Thurgau found, in the case of certain positively heliotropic stems, that curvature was most evident in the most rapidly growing zone, and he further found that this was also the case in the negatively heliotropic aerial roots of *Monstera Lennea* and of *Chlorophytum*. Wiesner has carefully investigated this point and concludes from his observations that, in stems which are only moderately sensitive to the heliotropic action of light, the greatest curvature takes place in the most rapidly growing zone, whereas in stems which are very sensitive the greatest curvature does not take place in the most rapidly growing zone. In the latter case the seat of greatest curvature is sometimes above and sometimes below the zone of most rapid growth; when the organ is young the former is the case, when it is older, the latter. The form of the curved organ will, of course, vary under these different circumstances.

It will be observed that in all cases heliotropic curvature is limited to the growing region, or, to put it more generally, to the region which is capable of growing. This is illustrated in an interesting manner by the behaviour of shoots, such as those of Caryophyllaceæ, Grasses, etc., in which the nodes are well-marked and the leaves sheathing. In these shoots the tissue at the lower end of each internode, surrounded by the sheathing leaf-bases, remains capable of growth (see p. 333). If now light is allowed to fall upon one side of such a shoot, it curves heliotropically, the curvature taking

place at the lower ends of the internodes. The same effect is produced even after normal growth in length has ceased, for the heliotropic action of light induces a resumption of growth.

In connexion with these considerations there naturally arises the question as to the seat of heliotropic irritability in growing organs. It would appear that, in most cases, the whole growing region is irritable, whereas in some cases the irritability is localised. Darwin concludes from his experiments with *Phalaris canariensis*, that the illumination of the upper part of the cotyledons of seedlings of this plant materially affects the capacity for curvature, and the extent of it, in the lower part; yet some observations seemed to render it probable that the simultaneous stimulation of the lower part by light greatly favours, or is almost necessary for, its well-marked curvature. Experiments made upon cotyledons of *Avena sativa* (Oat), on hypocotyls of *Brassica oleracea* (common Cabbage) and of *Beta vulgaris*, and on roots of seedlings of *Sinapis alba*, led him to much the same conclusions.

The experiments were performed by covering the tips of the organs with opaque screens, or by painting them black. In the majority of cases the organs thus treated remained upright when exposed to lateral light, whereas similar organs which had not been so treated became strongly curved.

With regard to the mode in which heliotropic curvature is effected, it may be stated generally that it is due to a change in the relative length of the two sides of the organ. When the organ is growing rapidly, both sides elongate, but the side which will be convex does so more rapidly than the side which will be concave; when the organ is growing slowly, the concave side elongates but little; when curvature takes place in an organ which is not growing, the concave side shortens.

In illustration of the relation between the elongation of the two sides, the following table of measurements made by Müller-Thurgau may be given. The numbers give, in millimetres, the elongation of the two sides of a portion, 20 millimetres long, of a growing shoot of *Valeriana officinalis*. In the column *A* are the successive increments in length of

the side most exposed to light (the concave side); in *B*, those of the shaded side. The time of growth was in every case a period of 5 hours.

<i>A</i>	<i>B</i>
0·5	0·7
0·7	1·1
1·0	1·7
1·0	1·9
0·9	1·6
0·6	1·1
0·4	0·7
0·1	0·3

We will now endeavour to arrive at some explanation of the phenomena of heliotropism. The fact which has to be explained is the change in the relative length of the two sides of the organ. Various explanations have been offered, but it would not be any advantage to discuss them all. We will confine our attention to that of de Candolle, for this one is assumed, implicitly at any rate, in much of the current botanical literature. De Candolle was of opinion that the curvature of a positively heliotropic organ is due to a difference in the intensity of the light to which the two opposite sides of the organ are exposed, the result being the more rapid elongation of the side which is exposed to the less intense light: in fact, he regards heliotropic curvature as a phenomenon of etiolation, the shaded side of the organ becoming to a certain extent etiolated. The reasoning upon which this theory is based is this. It is known that light retards growth in length; hence when the two sides of a growing organ are exposed to light of unequal intensity, the growth of that side will be the more retarded which receives light of the greater intensity. The assumption is that it is the shaded side of the organ which is active in producing the curvature.

The inadequacy of this explanation is at once apparent when negative heliotropism is considered. Here we have precisely the opposite effect produced under the same external conditions. It was thought that negatively heliotropic organs

might be so constituted that their growth should be promoted, instead of being retarded, by light. Were this the case de Candolle's explanation of positive heliotropism would also apply to negative heliotropism, and there would then be some ground for accepting it. But the researches of Müller-Thurgau, of F. Darwin, and of Wiesner, shew that also negatively heliotropic organs grow more rapidly in darkness than in light.

The endeavour which is usually made to explain heliotropic curvature by referring it to the direct action of light upon the elongation of the two opposite sides of the curving organ, is clearly unsatisfactory, and must be abandoned. If we sum up all the facts with which we have now become acquainted on the subject of heliotropism, we find that our knowledge amounts to this, namely, that the curvature is dependent upon the direction of the incident rays, and that the organ tends to place its long axis parallel to the direction of the incident rays, directing its apex sometimes towards and sometimes away from the source of light. Light affects the organ as a whole, and not merely the sides exposed to or turned away from it. The curvature, too, is effected by the organ as a whole, and is not merely the result of the direct influence of light upon the side most exposed to it. The difference in length of the convex and concave sides is the result, and not the cause; the organ, as a whole, is induced to take up a certain position with reference to the direction of the incident rays; to do this it must curve, and curvature can only be effected by heterauxesis, one side, the convex, becoming longer than the other, the concave.

It remains to explain the mechanism by which an organ performs its heliotropic curvature. Without entering at present into a full discussion of the subject, which we reserve for a subsequent lecture, it is clear that the heterauxesis is due to the greater turgescence of the cells of the convex side as compared with that of the cells of the concave side. The cells in question must necessarily be parenchymatous, and it appears that they belong to the cortical tissue, a point to which we shall revert when we are studying Geotropism.

Now that we have concluded our consideration of the directive influence of light upon growing radial organs, we turn to the study of the phenomena presented by bilateral organs. It will be convenient to consider separately the phenomena presented by isobilateral organs, and those presented by dorsiventral bilateral organs.

With regard to the former, of which the flattened leaves of some species of *Iris* and *Xyris* may be taken as examples, it will suffice to say that they are positively heliotropic.

The characteristic position of dorsiventral organs is such that, under normal conditions, their long axes are inclined at a greater or a smaller angle to the vertical. This position is, like that of all plant-organs, a resultant one, the resultant effect of the action of inherent tendencies and of external influences, and the problem now before us is to ascertain the extent to which light takes part in inducing this position.

It has been shewn in many cases that light is an important factor. Rauwenhoff, in particular, has called attention to the fact that whereas in a large number of plants the lateral branches are directed obliquely under normal conditions, in etiolated specimens they are more or less nearly vertical. Frank, again, has observed that the shoots of *Lysimachia Nummularia*, *Polygonum aviculare*, *Panicum Crus-Galli* and many other Grasses, *Atriplex latifolia*, *Chenopodium polyspermum*, *Matricaria Chamomilla*, and others, run horizontally along the surface of the soil when the plants are growing in sunny localities, whereas they grow erect when the plants are shaded or are kept in darkness. He has observed the same thing in the branches of thalloid Liverworts, such as *Marchantia*, which under these circumstances are narrow and channelled on the upper surface. Vöchting has made similar observations on the peduncles of *Erodium cicutarium* and of *Taraxacum officinale*, and Wiesner on the runners of *Fragaria vesca* and of *Glechoma hederacea*. This peculiar relation to the intensity of light is strikingly illustrated in *Vaucheria*. Stahl has found that in weak light the shoots of this plant are positively heliotropic, that is, that their apices are directed towards the source

of light, whereas in intense light their long axes are at right angles to the direction of the incident rays.

Finally, dorsiventral leaves are usually more or less nearly horizontal when growing exposed to light, whereas, when etiolated, they frequently tend to place themselves rather in a vertical than in a horizontal plane. This is especially marked in the case of radical leaves (Frank).

Some more definite information is afforded by the observations which have been made on the behaviour of dorsiventral organs when their dorsal (morphologically upper) and ventral (morphologically lower) surfaces are respectively exposed to light. With regard to dorsiventral shoots, de Vries found, in the case of runners of *Polygonum aviculare*, *Lysimachia Nummularia*, and others, that if such a shoot be placed vertically and light be allowed to fall upon its dorsal surface, the shoot curves away from the source of light. When on the contrary, the ventral surface is exposed to light, the shoot curves towards the source of light. He obtained similar results when he exposed the mid-ribs of leaves, freed from the mesophyll, under similar conditions. When the dorsal surface was exposed to light, the curvature, if any, was always such that the dorsal surface became convex to the source of light; when the ventral surface was exposed, there was in all cases a well-marked curvature such that the ventral surface became concave to the source of light. Similarly, both Frank and Sachs have observed that when the dorsal surface of a *Marchantia*-thallus is exposed to light, the thallus becomes convex towards the source of light, whereas when the ventral surface is exposed, it becomes concave.

De Vries attributes the curvature away from the source of light to the possession of negative heliotropic properties by these organs, an opinion which is shared by Frank as far as *Lysimachia Nummularia* is concerned. But the concave curvature when the ventral surface of the organs was exposed to the light remains unaccounted for. In order that this explanation of the phenomena may be consistent throughout it is necessary to assume that the two surfaces of the organ, in these cases, are endowed with different heliotropic proper-

ties; that the dorsal is negatively and the ventral positively heliotropic. This explanation was mentioned by Sachs, in his paper on orthotropic and plagiotropic plant-organs, but it appeared to him that the assumption was an impossible one. Wiesner, however, is more bold, and accepts and attempts to justify it. We shall not follow him in this, but will endeavour to shew that the phenomena can be satisfactorily accounted for without making this very doubtful assumption.

Such an explanation is not far to seek, and it is to Sachs that the first suggestion of it is due. In the paper mentioned above, when speaking of the influence of light upon the *Marchantia*-thallus, Sachs says: "So far as I can at present apprehend the facts, this negative heliotropism of the *Marchantia*-shoots, and that of many other shoots which behave in the same way, is the same phenomenon as the epinasty of foliage-leaves described by de Vries." Taking this statement in connection with Detmer's results (see *supra*, p. 383) that light promotes the epinasty of foliage-leaves, we arrive at once at an explanation of the phenomena in question. The dorsiventral organs which we have been considering are photo-epinastic; that is, that when exposed to intense light their dorsal surfaces grow more rapidly than their lower.

We will here digress for a moment and revert to the apparent reversal of the heliotropic properties of orthotropic organs to which allusion was made a short time ago (p. 429). It was then pointed out that the effect of intense unilateral illumination was to induce dorsiventrality in previously radial shoots (*Ivy*, *Tropæolum*). This being the case, we see that their apparent negative heliotropism is nothing more than the photo-epinasty which we have found to obtain in the dorsiventral organs now under consideration. It is probable that this explanation applies also to the apparent negative heliotropism of the tendrils of *Vitis* and *Ampelopsis* to which allusion was made above (p. 429).

We have come to the conclusion, then, that dorsiventral organs are not negatively heliotropic, and we may now go on to enquire if they are positively heliotropic; that is, if under

any circumstances, the dorsal surface becomes concave when light falls directly upon it. Sachs mentions that the leaves of a plant of *Tropæolum majus* grown in a window were positively heliotropic. De Vries found that neither dorsiventral leaves nor shoots ever exhibited positively heliotropic curvature when the light fell on the dorsal surface, but he is nevertheless inclined to attribute positive heliotropism to the former. Wiesner states that he has frequently detected positive heliotropism in leaves. But these statements as to the positive heliotropism of leaves are open to criticism. In the first place the apparent positive heliotropism may reside, not in the dorsiventral lamina, but in the petiole which may be radially-organised. And secondly, it may be that when it is exhibited, as in the cases adduced by Wiesner, in feeble light, it is simply the expression of a partial etiolation, a condition which, as we know, prevents the expansion of the blade so that its upper surface remains concave. A form of positive heliotropism, but not the one which we are considering here, has indeed been observed in dorsiventral organs. Sachs has pointed out, for instance, that when a leaf of *Fritillaria imperialis* was so placed that the incident rays fell upon one lateral margin, this margin became concave so that the blade assumed a sickle-shape: de Vries has found the same to occur in a number of cases (*Rhus typhina*, *Ailanthus glandulosa*, *Spiræa sorbifolia*, etc.), and Wiesner has made similar observations on the leaves of *Campanula persicifolia* and on the cotyledons of the Silver Fir (*Abies pectinata*).

We come then to the conclusion that when either the dorsal or the ventral surface of a dorsiventral organ is exposed to light it exhibits neither negative nor positive heliotropism, but only photo-epinasty (or photo-hyponasty). We must be careful not to regard photo-epinasty as belonging to the category of heliotropic phenomena, that is, as being a manifestation of the directive influence of light, for the same effect is produced whether the dorsal or the ventral surface of the organ is the one upon which the incident rays directly fall. And if any further proof of this is wanted, it is afforded by Detmer's observation that the lamina of a leaf (he experimented with the cotyledons of

Cucurbita) becomes expanded by means of epinasty when the light falls on its lateral margin. A similar result was obtained by de Vries, but he failed, apparently, to see the significance of it.

But light does, as a matter of fact, exert a directive influence on dorsiventral organs. It is a matter of common observation that these organs take up a definite position with regard to the direction of the incident rays, such that the dorsal (morphologically upper) surface of the organ is placed perpendicularly to it. This has been observed by Frank and others in the case of branches, and by Frank and Sachs in the case of the *Marchantia*-thallus, but, inasmuch as the actual influence of light has not been estimated by eliminating the effect of other directive forces—that of gravity, especially, by rotation on the clinostat—the further consideration of them would not lead to any conclusion. The phenomena are much more strikingly exhibited by dorsiventral leaves, and moreover they have, in this case, been to a certain extent investigated by the experimental method just mentioned. Leaves of this kind take up any definite fixed light-position. In the vast majority of cases, this position, when the plant is fully exposed on all sides to light, is such that the dorsal surface of the leaf is directed towards the sky, and the ventral surface towards the earth. But to this general rule there are exceptions. Frank mentions the remarkable fact that in *Allium ursinum* the fixed light-position of the leaf is such that the ventral (morphologically lower) surface is the one which is presented to the incident rays. In a great many cases the fixed light-position is such that the surface of the leaf is placed vertically so that one lateral margin is directed towards the sky and the other towards the earth.

Stahl mentions the following examples of the last-mentioned case :

Santalaceæ ; species of *Thesium*.

Compositæ ; *Picris hieracioides*, *Cirsium arvense*, *lanceolatum*, *eriphorum*, *Silphium laciniatum*, *Lactuca scariola*.

Labiatae ; *Marrubium vulgare*.

Cruciferae ;

Umbelliferae ; *Peucedanum cervaria*.

Also in the Hop, Vine, Lime, various Grasses (*e.g. Brachypodium pinnatum*), *Aspidium Filix-mas*, *Geranium sanguineum*, *Picea excelsa*, *Abies pectinata*.

Also in the following water-plants (aërial leaves), *Hydrocotyle bonariensis*, *Alisma Plantago*, *Sagittaria*, *Nymphæa*, *Nelumbium*.

It is in the assumption of the normal fixed light-position by leaves of this last description that the influence of light can be most readily traced, and we will therefore devote a short time to a more detailed consideration of the process. Of the plants mentioned, *Silphium laciniatum* and *Lactuca scariola* are those which respond the directive influence of light in the most marked manner. The leaves of these plants, namely, are not only vertical when fully exposed to light, but they place themselves in a vertical plane which more or less nearly coincides with the meridian of the locality, whence they have been spoken of as "Compass-plants."

Stahl describes as follows the mode in which this peculiar arrangement is attained. The leaves on the north and south sides of the stem, respectively, undergo a torsion of 90° , so that their morphologically superior (dorsal) surfaces are directed towards either the west or the east. The leaves borne on the east and west sides of the stem either simply curve upwards, so that they stand erect, or they undergo torsion such that their surfaces become vertical and curve at the same time so that their apices point towards either the north or the south: in any case, the upper surfaces of the leaves borne on the east side of the stem come to face the west, and those of the leaves borne on the west side to face the east.

The conditions which determine the assumption of the vertical position by dorsiventral leaves have been investigated by Stahl with reference to *Lactuca scariola*, and there can be little doubt that the facts which he has ascertained in the case of this plant are true also of the other plants which exhibit the same phenomenon. He finds, in the first place, that the vertical position of the surfaces is assumed only when the plant is growing fully exposed in a sunny spot; when it grows in the shade the leaves are horizontal. Secondly, if the plant is grown under such circumstances that it receives

the sun's rays only when the sun is high in the heavens, the leaves present their superior surfaces to the incident rays. Thirdly, if the plants are so situated that they receive only the oblique rays of either the morning- or the evening-sun, the leaves place their superior surfaces at right angles to the incident rays. The conclusion to be drawn from these observations is this, that it is the oblique rays of the sun which determine the vertical and meridian position of the leaves. The presentation of the upper surface of any leaf to the east or to the west is determined by the illumination to which its upper surface is exposed. Thus, the leaves borne on the east side of the stem have the sun's rays falling upon their upper surfaces principally during the afternoon, whereas those borne on the west side receive the rays of the sun upon their upper surfaces chiefly in the morning: hence the former direct their upper surfaces towards the west, and the latter towards the east.

The fixed light-position of most leaves is determined, as Wiesner has shewn, not by the direction of incidence of direct sunlight, but by the direction of incidence of the brightest diffuse daylight. He observed, for instance, that when plants were so situated that they received direct sunlight only for a time in the morning and diffuse daylight during the rest of the day, their fixed light-position was such that their upper surfaces were directed perpendicularly to the direction of incidence of the daylight and not to that of the rays of the morning-sun. In this respect the leaves of the Compass-plants behave differently. When exposed only to diffuse light, falling from above, they are horizontal, and it is not until they are exposed to direct sunlight that they take up the characteristic vertical meridian position. This difference in behaviour can only be accounted for by attributing to the two kinds of leaves in question differences in irritability. Diffuse daylight is insufficient to induce the assumption of their peculiar fixed light-position by the leaves of the Compass-plants, direct sunlight is necessary; in other plants, on the contrary, the fixed light-position is determined by the direction of incidence of the brightest diffuse daylight.

The cases which we have so far considered as to the directive influence of light upon leaves are such as present themselves in nature; we will now consider the facts which have been elicited by experiment. Bonnet long ago noted that most leaves are so placed that their morphologically superior surfaces are directed towards the sky, and their morphologically inferior surfaces towards the earth, and found that whenever he altered this, the normal position, the leaves resumed it by curvatures or torsions. More striking demonstration of the tendency of leaves to place themselves so that their dorsal surfaces are directed perpendicularly to the direction of incidence of the stimulating light is afforded by the observations of F. Darwin. In speaking of the positions taken up by plagiotropic branches under the directive influence of light, it was mentioned that it is at present impossible to estimate the extent and nature of their response in the absence of observations made in such a way as to eliminate as far as possible any effects which might be induced by other directive influences. This has, however, been done to a certain extent in the case of leaves by F. Darwin by observing the positions taken up by leaves under the influence of light whilst rotating on the clinostat. His observations are, unfortunately, not quite complete, inasmuch as they refer only to the curvatures, and not to the torsions, performed under these circumstances. Without entering into a detailed description of his experiments, it may be stated that the leaves were exposed in three positions to the incident rays of light: (1) so that the rays fell on the dorsal (morphologically upper) surface (zenith-position); (2) so that the rays fell upon the ventral (morphologically lower) surface (nadir-position); (3) so that the rays fell on the margin, the apices or bases being directed towards the light (lateral position). The plants to which reference will now be made were *Ranunculus Ficaria*, *Cucurbita orifera* (Vegetable Marrow), *Plantago media*. In so far as the various forms of experimentation were applied to these plants, it was found that under all circumstances their leaves so curved as to place their dorsal surfaces more or less nearly at right angles to the direction of the incident rays. With the plant in the zenith-position the leaves curved either

towards or away from the source of light, as the case might be, in order to reach the perpendicular plane: with the plant (*Ranunculus Ficaria*) in the nadir-position, the leaves curved concavely towards the source of light, until ultimately the morphologically upper surface came to be directed towards it: with the plant in the lateral position (*Ranunculus Ficaria*) the leaf which was so placed that its apex was at first directed towards the incident rays bent downwards until the dorsal surface of its blade was perpendicular to them, and the leaf which was so placed that its base was directed towards the incident rays bent upwards until the dorsal surface of its blade received the incident rays but failed to place itself quite perpendicularly to them though it moved through more than 100° in its attempt to do so.

The foregoing facts will suffice to prove that when dorsiventral organs respond at all to the directive influence of light, they exhibit a well-marked tendency so to place themselves that the dorsal surface shall receive rays of light falling perpendicularly upon it. In endeavouring to account for this behaviour, Frank finds himself compelled to assume that it is due to a kind of heliotropic irritability peculiar to dorsiventral organs, and different from that of orthotropic organs. Radial and isobilateral organs, as we have seen, respond to the directive influence of light in this way, that they tend to place their long axes parallel to the direction of the incident rays, the apex being directed either towards or away from the source of light. Dorsiventral organs respond in this way, that they tend to place their long axes perpendicular to the direction of the incident rays. This peculiar kind of irritability Frank terms *Transverse Heliotropism*. Darwin has proposed the less cumbersome term *Diaheliotropism*, and we will use it in preference in further discussing the subject. This suggestion is, however, by no means universally accepted. De Vries, in his searching criticism, rejects the assumption of a diaheliotropic irritability, and refers the movements performed by a leaf removed from its fixed light-position in its attempt to regain that position as being due, when the movement is one of simple curvature, to negative geotropism, and to negative or positive heliotropism,

and to epinasty, and when the movement is one of torsion, to these factors more or less interfered with in their operation by the mechanical moment of the heavy lamina. Wiesner also attributes these movements to negative geotropism, positive heliotropism, epinasty, weight of lamina, etc.

It would seem to be almost impossible to account for all these phenomena, especially those exhibited by the Compass-plants, in the way proposed by de Vries and by Wiesner, even admitting that all the agents above enumerated are in operation. We have, however, seen reason to come to the conclusion that dorsiventral organs are not endowed with either positive or negative heliotropism, and we have learned from F. Darwin's experiments that the movements in question are performed by leaves when rotating on the clinostat, that is, when the effect of gravity is eliminated. These movements, then, cannot be due in any degree to negative geotropism. Under these circumstances the only course left to us is to accept Frank's suggestion that these organs possess diaheliotropic irritability.

In concluding this subject we may advantageously sum up in a concise form the conclusions to which a full consideration of all the available facts has led us. We have found that dorsiventral organs are photo-epinastic and diaheliotropic. It is clear that when the photo-epinasty of an organ is well-marked, its diaheliotropism will be less so. Thus Frank observed that in *Lysimachia Nummularia* when growing on sloping ground, the shoots were directed downwards and were closely appressed to the sloping surface, so that their long axes made an angle of considerably more than 90° with the direction of the incident rays of light. In *Polygonum aviculare* he observed, on the contrary, that, under the same circumstances, the shoots proceeding from the lower side of the plant raised themselves from the soil so that their long axes made an angle of 90° with the direction of the incident rays. The explanation of these facts seems to be that in the former case the photo-epinasty overcomes the diaheliotropism, whereas in the latter the diaheliotropism overcomes the photo-epinasty. The same thing was observed by F. Darwin in the course of his experiments with leaves. As already mentioned, the leaves of

Ranunculus Ficaria, when in the zenith position, curved so as to place the upper surface of the blade at right angles to the direction of the incident rays : in the Cherry and in the Bean, under similar circumstances, the leaves curved epinastically backwards towards the stem, so that the angle which their upper surfaces made with the direction of the incident rays was much greater than a right angle. It seems probable that strongly marked photo-epinasty is peculiar to a certain period in the development of the leaf, the diaheliotropism asserting itself later, so that ultimately the fixed light-position, in which the dorsal surface is perpendicular to the direction of the incident rays, is assumed. This may also apply to dorsiventral shoots, but a fuller investigation of the whole subject is necessary before we can arrive at such definite conclusions as will enable us to give a completely satisfactory explanation of these complicated phenomena.

With regard to the mechanism by which the heliotropic curvature of dorsiventral organs is effected, it will suffice for the present to say that it is essentially the same as in the case of orthotropic organs.

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LECTURE XVIII.

IRRITABILITY OF GROWING ORGANS (*Continued*).

Gravity. In a previous lecture (p. 409) some account was given of the action of gravity in modifying the rate of growth. We now turn to the consideration of the influence of gravity in determining the normal direction of growth of growing organs and of the phenomena which present themselves when a growing organ is placed in a position other than that which it normally occupies with respect to the line of action of gravity, phenomena which are collectively designated by the term *Geotropism*, a term which we owe to Frank.

It must be premised that the effects produced by gravity are of two kinds, namely, those which are due to the mere weight of the parts, and those which are due to the stimulating action of gravity. It is only the latter which are referred to in using the word *geotropism*. It is of great importance that these two sets of effects should be clearly distinguished from each other, especially when we remember that Hofmeister ascribed geotropic curvature in certain cases to the bending of the organ under its own weight. Frank, however, demonstrated that this view was entirely erroneous. It will be worth while, in view of its importance, to illustrate this point rather fully. Pinot, Mulder, and Payen found, for example, that the primary root of a seedling will curve downwards into mercury, that is, that it will curve downwards against a considerable resistance, and Johnson observed that such a curvature was performed against a weight of ten grains. It requires in many

cases great care to distinguish true geotropic curvatures from curvatures due to mere weight. It was mentioned in a previous lecture (p. 342) that the pendent position of flower-buds is frequently due to the pliability of the upper growing portion of the peduncle. But this is not always the case, and a definite opinion can only be formed in any particular instance as the result of experiment. The decisive experiment consists in causing the stalk bearing the pendent flower-bud to rotate horizontally on the clinostat. If the curvature is due to the weight of the bud, the bud will continue to hang downwards during rotation; but if the curvature is geotropic then the original curvature will be retained, so that the bud in the course of each rotation will lie sometimes above, sometimes below, and sometimes at the side of the straight portion of the stalk. By experiments of this kind Vöchting has ascertained, for instance, that the pendent position of the buds of *Galanthus nivalis* and of *Helleborus* is due to the weight of the bud being too great for the stalks to bear erect; the pendent position of the buds of various species of Poppy and of *Tussilago Farfara*, on the other hand, is due to geotropic curvature, a conclusion which has been confirmed by Fünfstück as regards the Poppy.

It will be convenient in dealing with the facts of geotropism to take separately the phenomena presented by organs of different physiological properties. We will begin with those presented by radial organs, and these we shall further subdivide into those which are peculiar to orthotropic radial organs, and those which are exhibited by plagiotropic radial organs. We shall then consider those presented by bilateral organs, taking first those exhibited by isobilateral organs, and then those peculiar to dorsiventral organs.

It is a familiar fact, with regard to orthotropic radial organs, that primary shoots grow vertically upwards, and that primary roots grow vertically downwards into the soil. Inasmuch as this takes place at the most widely distant parts of the earth's surface, the fact may be more precisely stated thus, that the shoots grow outwards, that is, away from the centre of the earth, and the roots inwards, that is towards the centre of the earth.

The direction of growth thus definitely assumed is not a merely accidental one. Dodart and Bonnet, who appear to have been the first to investigate it scientifically, found that when shoots were inverted, they curved until they came to occupy again their normal position with respect to the vertical. It is, then, a direction which is assumed not passively but actively. The cause of it is not to be found in the influence of light, for orthotropic organs maintain their vertical direction of growth as well in darkness as in light. Duhamel shewed that the direction of growth of these organs is not an effect of the influence of moisture as Dodart suggested, nor an effect of differences of temperature on two opposite sides of the organ as Bonnet was inclined to believe. The true active cause was determined by Knight. He imagined that if the action of gravity were the cause of the downward growth of the radicle and of the upward growth of the plumule, its operation would be suspended by a constant change in the position of the germinating seed with regard to the vertical, and that it might be counteracted by the agency of centrifugal force. The first part of his idea is verified by the results of recent research. When a germinating seed is made to rotate slowly on a clinostat, so that its relation to the vertical is constantly being altered, its plumule does not grow upwards, nor its radicle downwards, but these organs tend to grow straight in a horizontal plane in virtue of their rectipetality (see p. 418). The second part of his idea was verified by himself. He found that when a germinating seed was attached to a wheel revolving round a horizontal axis with such rapidity that the centrifugal force was considerable, the radicle grew outwards and the plumule inwards, that these organs behave, in fact, to the influence of centrifugal force in precisely the same way as they do to the influence of gravity. He contrived, further, to combine the effects of centrifugal force and of gravity by causing the wheel to revolve round a vertical axis. Under these circumstances the radicle grew obliquely outwards and downwards, and the plumule obliquely inwards and upwards. He states his conclusions as follows: "I conceive myself to have proved that the radicles of

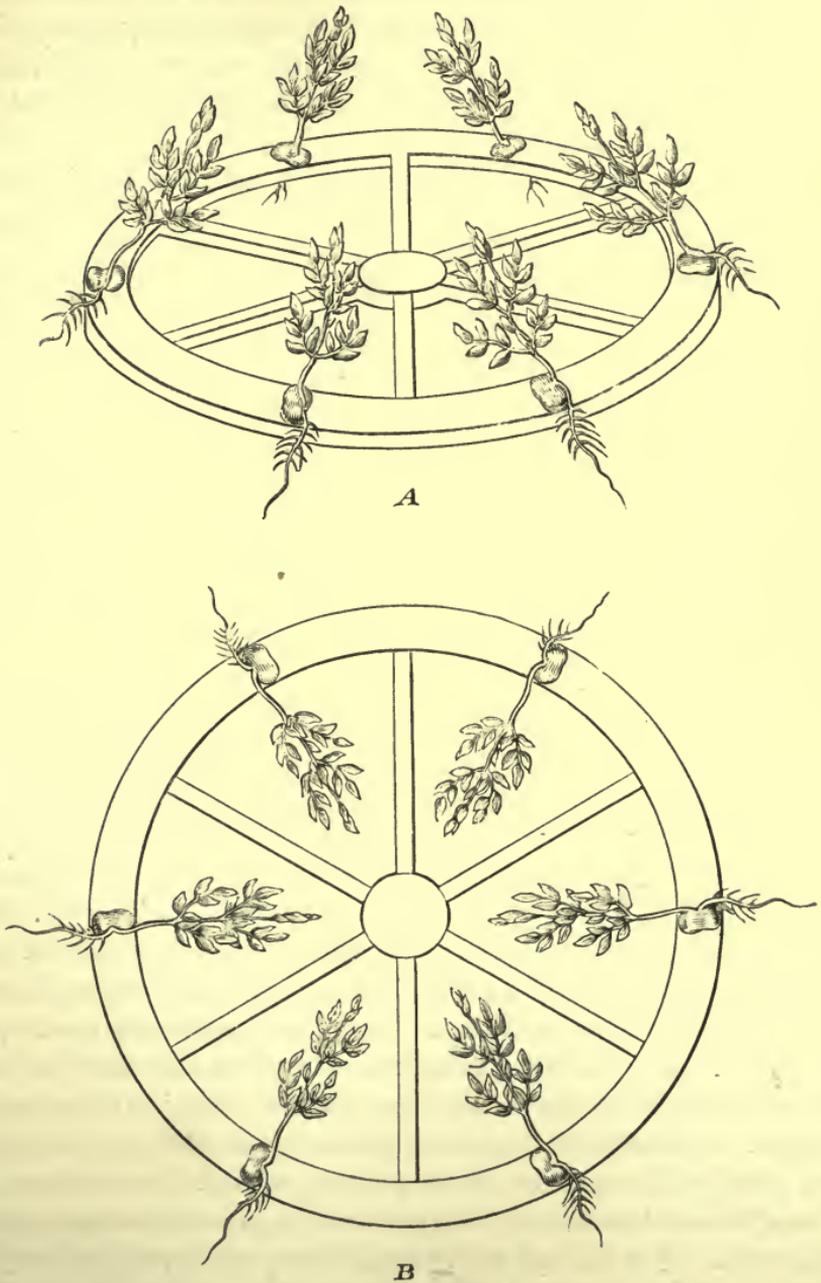


FIG. 51. (after Knight). Diagrams illustrating Knight's experiments. *A* wheel rotating horizontally; the plants grow under the combined influence of gravity and centrifugal force. *B* wheel rotating vertically; the direction of growth is determined by the centrifugal force alone.

germinating seeds are made to descend, and their plumules to ascend, by some external cause, and not by any power inherent in vegetable life ; and I see little reason to doubt that gravitation is the principal, if not the only agent employed in this case by Nature."

The downward direction of growth of orthotropic roots and the upward direction of growth of orthotropic stems are due, then, to the action of gravity ; the direction of growth is, in fact, the response of the growing organ to the stimulating effect of gravity, just as the assumption of a definite direction of growth under the influence of light is the response of the growing organs to its stimulating action. Further, just as we found organs which curve towards or away from the source of light, organs which are respectively said to be positively or negatively heliotropic, so we find organs which grow towards or away from the centre of the earth, and they are respectively said to be *positively* or *negatively geotropic*, or, to use Darwin's terminology, *geotropic* or *apogeotropic*.

We have already cited primary stems as examples of negatively geotropic shoots, and primary roots as examples of positively geotropic roots ; but to these many more may be added. The stipes of Mushrooms, the sporangiferous hyphæ of Moulds, the stems of Characeæ, the stalks of the receptacles of Liverworts, the seta of the Muscineæ, the peduncles of many flowers, are examples of negatively geotropic shoots : the hyphæ of Moulds which penetrate into the substratum, the root-like filaments of Vaucheria, Caulerpa, and other Algae, the rhizoids of Muscineæ, are examples of positively geotropic roots. The long narrow radial leaves of some Monocotyledons, such as the Onion, are further examples of negatively geotropic organs. Orthotropic shoots are generally negatively geotropic, but not in all cases, for Sachs points out that the rhizomes of *Yucca filamentosa* and of *Cordyline rubra* grow downwards like tap-roots. Nor are all orthotropic roots positively geotropic, for, as Schimper has found, the climbing roots of various Epiphytes are negatively geotropic.

Cases of the absence of geotropic irritability are afforded by the hypocotyl of the Mistletoe (*Viscum*) which, as Duhamel

first pointed out, maintains any direction of growth which it may originally have assumed, and by the aërial roots of various Epiphytes.

A reversal of the geotropic properties of an organ may take place in the course of its development. Vöchting has found, for instance, that the peduncle of the Poppy is positively geotropic whilst the flower is in the bud, but negatively geotropic during flowering and fruiting: similarly, the peduncle of *Tussilago Farfara* is negatively geotropic during the period of flowering; during the development of the fruit the upper part of the peduncle becomes positively geotropic; and finally, when the fruit is mature, the whole peduncle is negatively geotropic.

The foregoing are some examples of the phenomena of geotropism as exhibited by orthotropic organs. In passing now to study the action of gravity in producing them, we shall subdivide the subject as we did in treating of the heliotropic action of light (p. 431); we shall consider first the effect of variations in the angle of deviation—that is, of the angle made by the long axis of an organ when in an abnormal position, with its long axis when in the normal position of equilibrium with regard to gravity—and secondly the effect of variations in the intensity of the force. It is true that the force of gravity is constant; but since, as we have seen, centrifugal force induces curvature just as gravity does, we can, by substituting this variable force for the constant one, obtain results which are probably the same as those which would be obtained could we vary the force of gravity.

We have learned that the heliotropic effect of light is determined by the angle of incidence of the rays, and we shall now find that the geotropic effect of gravity exhibits a similar relation to the angle of deviation. From his experiments on stems and roots Sachs comes to the conclusion that the geotropic influence of gravity is greatest when the long axis of an orthotropic organ is at right angles to the vertical, and that it is zero when the long axis of the organ coincides with the vertical, whether the apex of the organ point upwards or downwards, or whether the organ be positively or negatively geo-

tropic. In other words, if we resolve the force of gravity into two forces, the one acting at right angles to the long axis of the organ, and the other along it, it is only the former that is active in producing a geotropic effect. It is clear that such a resolution cannot be made when the organ is either horizontal or vertical; in the former position the force of gravity acts wholly at right angles to the long axis of the organ, in the latter, along it; hence the geotropic effect is greatest in the former position, and it is zero in the latter, and the greater the angle of deviation of the long axis of the organ from the vertical towards the horizontal, the more marked will be the geotropic effect. Sachs bases this view upon the fact that geotropic curvature is more rapidly produced when an organ is horizontal than when it is in any other position.

The correctness of this view is rendered somewhat doubtful by the observations of Elfving. He found, namely, that when primary roots, growing in moist air, were placed so that their apices were directed upwards, that is, at an angle of 180° to their normal direction, they curved downwards indeed, but never so much as to assume their normal vertically downward direction; that is, the apex in no case travelled through 180° . In some cases the angle described was only a small one; in others it was 90° , so that the roots remained horizontal; in others it was as large as 130° . The angle finally assumed in each case is clearly the angle at which gravity ceased to exert a geotropic influence, the differences in the size of the angle being the expression of individual peculiarities of irritability. In no case did a root grow vertically upwards, but all curved downwards more or less. The conclusion which Elfving draws from these observations is that the geotropic effect of gravity is greatest when the angle of deviation is 180° .

It may be objected that the geotropic irritability of the roots may have been interfered with in these experiments by the abnormal conditions under which the roots were placed. Sachs has, in fact, proved that this is the case. Elfving himself states that when roots growing in earth were placed in the inverted position, they curved downwards so as nearly or

completely to bring about the normal vertically downward direction of the apex. Doubtless the geotropic irritability of the roots growing in earth was greater than that of those growing in moist air. But the latter retained considerable geotropic irritability nevertheless. This is shewn by the fact that when, after having curved as a consequence of their reversed position, they were so moved that the apices again pointed vertically upwards, they again curved downwards to a greater or a less extent. It is shewn further, and perhaps more strikingly by another experiment. Seedlings were placed with their radicles pointing radially inwards on a wheel rotating with such a velocity that the acceleration of the centrifugal force was about $50g$ (g being the acceleration due to gravity), and care was taken to ensure a moist atmosphere. Under these circumstances they naturally tended to curve outwards, as in Knight's experiment already described (p. 456), for they were in an inverted position as regards the direction of the centrifugal force; and they did so to a much greater extent than in the previous experiments under the action of gravity. In no case was the ultimate angle of deviation from the normal position (radially outwards) greater than 45° . These roots, then, possessed geotropic irritability, though in a less degree than roots grown under normal conditions. This, far from being an objection, is a support to Elfving's view. These feebly geotropic roots afforded a better means of estimating the geotropic effect of gravity at different angles than highly irritable roots.

A further objection to Elfving's conclusion might be based on Sachs' observation that geotropic curvature is more rapidly produced when an organ is placed horizontally than when it is in any other position. Elfving has anticipated this objection, and urges that this may be due to the fact, mentioned in a previous lecture (p. 409), that when an organ is placed in the inverted position its growth is retarded by the action of gravity, and consequently its curvature is slowly produced.

Elfving's experiments are obviously incomplete; they require to be extended to shoots and to other organs. But they seem to point to this general conclusion, that the geotropic

action of gravity upon an orthotropic organ is greatest when that organ is removed as far as possible from its normal relation to the vertical.

The discussion of these observations of Elfving's naturally leads us on to the phenomena presented by radial but plagiotropic organs. We begin with lateral roots. The lateral roots which spring from a tap-root, do not grow vertically downwards like the latter, but nearly horizontally outwards with a downward inclination. It might be supposed from this that lateral roots are not at all geotropic, and that their normal direction of growth is determined simply by their relation to the axis which bears them, by their "proper angle" (see p. 421). They are, however, positively geotropic, as Sachs has shewn. He found that when a pot in which a seedling was growing was turned upside down, and was kept for some time in that position, the lateral roots curved downwards so as to assume their normal position with regard to the vertical. He found, further, that when seedlings of *Vicia Faba* were made to rotate with such a velocity that the acceleration due to the centrifugal force was $4g$ (g representing the acceleration due to gravity), the lateral roots of the first order curved outwards so that their long axes approached the direction of action of the centrifugal force. He ascertained also that the greater the centrifugal force, the more strongly marked was the curvature, though the curvature did not increase in direct proportion to the acceleration due to the centrifugal force, but in some smaller proportion.

These lateral roots are clearly organs endowed with low geotropic irritability. Their behaviour is of the same kind as that of the primary roots in Elfving's experiments. Their normal direction of growth is just that which is determined by their feeble positive geotropism. Their plagiotropism is simply the expression of their feeble geotropic irritability, just as the orthotropism of other radial organs is the expression of their high geotropic irritability.

We come now to certain cases of plagiotropism in radial organs which cannot be explained in this way. Elfving has observed, in the case of the horizontally creeping rhizomes of

Heleocharis palustris, *Sparganium ramosum*, and *Scirpus maritimus*, that their normal direction of growth is horizontal, and that in whatever position they may be placed, whether their apices are directed upwards, or downwards, or at any angle to the horizontal, they curve so as to assume the horizontal direction of growth. It is clear that the plagiotropism of these organs cannot be ascribed to a lack of geotropic irritability. This they undoubtedly possess, but apparently of a peculiar kind, of such a kind, namely, that equilibrium is only attained when their long axes are horizontal. This kind of geotropic irritability is termed *Transverse Geotropism* (Frank) or *Diageotropism* (Darwin).

Similar facts have been brought to light by Vöchting with regard to peduncles. He observed that the flower-buds of *Narcissus Pseudo-Narcissus* (Daffodil) and those of *Agapanthus umbellatus* are vertical until just before they open, when they assume a horizontal position. He ascertained by appropriate experiments that this change in position is due to a change in the geotropic irritability of the pedicels. At first they are clearly negatively geotropic, but their negative geotropism gives place to diageotropism. Their diageotropism is not, however, so well marked as that of the rhizomes mentioned above; it is materially affected by their relation to the vertical. We have here, in fact, another illustration of the relation of the stimulating effect of gravity to the angle of deviation. If a scape bearing a flower about to open be placed horizontally, no curvature will be produced, but the pedicel will remain horizontal, that is, the long axis of the flower will continue to form one straight line with that of the scape. If now, the scape be raised gradually until it becomes vertical, the pedicel will curve so that the horizontal direction of the long axis of the flower will be maintained, the curvature increasing as the angle with the horizontal increases. If, however, the inclination of the scape be such that it is directed obliquely downwards, no curvature of the pedicel will take place, but the long axis of the flower and that of the scape will continue to form one straight line. The irritability of the pedicels in these cases is such that they will only respond

geotropically when the angle made by their long axes with the vertical lies between 90° and 0° in the upper quadrant, the response being greatest when the angle is 0° .

The question as to the validity of the assumption of Diageotropism as a special form of geotropic irritability will be discussed in connexion with the geotropic phenomena presented by dorsiventral organs.

Just as in the case of the action of light upon growing organs, so also in that of the action of gravity, the response of the organ to the action of the stimulus, as indicated by commencing curvature, is not at once exhibited, but a longer or shorter "latent period" precedes it. Sachs observed, for instance, in the case of slender stems, that when they were laid horizontal, the upward curvature could first be detected at the end of $\frac{1}{2}$ —2 hours. Similarly Darwin observed that the stem of a young plant of *Cytisus fragrans* began to curve upwards after having been in a horizontal position for three quarters of an hour. Again, as in the case of the action of light, so also in that of gravity, the induced effect persists after the stimulus has ceased to act; this is, in fact, an induction of geotropism similar to the induction of heliotropism. Sachs observed that when shoots were kept in a horizontal position until they began to exhibit a distinct upward curvature, and were then either placed vertically or were turned through 180° round their own axes so that their position was reversed, the curvature continued to increase during the next 1—3 hours. In roots this persistent after-effect, this induced geotropism, is less marked: Sachs was in fact unable to detect it, but Frank and Ciesielaki state that they have done so.

Now that we know something as to the conditions of the action of gravity upon orthotropic radial organs, we may pass to the consideration of the manner in which these organs perform geotropic curvature. It is, like heliotropic curvature, a phenomenon of induced heterauxesis. It is effected in a rapidly growing organ by the greater elongation of the side of the organ which becomes convex as compared with that of the side which becomes concave; when, however, the organ is

growing slowly or not at all, it is probably due to the shortening of the side which becomes concave. It appears, namely, that just as we may have heliotropic curvature without growth in length (p. 436), so we may have geotropic curvature. Kirchner observed geotropic curvature in roots of Peas and Beans, at a temperature of 2—3.5° C., a temperature at which their growth in length must have been very slow if it took place at all. When the curvature is distinctly accompanied by growth in length, the rate of growth of the convex side is greater than the mean rate of growth of the whole organ, whereas that of the concave side is less. The relation between the rate of growth of the convex and concave surfaces of a geotropically curving organ, as well as the relation of the rate of growth of the organ as a whole to that of a similar organ growing in the normal direction is well illustrated by Sachs' observations on the roots of *Vicia Faba*, an example of which is given below.

One seedling was placed with its root vertical, and another similar seedling was placed with its root horizontal: each root was marked out into lengths of 2 m.m. each. At the end of 14 hours the four apical lengths of the horizontal root (*i.e.* a portion 8 m.m. long) had grown and become curved.

Increment of length of convex side	...	10.8 m.m.
" " concave "	...	6.1 "
Mean increment	8.4 "

The corresponding portion of the vertical root had grown in the same time to the extent of 10.5 m.m.

Comparing these results, and taking 10.5 as the normal increment of growth of the root, we find that

1. The increment of the convex side exceeds the normal by 0.3 m.m.
2. " " concave side falls short of " 4.4 "
3. Mean " " curving root " 2.1 "

Sachs has arrived at the same result by comparing the length of the cortical parenchymatous cells of the convex and concave sides of the curving region of roots with that of the cells of the straight portion: the numbers refer to divisions of the micrometer; the measurements here given refer to the root of *Aesculus Hippocastanum*.

Mean length of cells of straight portion of root	20·1
„ „ convex side	28·1
„ „ concave side	9·3
„ „ curved portion of root	18·7
		Difference	1·4

The action of gravity induces growth in organs which have ceased to grow but which are still capable of growth, or more rapid growth in organs which are growing but slowly, provided that they are geotropically irritable. A case in point is afforded by the haulms of Grasses, to which allusion was made in a previous lecture (p. 333). After they have entirely or nearly ceased growing in the normal vertical position, they will, if laid horizontally, begin to grow again at the nodes with considerable activity, the result being an upward curvature. Elfving has compared the rate of growth of Grass-haulms, which had nearly ceased growing, when in the vertical position and when rotated horizontally on a clinostat. In one set of observations he found that the mean increment in 44 hours was, for the vertical haulms 2·4 (micrometer-divisions), and 6·4 for the haulms on the clinostat; in another set the figures are respectively 1·3 and 11·3. The effect of the slow rotation on the clinostat is that each side in turn tends to become convex, that is, begins to grow more rapidly, and thus the rate of growth of the whole haulm is increased.

Growth, we know, depends upon turgescence; hence the geotropic curvatures of growing organs depend upon the turgidity of their cells; and since it is only living cells containing protoplasm which can be turgid, it must be by such cells of the organ that its curvature is effected. Such cells constitute the parenchymatous tissue of the organ. It might be thought that the pith plays an important part in producing curvature, but it appears that this is not the case. Sachs found, namely, that the pith of shoots, when freed from the other tissues, cannot be induced to curve geotropically, and de Vries found the same to be the case with the medullary tissue of the nodes of Grass-haulms. Sachs has also observed, in a shoot of *Nicotiana Tabacum* which had become geotropically curved, that when the pith was isolated it at

once became perfectly straight, an observation which has been repeated in various plants with similar results by Frank. Again, as Frank points out, organs which have no pith, such as the hollow leaves of the Onion, are capable of becoming geotropically curved. It appears that it is the cortical parenchyma which is most concerned in producing the curvature.

With regard to the seat of the geotropic curvature, it appears from the observations of Frank and of Sachs on roots, and from those of Sachs on shoots, that the most rapidly growing zones are those which curve most, but it is probable that, as in the heliotropic curvature, this is not always the case.

We pass to enquire, in concluding the subject, whether the geotropic irritability is confined to a particular portion of the growing region of an organ, or whether it is distributed throughout it. The view which, until recently, has been generally accepted is that the region of most active curvature is the seat of the greatest irritability. We have at present no grounds for doubting the correctness of this view, except with regard to roots, in which, as Darwin first pointed out, there appears to be some reason to believe that a coincidence of the seat of the most active curvature with that of the greatest irritability does not obtain, but that they are more or less widely separated. This view was suggested by Ciesielski's observation that when the roots of seedlings (*Pisum*, *Ervum*, *Vicia*) which had had their tips cut off, were laid horizontal, they did not curve geotropically; when, however, the roots which had had their tips cut off were left for some days, they formed new growing points, and then they at once began to curve geotropically. From these facts Ciesielski inferred that the geotropic curvature of a root can only take place when the root possesses an uninjured growing-point. Darwin repeated Ciesielski's experiments with numerous variations, and obtained confirmatory results. In explaining the facts, Darwin goes much further than Ciesielski. He considers the importance of the tip in relation to the geotropic capability of the root to be this, that it is the seat of the geotropic irritability, that it receives the stimulus and transmits it

to the growing zones behind it in which the curvature takes place.

The assertion by Darwin of the localisation of geotropic irritability in the tips of roots has given rise to a number of researches on the subject the results of which are conflicting. The cause of this conflict is the difficulty of ensuring the normal growth of roots under conditions favourable for observation, and the fact, to which Sachs first drew attention, that the removal of the tip causes roots to undergo the most various curvatures. This irregularity is due, as Darwin and Kirchner state, to an oblique, that is not exactly transverse, "decapitation", a curvature taking place towards the longer side of the injured root, but Detlefsen replies that when roots are vigorous, irregular nutations follow decapitation even when the section is as nearly as possible transverse. Some observers, such as Sachs and Detlefsen, deny altogether that decapitated roots are incapable of geotropic curvature. Wiesner admits that the capability of performing geotropic curvature is diminished by decapitation, and ascribes the diminution to a diminished turgidity of the growing cells. He finds also that a decapitated root grows in length less rapidly, when in moist air, than an uninjured root—an observation which has been confirmed by Molisch—though it grows more rapidly when in water. On the other hand Darwin's view is supported by the observations of F. Darwin, Kirchner, Krabbe, and Brunchorst. F. Darwin finds, in repeated experiments, that decapitated roots do not curve geotropically, and that decapitation does not so diminish the activity of growth in length of a root as to account for its loss of geotropic irritability. Kirchner also denies that there is any such difference in the rate of growth in length of normal and decapitated roots as Wiesner and Molisch assert, and points out that, even admitting this to be the case, geotropic curvature is not proportional to the rate of growth in length. From Krabbe's observations it would appear that decapitated roots grow in moist air rather more rapidly than normal roots. Brunchorst has made the very remarkable observation that if the communication between the region of curvature and the tip of

the root be impaired by the removal of a ring of cortical tissue, the root will not curve when placed horizontally. Both Brunchorst and Wiesner have investigated the effect of centrifugal force on decapitated roots. They both found that when the roots are in a moist chamber, they curved outwards under the influence of this force like normal roots, but Brunchorst observed that they did not so curve when the chamber was loosely filled with damp sawdust. Brunchorst concludes from this that the curvature observed in the moist chamber is not a response to the stimulus of the centrifugal force, but is a purely mechanical result which is prevented by the introduction of the moist sawdust. On the whole, then, the evidence is clearly in favour of Darwin's view that geotropic irritability is localised in the tips of roots.

We go on now to consider the geotropic phenomena of bilateral organs, and we begin with those of isobilateral organs. The long narrow flattened leaves of Monocotyledons such as Iris are already familiar to us as examples of organs of this kind. All that we have to say with regard to them is that they are orthotropic and negatively geotropic.

We have to consider, finally, the geotropic phenomena of those bilateral organs which are dorsiventral. We find, in the first place, that many organs which, when exposed to light, take up the plagiotropic position characteristic of dorsiventral organs, do not do so in the absence of light, but that, under these circumstances in which gravity is the one external directive influence which acts upon them, they grow erect, they are orthotropic. This is the case, as Frank has shewn, with the creeping shoots of *Lysimachia Nummularia*, *Polygonum aviculare*, *Atriplex latifolia* and other plants, with radical leaves, and with the thalloid shoots of *Marchantia*. Other instances are doubtless afforded by the shoots of *Tropæolum* and of the Ivy to which reference was made in our discussion of heliotropism (p. 443). We know already that, in the case of the creeping shoots above-mentioned, their dorsiventrality is induced by the action of light, and we cannot be surprised to learn that in the absence of light they should exhibit the negative geotropism characteristic of

orthotropic radial shoots. Radical leaves, and the shoots of *Marchantia*, afford us examples of permanently dorsiventral organs which are negatively geotropic.

But all organs which are dorsiventral, and therefore plagiotropic under normal conditions of growth, do not behave in this way. Frank has observed, for instance, that the runners of *Fragaria lucida*, the lateral branches of Conifers and of many dicotyledonous shrubs and trees maintain their plagiotropic habit even in darkness. When they are placed with their apices directed upwards or downwards, they curve so as to assume a more or less horizontal direction. And further, when they are placed horizontally in the inverse position so that their morphologically inferior surfaces are directed upwards and their morphologically superior surfaces downwards, they twist on their own axes until the normal relation of these surfaces with respect to the vertical is attained. Many leaves were also found to behave in this way.

In considering the geotropic phenomena presented by these dorsiventral organs, two facts are to be clearly distinguished from each other, namely, the maintenance of the horizontal direction of growth, and the maintenance of the normal relative position of the two opposed sides of the organ. As far as the former is concerned these organs behave precisely like those radial organs which we have already considered (p. 463): the latter is a peculiarity of dorsiventral organs. The maintenance of the horizontal position in both cases may be ascribed to Frank's diageotropism: but there is this difference between the diageotropism of plagiotropic radial organs and that of dorsiventral organs, that, in the former case, it is indifferent which side of the organ lies uppermost, whereas in the latter there appears to be a tendency to maintain the morphologically superior surface uppermost in all cases, and the morphologically inferior surface undermost.

The assumption of the existence of diageotropism has naturally been exposed to a good deal of criticism; but this criticism has, so far, been confined to the diageotropism of dorsiventral organs. With regard, first of all, to the maintenance of the horizontal direction of growth, de Vries has

found that the runners of *Fragaria canadensis* do not remain horizontal when kept in darkness, but curve upwards, and he rightly infers that they are negatively geotropic. He has likewise found that the lateral branches of Conifers and dicotyledonous trees do not in all cases maintain their horizontal direction of growth in darkness, and when this is the case he accounts for it in a different way. For instance, he found that the upward curvature of such branches was in some cases interfered with, and in others prevented, by the weight of the leaves: here the cause of the more or less complete maintenance of the horizontal direction of growth is a purely mechanical one. In other cases he observed that the leafless branch (*Tilia*) maintained its horizontal direction of growth in darkness when its morphologically superior surface was uppermost, and that it did not do so, but curved upwards, when its morphologically superior surface was undermost. The branch, he says, was clearly epinastic; the maintenance of the horizontal direction of growth in the first instance, was due to the exact counterbalancing of negative geotropism by epinasty; the upward curvature in the second instance, to the cooperation of negative geotropism and epinasty. In other cases (*Ulmus*, *Corylus*, *Picea*) he found that leafless shoots, when placed in the normal horizontal position, curved upwards, and when placed in the inverse position, downwards. These shoots were hyponastic. In the former position hyponasty and negative geotropism cooperated and produced the upward curvature; in the latter they acted antagonistically, but the former was sufficiently strong to overcome the latter, and the downward curvature resulted. In a word, the positions assumed by dorsiventral shoots growing in darkness are regarded by de Vries as the results of the simultaneous action of spontaneous heterauxesis and negative geotropism.

With regard now to the special peculiarity of the dia-geotropism of dorsiventral organs, the maintenance of the morphologically superior and inferior surfaces in their normal relative positions. The torsions which Frank found to take place when dorsiventral shoots were placed with their superior

surfaces downwards, are ascribed by de Vries to the unequal weight of the leaves on the two sides. He found that when lateral branches (*Ulmus campestris*, *Celtis australis*, *Rhodotyphus kerrioides*, etc.) from which the leaves had been removed, were fixed horizontally in the inverse position, whilst still in connexion with the plant, they curved upwards without undergoing any torsion; whereas branches bearing leaves, when treated in a similar manner, underwent torsion as they attempted to curve upwards. De Vries explains the torsion in the latter case by saying that the leaves, when in the inverse position, curved upwards in consequence of negative geotropism and of epinasty, and since the curvatures were not quite uniform, the mechanical moment of the weight of the leaves on the two sides of the branch was unequal, and tended to twist the branch on its own axis. He points out that the normal torsions which take place in the internodes of branches bearing decussate leaves, which are such that the leaves come to lie in two planes, are due, not as Frank suggested in the case of *Deutzia scabra*, to diageotropism, but simply to the mechanical effect of the unequal weight of the leaves. The same cause, de Vries believes, induces the torsion of leaves when placed in the inverse position. When a mid-rib, freed from the lamina, is placed in this position, it curves upwards without torsion; when, however, the leaf is entire torsion results so that the morphologically superior surface curves to the uppermost. This torsion de Vries ascribes to the fact that the mid-rib does not curve upwards exactly in a vertical plane, but tends somewhat to one side; consequently the strain on the two sides is unequal and torsion results.

In support of the assumption of the diageotropism of dorsal-ventral shoots it may be pointed out, as Frank does, that it is not obvious in de Vries' explanation why the torsion should just cease when the leaves come to lie horizontally again, for it is precisely in this position that the inequality of the mechanical moment on the two sides of the shoot would exert its greatest twisting effect. It would be quite intelligible that they should so twist the axis as to come to lie in a vertical plane, but this is not the position which they assume.

In summing up the evidence for and against the assumption of diageotropism, we find that it is unassailed as regards radial organs, and in fact, with the case of the rhizomes observed by Elfving (p. 462) in view, it seems to be unassailable. But the case for the diageotropism of dorsiventral organs has not been as clearly made out as that for their diaheliotropism (p. 449); before the question can be regarded as finally settled more experimental evidence must be forthcoming.

A full discussion of the details of the mechanism by which geotropic curvature is effected will be given in a subsequent lecture when the general question of curvature will be gone into. It need only be urged here, as it was previously with regard to heliotropism—and it is more obviously true in the case of geotropism—that curvature is not the expression of the directive action of the force on the cells or cell-walls, retarding the growth of one side of the organ and accelerating that of the other, but that it is the response of the organ as a whole to the action of the force, whereby it is stimulated to take up a definite position with regard to the direction in which the force acts.

Current of Water. Jönsson has observed that the direction of growth of plant-organs is affected when they are exposed to the influence of a current of water; he designates the induced phenomena by the term *Rheotropism*. Organs grown under this condition, place themselves so that their long axes lie in the direction of the current. The hyphæ of Moulds (*Phycomyces*, *Mucor*) took up such a position that their direction of growth coincided with the direction of the current, they were, as Jönsson puts it, positively rheotropic. The hyphæ of *Botrytis cinerea*, however, took up such a position that their direction of growth was opposed to that of the current; they proved themselves to be negatively rheotropic. The radicles of Maize-seedlings likewise proved themselves to be negatively rheotropic, as did also those of Rye- and Wheat-seedlings.

It appears, then, that the force of a current of water exercises a directive influence, that it, in fact, induces heterauxesis, and so give rise to curvatures of plant-organs.

Constant Galvanic Current. Elfving, in his researches on the effect of the passage of electric currents through growing organs (p. 410), found that when a root is placed in a vertical position between two electrodes, it usually curves towards the positive electrode, that is, against the direction of the current. He found that a similar curvature takes place when the root is traversed longitudinally by a descending current; only in the case of *Brassica oleracea* was the curvature towards the negative pole. These phenomena may be conveniently designated by the term *Galvanotropism*.

Müller-Hettlingen, in his investigation of the same subject, found that the curvature of the roots of seedlings was always such as to tend to place their long axes in the direction of the current, the curvature being towards the negative pole. In his experiments, in which the mode of experimentation was somewhat different from Elfving's, the roots did not, except in a few cases, die. Müller concludes that the curvature observed by him is the true galvanotropism, whereas that observed by Elfving is a pathological phenomenon, not dependent necessarily on growth, for it could be induced after cutting off the tip of the root as Elfving himself states. It may be pointed out that Elfving used 2, 4, or 6 Leclanché cells, and Müller 4 Grove's cells. Müller found, further, that the curvature was induced when the current traversed only the tip of the root, an observation which confirms Darwin's view, to which allusion has already been made, that irritability is localised in the root-tip.

It is clear that the passage of a current through a root exercises a directive influence, that it induces heterauxesis and so alters the direction of growth. If we accept Elfving's results, we must regard the majority of roots as being negatively galvanotropic, and some as being positively galvanotropic; if we accept Müller's results, we must regard roots as being all positively galvanotropic.

The Substratum. Dutrochet observed that the hypocotyl of the Mistletoe, in whatever position the seed may have been placed, assumes such a direction of growth that its long axis is perpendicular to the surface of the branch or other body

upon which the seed has germinated, and he recalled and confirmed Spallanzani's observation that the sporangiferous hyphæ of Moulds grow perpendicularly outwards from their substratum. He proved, moreover, that the influence of the substratum on the growing organ is not due to the mere physical attraction between them, that is the result of a stimulating effect on what he terms the "nervimotility" of the organ.

Dutrochet's observations on Moulds have been comparatively recently confirmed by Sachs, who has found that when Mucor-spores are sown on a suspended cube of bread, in darkness, the sporangiferous hyphæ developed on the upper surface of the cube grow vertically upwards, whereas those developed on the lateral and inferior surfaces grow for a time perpendicularly outwards, but subsequently curve upwards in consequence of negative geotropism. The perpendicular direction of growth of the hyphæ growing on the lateral and inferior surfaces of the cube is maintained, in opposition to geotropism for a time, until they attain a certain length, and then geotropic curvature takes place. The directive influence of the substratum thus appears to be limited to a certain distance from its surface. Mycelial hyphæ were only developed on the lateral and inferior surfaces of the cube of bread, in no case on the upper surface; those that projected from the lateral surfaces behaved just like the sporangiferous hyphæ, only they subsequently curved downwards; those which projected from the inferior surface grew straight downwards. Similar results were obtained by Sachs with *Pilobolus* and *Coprinus*.

From these observations it is clear that the substratum exerts, for a time at least, a directive influence on growing organs, which is spoken of as *Somatotropism*; and growing organs may be classified according to their response to this influence, into two classes, the positively and the negatively somatotropic; the former are represented in the above observations by the radicle of the Mistletoe, and the mycelial hyphæ of the Fungi, which tend to grow perpendicularly inwards into the substratum; the latter, by the primary stem of the Mistletoe, and by the sporiferous hyphæ of the Fungi. We may go so

far as to make this generalisation, that shoot-organs are negatively, and root-organs are positively somatotropic.

But the observations before us, valuable as they are, are not quite conclusive, for the directive influence of gravity was not eliminated. In the case of the Mistletoe this is not a point of great importance, for, as has been already mentioned (p. 458), the hypocotyl is scarcely at all geotropic, but in the case of the Fungi it is of importance for their hyphæ are markedly geotropic. It is easy to imagine that although an organ may tend to conform to this law of perpendicular growth, yet its

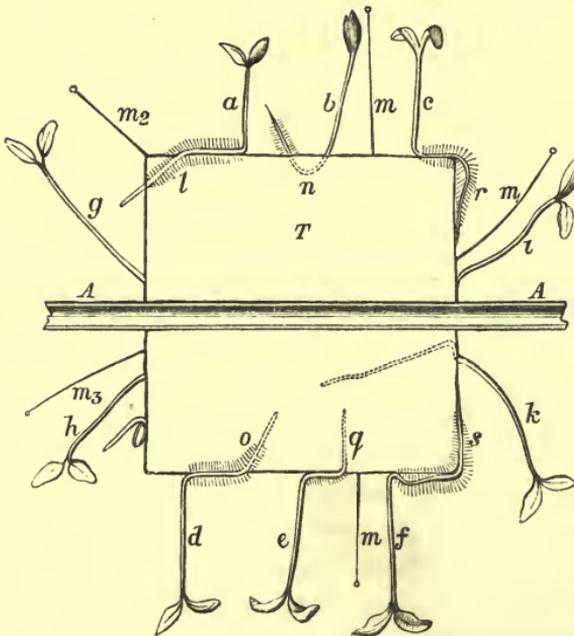


FIG. 52 (after Sachs). *A*, the axle of rotation; *T*, the cube of turf; *a*—*k*, seedlings of *Lepidium sativum* and *Linum usitatissimum* developed during rotation; *m*—*m*₃, sporangiferous hyphæ of *Mucor Mucedo*. The obliquity of the organs growing on the flanks of the cube is due to the throwing of a shadow by the thick axle.

irritability to the action of other directive influences may be such as to induce effects which entirely mask the effort towards perpendicular growth. The influence of light can be eliminated, either by keeping the plant in darkness, or by causing the plant to rotate slowly round either a vertical or a horizontal

axis in such a position with regard to the direction of the incident rays that each side of the organ under observation receives an equal amount of illumination, when heliotropic curvature is an impossibility. The influence of gravity can be eliminated by rotation on a clinostat. In experiments performed under these conditions, Sachs found the tendency towards perpendicular growth to exhibit itself in an unmistakable manner, in the growth of the sporangiferous hyphæ of Moulds and of the shoots of seedlings of various kinds. The radicles of the seedlings did not, in most cases, grow straight inwards into the piece of turf, as the accompanying figure shews. This is due to the disturbing influence of another directive agent, the moistness of the substratum, an influence which we shall shortly proceed to consider.

These facts clearly prove that the substratum exercises a directive influence upon the growth of organs developed upon it. This influence is sufficiently powerful, as the above figure shews, to induce heterauxesis and thus to give rise to curvatures.

Moisture. The fact that roots, when brought into the neighbourhood of moist surfaces, curve towards them, appears to have been long known to physiologists. Bonnet mentions it, but Knight seems to have been the first to make it the subject of experiment, and in this he has been followed by Johnson, Duchartre, Sachs, Darwin, Wiesner, and Molisch. The mode of experiment is very much the same in all cases. Seeds are sown in damp moss or sawdust contained in a vessel, suspended vertically or obliquely, the bottom of which is perforated with holes large enough to allow the roots of the seedlings to pass through them. In consequence of their positive geotropism, the primary roots of the seedlings grow downwards till they pass out into the air through the holes in the bottom of the vessel. Then their direction of growth alters. They no longer grow vertically downwards, but curve upwards so as to apply themselves to the moist surface: the influence of gravity has been overcome by the action of another stimulus which calls forth from the roots a more powerful response. These observations do not, however,

prove that the stimulus in question is due to the dampness of the moist surface, but special experiments have been made which supply the necessary evidence. Knight and Johnson found, for example, in the course of their experiments, that when the air into which the roots of the seedlings penetrated, after escaping through the holes in the vessel, was saturated with moisture, the roots continued to grow vertically downwards. The curvature is, then, the response of the root to the stimulating influence of the moist surface, and it is to this that Darwin has applied the term *Hydrotropism*.

We see that a root behaves to the stimulating action of a moist surface much in the same way as it does to the action of gravity; so we may say that a root is positively hydro-tropic just as we say that it is positively geotropic. We may also go a step further and enquire if there are such things as negatively hydrotropic organs; we might expect, for instance, that since roots are positively hydrotropic, stems would be negatively hydrotropic. It appears, from the researches of Molisch, that stems, with the possible exception of the hypocotyl of *Linum usitatissimum* which exhibited some signs of negative hydrotropism, are not hydrotropic at all. Wortmann has, however, observed that the sporangiferous hyphæ of *Phycomyces*, are distinctly negatively hydrotropic, for they curve away from any moist surface which may be brought near to them. Wortmann's observations have been confirmed by Molisch, who has further found that the subaerial hyphæ of *Mucor stolonifer* and the stipes of *Coprinus*, are also negatively hydrotropic, whereas the rhizoids of *Marchantia* and other Liverworts are positively hydrotropic.

Molisch points out with regard to the hydrotropism of roots, that, as might be expected, they curve out of the vertical towards a moist surface the more readily the less they are acted upon by gravity. For instance, we have learned that lateral roots are less geotropically irritable than primary roots, and Molisch has observed that the former curve hydrotropically more readily than the latter.

These are the principal facts which are at present known concerning hydrotropism. We see, at once, that we have to

deal here with phenomena resembling those of heliotropism and of geotropism. Here, too, we have a stimulus acting upon a growing organ which responds by altering its direction of growth, by becoming curved; in this case also heterauxesis is induced, the curvature being due to the more active growth of the convex as compared with the concave side. The resemblance is further brought out by the observations of Molisch, that, in the hydrotropic curvature, as is usually the case in the heliotropic and geotropic curvatures, the region of greatest curvature, in roots at least, coincides with the region of most active growth. Until the time of the publication of Darwin's observations, it was thought that the hydrotropic irritability, like the geotropic irritability, resided in the curving cells; but Darwin came to the same conclusion, from his experiments, with regard to hydrotropism as with regard to geotropism, that the irritability is localised in the root-tip, and that the stimulus is transmitted to the actively growing region. He found, namely, that when the tips of the roots of seedlings (*Phaseolus*, *Vicia Faba*, *Avena*, *Triticum*), were coated for a length of 1 or 2 mm. from the apex with a mixture of olive-oil and lamp-black which formed a water-proof covering, or when the tips were cauterised with nitrate of silver, the roots performed hydrotropic curvature rarely and in a slight degree only.

Darwin's experiments were made in the following way. The seeds were sown in damp sawdust contained in a sieve inclined at an angle of 40 degrees with the horizon. After germination the radicles protruded through the holes of the sieve, and were exposed to the hydrotropic influence of the inclined surface of moist sawdust: the projecting radicles could easily be coated with grease or cauterised.

The following may serve as an example of his numerical results:

Phaseolus multiflorus.

- a. Of 29 untouched radicles, 24 curved hydrotropically so as to come into contact with the sieve.
- b. 8 radicles had their tips greased for a length of 2 m.m., and 2 radicles for a length of $1\frac{1}{2}$ m.m.
 - for the first 24 hours they were all either vertical or nearly vertical, some had curved towards the damp surface to the extent of 10° .
 - at the end of 48 hours, three of the radicles had become considerably curved towards the sieve.

- c.* 10 radicles had their tips greased for a length of only 1 m.m. of these, four curved to the sieve within 24 hours, and four more curved in the succeeding 24 hours.
- d.* 5 radicles cauterised to a length of about 1 m.m. with nitrate of silver : in 24 hours one had curved into contact with the sieve, another was coming towards it, and the remaining three were vertical.

He suggests that in those cases in which the radicles became curved, it is possible that the layer of grease was not sufficiently thick wholly to exclude moisture, or that a sufficient length was not thus protected, or, in the case of caustic, was not destroyed ; and he accounts for the fact that in some cases curvature took place after an interval of one or two days by pointing out that when radicles with greased tips are left to grow for several days in damp air, the grease becomes drawn out into the finest reticulated threads with narrow portions of the surface left clean which would probably be able to absorb moisture.

The validity of Darwin's conclusion as to the localisation of the hydrotropic sensibility in the root-tips has been questioned by Wiesner and Detlefsen. Wiesner urges, as he did also with reference to geotropism, that the greasing or cauterising of the root-tips induces altogether abnormal modes of growth. He points out that though Darwin indeed mentions that the roots with greased tips continued to grow satisfactorily, yet they do not grow nearly so actively as uninjured roots, but he admits that there is no ground for asserting a proportionality between hydrotropic curvature and growth in length. Both he and Detlefsen observed, in experiments with decapitated roots, that some of them curved hydrotropically, but the great difficulty of obtaining accurate results in experiments of this kind, as mentioned above in speaking of geotropism (p. 468), must be borne in mind.

On the other hand, Darwin's observations are confirmed by those of Molisch. The method which Molisch employed is not open to the objections which may fairly be made against the methods of greasing and decapitation, for it does not inflict any injury upon the root. It consists in enveloping the whole root, except the tip which is left uncovered, in wet paper, and exposing it to the influence of a moist surface. If, now, a curvature of the root takes place, it can only be due to the action of the moist surface upon the apex, for the rest of

the root, being surrounded by the wet paper, cannot be supposed to be at all affected by a moist surface at some little distance from it. Molisch found, as a matter of fact, that roots thus arranged, with tips projecting to the extent of 1—1.5 mm., curved towards the moist surface in six hours. These facts, it must be admitted, go far to prove that the hydrotropic irritability of roots is localised in their tips.

With regard to hydrotropism also, we shall defer a full discussion of the mechanism of the curvatures to a subsequent lecture. But it must be urged in this case also that the curvature is not due to the stimulation of one side or other of the organ, to the stimulation, for instance, of the concave side by the moist surface, or, as Molisch insists, to the stimulation by the relative dryness of the air, of the side which becomes convex. The whole organ is stimulated, and the curvature is merely a mechanical necessity for the expression of the response of the whole organ to the stimulus.

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LECTURE XIX.

IRRITABILITY OF GROWING ORGANS (*continued*).

Contact.

IN previous lectures we became acquainted with the effect of continued and considerable pressure, upon growth, and we have now to study more particularly the effect of slight pressure continued during a relatively short space of time.

The most familiar instances of the effect of contact on growing organs are afforded by tendrils, the well-known twining properties of these organs being simply the expression of their sensitiveness to contact. A slight touch, in the case of very sensitive tendrils, such as those of *Passiflora gracilis* and of *Sicyos angulatus*, is sufficient to induce a very perceptible curvature. Darwin found the tendrils of *Passiflora gracilis* to be the most irritable. He says with reference to it: "a single delicate touch on the concave surface of the tip soon caused a tendril to curve, and in two minutes it formed an open helix. A loop of soft thread weighing $\frac{1}{32}$ of a grain placed most gently on the tip thrice caused distinct curvature. A bent bit of thin platinum wire, weighing only $\frac{1}{60}$ of a grain, twice produced the same effect; but this latter weight when left suspended, did not suffice to cause a permanent curvature." In this case also, the movement after a touch is very rapid: it is generally perceptible, according to Darwin, in half a minute after a touch. It will be readily understood that, in

the case of less highly irritable tendrils, the stimulus must be more powerful in order to produce a perceptible curvature, and the time which elapses between the moment of stimulation and the commencement of the curvature is longer.

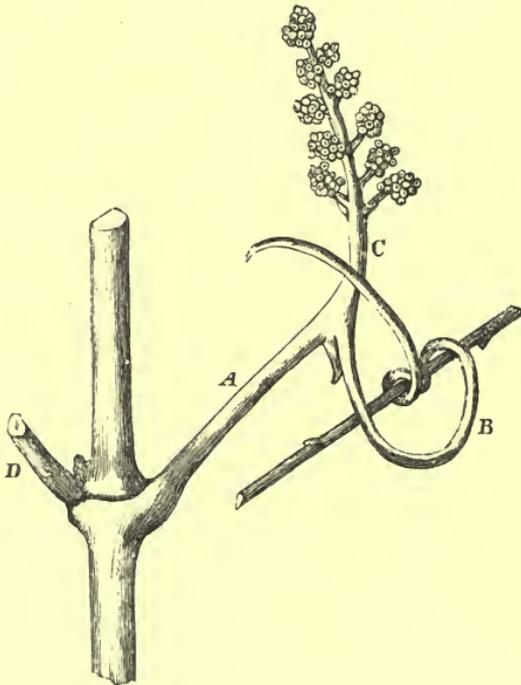


Fig. 53 (after Darwin). Tendril of *Vitis*.

If the contact be not too long-continued, the tendril will straighten out the curvature which it has made. Darwin, in endeavouring to ascertain how often the tendril could thus straighten itself after stimulation, found that it did so no less than twenty-one times in fifty-four hours. After the cessation of the stimulation, the curvature of the tendril continues to increase for a considerable time, it then ceases, and after a few hours the tendril uncurls itself and is again ready to act.

Now with regard to the period during which tendrils are irritable, and to the distribution of the irritability in a tendril, Darwin has clearly shewn that a tendril is not irritable during the whole of its existence. Speaking generally, tendrils do not possess irritability when they are either very young or

mature, but exhibit it most conspicuously when they are about three-fourths grown. An exception to this general rule is afforded by the tendrils of *Echinocystis lobata* which retain their irritability for a short time after they have ceased to circumnutate, that is in fact, to grow. Darwin has also found that the irritability of tendrils is localised. In the case of most tendrils, the lower or basal part is either not at all sensitive, or it is sensitive only to prolonged contact. Most tendrils have their tips slightly but permanently curved or hooked, and their irritability is localised in the concavity of this curvature: those of *Cobæa scandens* and of *Cissus discolor* are irritable on all sides: the inferior and lateral surfaces of the tendrils of *Mutisia* are sensitive, but not the superior surface.

In some cases the effect of the stimulus is confined to the point of contact, whereas in others its effect is manifested by portions of the tendril at some little distance from the point of contact. As an instance of the latter de Vries' observation may be mentioned. He found, namely, on stimulating a tendril of *Cucurbita* and immoveably fixing the stimulated region, that the tendril curved sharply for a distance of 5 mm. and 4 mm. respectively above and below the point of stimulation. In cases of this kind there is evidently a transmission of the stimulus.

The consideration of this point naturally leads us to briefly describe the general mode of action of tendrils. As a rule, tendrils are in active circumnutation at the time when their irritability is at its height, and the internodes which bear them are, in certain cases, circumnutating as well. The tendrils thus range over a large area, and consequently there is considerable probability that they will come into contact with some body around which they can twine.

With regard to the circumnutation of tendrils and of the internodes bearing them, Darwin gives the following information: in *Cissus*, *Cobæa*, and most *Passifloræ*, the tendrils alone circumnutate: in other cases, as *Lathyrus Aphaca*, only the internodes circumnutate, carrying with them the motionless tendrils: lastly, neither internodes nor tendrils circumnutate, as in *Lathyrus grandiflora* and *Ampelopsis*. In most *Bignonias*, *Ecremocarpus*, *Mutisia*, and the *Fumariaceæ*, the internodes, petioles, and tendrils, all move harmoniously together.

When, now, a tendril is brought into contact with a support, either by its circumnutation or by the wind, in such a way that its irritable surface is touched, it begins to curve round the support. As it does so, new areas of the irritable surface are stimulated, and the curvature increases and extends until the whole of the tendril lying between the original point of contact and the apex is wound in a spiral round the support. In some few cases, which are naturally also those in which there is no transmission of the stimulus, this is all that happens. In the great majority of cases, however, this coiling of the apical portion of the tendril round the support is followed by the spiral coiling of some part of that portion which lies between the point of contact and the insertion of the tendril upon the stem, provided that it is mechanically possible for the spiral coiling, which necessarily involves considerable shortening, to take place. It cannot possibly take place, for instance, when the stem bearing the tendril and the support around which its apical portion has twined are both immovably fixed. The turns of the spiral coiling are not, however, all in the same direction: they are grouped into two or more spires, separated by short straight portions, the turns of any two successive spires being in opposite directions. This is a mechanical necessity of the spiral coiling of a filament attached at both ends.

As a rule, according to Darwin, the spiral coiling usually begins in the attached tendril close to the support and then travels downwards towards the base. If, however, the tendril is very slack, the unattached portion becomes at first flexuous throughout nearly its whole length, and then it gradually becomes spirally coiled.

The especial physiological interest of this spiral coiling of the free portions of tendrils is that it offers a striking example of the transmission of a stimulus: the free portion is stimulated to coil spirally by the stimulus transmitted from the portion which had coiled round the support. Its general biological importance is also great. By the spiral coiling of the tendrils the stem bearing them is raised, and is held firmly in position, but not rigidly, for the spirally coiled tendrils act

as so many springs giving the stem a certain freedom of play when it is swayed by the wind.

It may be mentioned here that the tendrils of many plants, if they fail to become attached to a support, likewise coil spirally; but this is a very different matter from the spiral coiling of attached tendrils of which we have just been speaking. It is a much slower process, and it only begins at the time when the tendrils are ceasing to grow and to be irritable: moreover, inasmuch as the spontaneously coiling tendril is attached at one end only, the turns of the spiral are all in the same direction. In some few cases, as in *Bignonia* and in three genera of *Vitaceæ* (Darwin), this spontaneous coiling of unattached tendrils does not take place, but they simply remain straight, wither, and fall off.

Darwin gives the following instances to illustrate the relative time of commencement of the spiral coiling of attached and of unattached tendrils. In *Echinocystis*, the tendrils usually begin to coil spirally in 12–24 hours after being attached, whilst unattached tendrils do not begin to coil until two or three days, or even longer, after circumnutation has ceased. A full-grown tendril of *Passiflora quadrangularis* which had caught a stick began to coil in 8 hours, and in 24 hours formed several spires: a younger tendril, only two-thirds grown, showed the first trace of coiling two days after clasping a stick, and in two more days formed several spires. Another young tendril, of about the same age and length as the last, did not become attached; it acquired its full length in four days; in six more days it first became flexuous, and in two more days formed one complete spire; the first spire was formed towards the basal end, and the coiling steadily but slowly progressed towards the apex, but the whole was not closely wound up into a spire until 21 days had elapsed from the first observation, that is, until 17 days after the tendril had grown to its full length.

With regard to the mechanism by which the coiling of a tendril is effected, it may be at once stated that here too, as in all the curvatures which we have hitherto considered, it is due to an elongation of the side which becomes convex; and in this case also, the general law holds good, that, if the organ is actively growing at the time of curvature, the concave side also elongates, but not to the same extent as the convex side, whereas, if the growth of the organ is slow, the con-

cave surface does not elongate at all and may even become shorter.

In illustration of the relation existing between the rates of growth of the two sides of the coiling portion of a tendril, and between these and the rate of growth, the following observations of de Vries are cited.

A young tendril of *Curcubita Pepo*, 12 cm. long and 0.65 mm. thick, was marked out into lengths of 1 cm., and the fourth and fifth of such lengths (counted from the apex) were also marked out into millimetres. The portion marked out into millimetres was then brought into contact with the support, an iron wire 1.55 mm. in diameter. At the end of the experiment the tendril had made $1\frac{1}{2}$ turns round the support, the rest of it being straight.

On measuring, it was found that

the length of the concave surface of one complete turn of the tendril	=4.87 mm.
the length of the convex surface of one complete turn of the tendril	=8.79 „
the length of the curved portion having been, when straight	=4.60 „
hence, for each millimetre of original length there had been a growth, on the inside	=0.05 „
on the outside	=0.9 „
The mean rate of growth of the straight portions of the tendril, above and below the curved portion, was found to have been, per millimetre	=0.15 „

From these results it appears that the rate of growth of the concave side was considerably less than the mean, whereas that of the convex side was considerably greater.

It has been observed that the twining of a tendril round a support is dependent upon the thickness of the support, and upon that of that tendril. Most tendrils, inasmuch as they are very thin, can twine round strings, but those which are thicker can only twine round a support of some thickness. This is simply a mechanical necessity, inasmuch as there appears to be a limit to the excess of elongation of the convex over the concave side.

For example, Sachs noticed that a tendril of a Vine had made one turn round a support: the thickness of the support was 3.5 mm., and the mean thickness of the coiled portion of the tendril was 3 mm., hence the length of the concave side was 11 mm., and that of the convex side was about 29 mm., the lengths of the two sides being in the proportion of

1 : 2·6. Supposing now, the tendril had to curve round a support 0·5 mm. thick ; the length of the concave side would be 1·6 mm., and that of the convex side 20·4 mm., and the proportion would be 1 : 13. It seems that such a great difference in length cannot possibly be attained.

It is for the same reason that relatively thick tendrils do not apply themselves closely to the sides of flattened supports, but only touch the projecting angles, whereas thinner tendrils apply themselves to the flat sides, for they are capable of curving sharply round the angles. Von Mohl observed tendrils of *Lathyrus odoratus* and of *Pisum sativum* twining closely round strips of tin.

If the support is so thick that the tendril is not long enough to make one turn round it, it is impossible for the tendril to twine round it. When the support is rather thick, but not so as to prevent twining, the coils formed around it by the tendril are not even, but present undulations. De Vries attributes this to the fact that the general tendency of tendrils to make coils smaller than the diameter of the support is very strongly marked in this case. Small lengths of the tendril are in consequence made to bulge away from the support, and subsequently apply themselves to it again, the displacements causing the tendril to become wavy.

According to von Mohl's observations, the position and the nature of the support do not in any way affect the twining of tendrils around it. Darwin has made some very remarkable observations with regard to the latter point. He found, namely, in the case of *Echinocystis lobata* and of *Passiflora gracilis*, that a tendril is not stimulated by contact with another tendril. He observed a singular fact in *Echinocystis lobata*. In this plant the tendril forms a very acute angle with the projecting extremity of the stem or shoot bearing it, and the tendril would, were it to perform its circumnutation without deviation, probably come into contact with the end of the shoot. In order to avoid this, as it were, it becomes stiff and straight as it passes near the shoot. The advantages which these singular adaptations secure for the plants which possess them are obvious : they may be summed up by saying that a waste

of tendril-power is prevented. Darwin also observed that the tendrils of the two plants mentioned above are not irritated by the impact of drops of water. This is an important biological arrangement, for it prevents the disadvantage which would ensue were the tendrils capable of being stimulated to curvature by rain.

Tendrils are not, however, the only organs which are possessed of sensitiveness to contact. Other instances of this are afforded by the petioles of most leaf-climbers. It is not necessary to go into detail concerning them, for these organs closely resemble tendrils in their irritability and in their mode of response to a stimulus. Usually, the petioles are irritable only whilst young, but in different degrees in different plants, and they are sensitive on all sides.

In some cases shoots are sensitive to contact. It was first observed by Dutrochet that the twining stem of *Cuscuta*, the Dodder, is irritable like a tendril. Von Mohl indeed suggested that all twining stems are irritable, but both Darwin and de Vries were unable to detect any trace of such irritability. This view of von Mohl's has, however, been recently revived by Kohl, who finds that the twining internodes of climbing plants are sensitive to long continued contact, and that the side in contact with the support grows less rapidly than the opposite side. In *Calystegia* the irritability is so great that contact with a thin thread of silk, or with a piece of thin platinum wire, or a somewhat prolonged friction, suffices to induce a considerable difference in growth between the side thus treated and the side opposite to it. It must be mentioned here that Darwin found the young internodes of *Lophospermum scandens*, which is not a stem-climber, as also the peduncles of *Maurandia semperflorens*, to be sensitive to touch; Kerner states that the peduncles of many flowers (Poppies, Anemones, Ranunculuses, Tulips) are also thus irritable; and Sachs gives instances of the manifestation of sensitiveness to contact by roots.

From the observation of the behaviour of the radicles of seedlings in their attempts to pass over obstacles which they meet with in the soil, Darwin was led to suspect that the tip

of the radicle is sensitive to contact, and that the stimulus is transmitted from this, the sensory organ, to the growing zones behind it in which the necessary curvature was then effected. In order to ascertain whether or not this was the case, he made a number of experiments by attaching small objects to one side of the tip of the radicle, in various plants, by means of shellac or gum-water, or by touching one side with dry caustic, or by cutting a thin slice off one side. He vindicates his method of experimentation by pointing out, in the first place, that it is evident that a small object attached to the free point of a vertically suspended radicle can offer no mechanical resistance to its growth as a whole, for the object is carried downwards as the radicle elongates, or upwards as the radicle curves upwards. Nor can the growth of the tip itself be mechanically checked by an object attached to it by gum-water, which remains all the time perfectly soft. Finally, when the tip is lightly touched on one side with dry caustic (nitrate of silver) the injury caused is very slight. The general result which Darwin obtained in a very large number of experiments of this kind was that the radicle was sensitive to one or other of these stimuli, the response being that it curved in such a way that the side to which the small object (a small piece of card) was attached, or which had been touched with caustic, or from which a small slice had been cut off, became convex. This result is a remarkable one; it appears that the response of the root to stimulation is different from that of all other sensitive plant-organs. In all the instances of sensitiveness given above, the induced curvature was such that the stimulated side of the organ became the concave side. Sachs, as already mentioned, found that roots offer no exception to this rule, whereas, according to Darwin, they do. The peculiar curvature observed by Darwin in roots may be conveniently spoken of as the "Darwinian curvature."

The following details will illustrate the general nature of Darwin's experimental results :

Vicia Faba; tip of radicle sensitive to attached objects, to caustic, to lateral slicing.

Pisum sativum; tip of radicle sensitive to attached objects, to caustic, to lateral slicing.

Phaseolus multiflorus; tip of radicle slightly sensitive to attached objects, to caustic, to lateral slicing.

Tropæolum; tip highly sensitive to attached objects.

Gossypium herbaceum; tip certainly sensitive to caustic.

Cucurbita ovifera; tip moderately sensitive to attached objects, highly so to caustic.

Raphanus sativus; a doubtful case.

Aesculus; tips indifferent to attached objects, sensitive to caustic.

Quercus Robur and *Zea Mais*; tip highly sensitive to attached objects, and in the latter plant, to caustic.

The curvature of the radicle sometimes occurred within 6—8 hours after the tip had been irritated, and almost always within 24 hours. The curvature often amounted to a rectangle,—that is, the lower end of the radicle bent upwards until the tip projected almost horizontally; occasionally the tip, from the continued irritation of the attached object, continued to bend up until it formed a hook with the apex pointing straight upwards, or a loop, or even a spire. After a time the radicle apparently becomes accustomed to the irritation, as is the case also with tendrils, for it again grows downwards, although the bit of card or other object may remain attached to the tip. In some of the experiments the radicles were placed horizontally, and the lower sides were stimulated: under these circumstances the upward curvature did not take place, as it did when the radicles were vertical, in consequence of the stronger opposing influence of geotropism.

The length of the apex which is sensitive is 1—1.5 mm., and the length of the curving portion of the radicle, which lies immediately behind the sensitive apex, is 6—12 mm. The curvature which results from stimulation is generally symmetrical. The part which bends most, is apparently the part which is growing the most rapidly: the tip and the basal part grow very slowly and they bend very little.

With respect to the degree of sensitiveness, Darwin found that a very minute square of writing-paper, attached by shellac, sufficed to cause the radicle of *Vicia Faba* to curve:

short bits of moderately thick bristle, fixed on with gum-water, acted in three only out of eleven trials, and beads of shellac weighing less than $\frac{1}{200}$ grain acted only twice in nine cases. The most interesting evidence of the delicate sensitiveness of the tip of the radicle was afforded by its power of discriminating between equal-sized squares of card-like and of very thin paper, when these were attached on opposite sides the radicles curved away from the heavier object, as was observed in the Bean and the Oak.

Darwin's observations on this peculiar manifestation of irritability by radicles have given rise to considerable discussion. Wiesner confirms Darwin's statement that the Darwinian curvature is not induced by friction, and he regards it as a pathological phenomenon. With regard to the experiments with attached objects, he points out that the curvature cannot be due to a stimulating action of the small piece of card or paper, for, as we have seen already, a radicle will grow straight against a considerable resistance, for instance, when it grows downward into mercury, and he himself observed, in special experiments, that radicles in their downward growth exerted a pressure of about a gramme, and that radicles growing horizontally pushed weights of 0.75—1.25 grme. out of their way without becoming curved. Darwin himself has estimated the pressure of a Bean-root growing straight downward at a quarter of a pound. Wiesner concludes that the curvatures observed in Darwin's experiments with attached objects were due, not to the pieces of card, bristle, etc., but to the irritating effect of the shellac. He found that when small pieces of wood or grains of sand were made to adhere to radicles, without the use of any adhesive material, no curvature took place, and also, that the curvatures were induced equally well when a drop of shellac was employed without anything else. Microscopical examination shewed that the part of the tip touched by the shellac had died away. Wiesner concludes that the effect of irritating one side of the tip of a radicle in any of the ways mentioned is to cause, in the first instance, a slight concavity of the irritated side, in consequence of the

injury, which is followed by a more active growth of that side so that it becomes curved. The investigations of Detlefsen and of Burgerstein have led them to conclusions similar to those of Wiesner. They find that the root can grow, without deflection, against a considerable resistance: for instance they observed that radicles of *Vicia Faba* are capable of perforating tin-foil of the thickness of 0.02 mm.; and they attribute the Darwinian curvature simply to the injury which is inflicted, in making the experiment, on one side of the root-tip. Detlefsen points out that the adhesive materials used by Darwin, including gum-water, injure the root in greater or less degree and induce curvature, and that the application of a very thin film of glass to the root, without any adhesive material, caused at first the Darwinian curvature and subsequently the disorganisation of the tissue in the area covered by it. He finds, too, that a Darwinian curvature can be induced in other organs—he instances the younger leaves of the Onion—by injury of one side of the growing region. He shews, further, that the curvature depends upon injury of the root-cap, and not upon irritation of the actual growing-point of the radicle: injuries inflicted upon the radicle as far as 5 mm. from the apex, to which length the root-cap extended, caused distinct curvature.

Taking all these observations into consideration, and especially the fact that the Darwinian curvature differs from all other curvatures induced by contact or pressure in that it is the irritated side of the organ which becomes convex, it seems probable that Wiesner is right in regarding it as a pathological phenomenon due to injury, or at least to a disturbance of the normal conditions of growth.

The curvatures which are the result of contact are, like those produced by light, gravity, etc., to be regarded as phenomena of induced heterauxesis. A discussion of the mechanism by which they are effected will also be deferred to a subsequent lecture.

Combined Effects.

We pass now to consider the combined effect of the various directive influences which, as we have seen, determine the direction of growth of plant-organs, and which we have so far studied individually.

The ultimate position assumed by a plant-organ in the course of its development and growth is a resultant one: it is the resultant of the action of the inherent directive influences, and of the external directive influences to which the organ is sensitive.

With regard to the inherent directive influences, we have found them (pp. 421, 418) to be two: the relation of the organs to each other, and their own rectipetality. The former determines what the relative directions of growth of the organs of a plant are and these directions they maintain in the absence of any disturbing external stimulus. An evident manifestation of this can, in fact, only be obtained when the plant is grown under such conditions that its organs are exposed as little as possible to the action of external directive influences, as, for instance, when it is grown in darkness and is rotating horizontally on the clinostat. Let us consider the case of a plant growing under these conditions. Assuming that the soil in which the root is imbedded is uniformly moist, the only external directive influence acting upon the primary shoot and the primary root will be that of the substratum; but, inasmuch as this is clearly not acting so as to cause somatotropic curvature, its effect may be neglected. The primary shoot will continue to grow in a straight line horizontally outwards, and the primary root to grow in a straight line horizontally inwards, in virtue of the opposition of the directions of growth of these organs (p. 419). The lateral shoots will arise from the primary shoot and the lateral roots from the primary root at their own proper angles, and will continue to grow in a straight line in the directions thus impressed upon them.

It is clear that plant-organs growing in obedience to these internal directive influences will offer a certain resistance to the action of a directive influence acting from without. It is perhaps to this that the occurrence of the latent period (pp. 435, 464) is to be attributed.

With regard to the combined action of the external directive influences, it was pointed out in a previous lecture (p. 424) that the direction of growth of a plant-organ depends upon its peculiar irritability, and upon a certain balance between the responses given by it to the various directive influences which act upon it. We will now discuss this subject in detail.

It has been sufficiently shewn in previous lectures that plant-organs are sensitive to a variety of external directive influences, and it has been pointed out (p. 374) that each organ possesses a specific irritability to the action of each such influence. In endeavouring to account for the position assumed by different plant-organs under their several conditions of growth, we must bear in mind that they may differ from each other both in the kind and in the degree of their specific irritabilities; and further, inasmuch as we have seen that the response to the action of any given external influence varies with the strength of that influence, we must in all cases enquire into the strength of the directive influences at work.

We will begin with orthotropism. We have found, namely, that certain organs, which are radially or isobilaterally organised, grow vertically either upwards or downwards under what may be regarded as the normal conditions of their growth; that, for instance, primary shoots and isobilateral leaves grow vertically upwards when they are fully exposed to light, and that primary roots grow vertically downwards in a uniformly moist soil.

Taking first the case of the shoots and leaves, we find that their orthotropism is the result of their negative geotropism and of their positive heliotropism. The action of the directive influence of gravity upon these organs is clearly demonstrated by the fact that they grow vertically upwards in darkness; and,

inasmuch as under the given conditions the incident rays of light may be regarded as falling vertically downwards, the directive influence of light upon these organs is likewise such as to cause them to maintain a vertically upward direction of growth.

But it occasionally happens that these organs grow under conditions other than these, as, for instance, when they grow in hedges. One side of the organ is then more exposed to light than the other, in other words, the light falls not vertically but obliquely upon them. Under these circumstances gravity and light act somewhat antagonistically; the organs tend to grow vertically in virtue of their negative geotropism, and to grow obliquely in virtue of their positive heliotropism; their direction of growth will depend upon the relative strength of the geotropic and heliotropic effects produced. In the majority of cases, as mentioned in a previous lecture (p. 430), the heliotropic effect is the greater, so the organs grow obliquely towards the light; but in some cases (p. 431) the geotropic effect is the greater, so they grow erect.

The relative strength of the geotropic and heliotropic effects produced in these organs depends upon their relative geotropic and heliotropic irritability, and upon the intensity of the incident light. This has been investigated in some cases. Müller-Thurgau observed, for instance, that when a shoot of *Helianthus* was placed horizontally and light was directed upon it from below, it curved upwards, whereas a shoot of *Fritillaria* remained straight under similar conditions. The intensity of the light being the same in the two cases, it is clear that either the geotropic irritability of *Helianthus* is greater than that of *Fritillaria*, or that the heliotropic irritability of *Fritillaria* is greater than that of *Helianthus*. It appears that, as a rule, the heliotropic irritability of the primary shoots of seedlings is greater than their geotropic irritability, for, when they are placed horizontally and are illuminated from below, they curve downwards, as von Mohl and Müller-Thurgau have found. Wiesner has carefully investigated this subject with special reference to the intensity of the light. When the primary shoot of a Bean-seedling growing vertically

upwards was exposed to light of optimum intensity (p. 432), falling perpendicularly upon one side of it, it curved towards the light so that its direction of growth was at an angle of 45° with the vertical. Taking the direction of growth as the resultant of the action of gravity and of light, it appears that in this case the geotropic is equal to the heliotropic irritability. In the case of the primary shoot of the Vetch-seedling, the organ curved, whatever its original position and whatever the intensity of light, so that its long axis became parallel with the direction of the incident rays of light. The heliotropic irritability of this organ is much greater than its geotropic irritability, so much greater in fact that the latter leads to no perceptible response when the directive influence of light is in operation. This is even more strikingly shewn in Wiesner's comparative observations on the occurrence of the first indication of heliotropic curvature in Vetch-shoots, some of which were growing erect whilst others were rotating horizontally on the clinostat. Müller-Thurgau had observed in the case of other shoots that the first indication of heliotropic curvature could be perceived somewhat earlier when they were rotating horizontally on the clinostat than when they were growing erect. In the Vetch-shoots Wiesner failed to detect any such difference.

The relation between geotropic and heliotropic irritability, and the influence of the intensity of light, is very clearly brought out by Wiesner's observations on the shoots of Cress-seedlings. Some of these rotating horizontally on the clinostat and others growing erect were placed at a distance of 2.5 metres from the source of light (Wiesner's normal gas-flame), a distance at which the intensity of the light was the optimum. In 35 minutes all the shoots had begun to curve heliotropically, and in 45 minutes more they had all curved so that their long axes were parallel to the directions of the incident rays. When removed half a metre nearer the gas-flame, or half a metre further away from it, the same curvature took place in all cases, but more slowly, and the shoots on the clinostat curved about an hour earlier than those which were growing erect. At greater distances from the optimum-position the shoots

growing erect no longer curved so as to become horizontal, whereas those on the clinostat became horizontal in eight hours.

In the following table are given Wiesner's determinations of the angles which the secants of the curvatures of the cress-shoots which were not rotating made with the vertical at different distances from the source of light.

Distance from the flame.	Angle with the vertical.
0·25 metres	30 ⁰
0·30 „	35 ⁰
0·75 „	55 ⁰
1·25 „	70 ⁰
2·50 „	80 ⁰ (optimum)
3·00 „	65 ⁰
3·75 „	35 ⁰

The foregoing results clearly shew that the relation between the geotropic and the heliotropic irritability is by no means the same in the shoots of all plants, and this affords an explanation of the different directions of growth assumed by the shoots of different plants growing under the same conditions.

Turning now to primary roots, when they are growing in soil, the external directive influences which may act upon them are those of gravity and of an unequally distributed moisture (p. 477). They grow vertically downwards, in consequence of their positive geotropism, when the soil around them is uniformly moist, but, inasmuch as their hydrotropic irritability is greater than their geotropic, they will, when the soil is not uniformly moist, curve out of the vertical and grow towards the damper area.

The relation between the geotropic and heliotropic irritability is of interest only as a matter of experiment in the case of earth-roots, but it is a matter of biological importance in the case of aërial roots. It has been already pointed out (p. 436) that the heliotropic irritability of the former is slight, so slight in most cases that it can only be detected, if at all, by eliminating the action of gravity by means of the clinostat. The heliotropic irritability of aërial roots is, on the contrary, frequently well-

marked, but I am not aware that any comparison of their heliotropic with their geotropic irritability has as yet been instituted.

We pass now to plagiotropic organs. The oblique direction of growth is, as we have seen in previous lectures, assumed by both radial and dorsiventral organs, including shoots, roots, and leaves.

The simplest cases of plagiotropism are those offered by radial organs, such, for instance, as certain rhizomes, and lateral roots. Elfving observed, namely (p. 462), that certain rhizomes (*Heleocharis palustris*, *Sparganium ramosum*, *Scirpus maritimus*), grow horizontally beneath the surface of the soil. The only external directive influence, apparently, which determines their direction of growth is that of gravity, and their irritability to its action is of the kind with which we have become acquainted as Diageotropism. The same behaviour has more recently been observed by Stahl in the rhizomes of *Adoxa moschatellina*, *Circæa lutetiana*, and *Trientalis europæa*.

Though light takes no part, under ordinary conditions, in determining the direction of growth of these rhizomes, yet their behaviour when exposed to light is of interest. Stahl has observed that when a rhizome of *Adoxa* is exposed to light, it curves so that its direction of growth becomes either obliquely or vertically descending. He explains this change in the direction of growth by assuming that exposure to light alters the nature of the geotropic irritability of the rhizome, so that from being diageotropic it becomes positively geotropic. The downward curvature is clearly not due to negative heliotropism, for Stahl has conclusively proved that the rhizomes do not respond to the directive influence of light. This is a point which merits further investigation, for it is difficult to conceive that exposure to light should thus modify the geotropic irritability. In view of what we know as to the influence of light upon the physiological properties of the shoots of *Tropæolum* and of the Ivy (p. 425), it would seem not impossible that exposure to light induces dorsiventrality in the rhizomes, and leads to photo-epinasty. If this be so, then the downward direction of growth of the

rhizomes when exposed to light is the resultant of diageotropism and of photo-epinasty, the latter being much the more powerful factor. But this suggestion is scarcely to be reconciled with the fact that very faint light, as I have observed, suffices to cause the downward curvature.

The plagiotropism of lateral roots is not, like that of these rhizomes, due to Diageotropism, but depends simply on their slight geotropic irritability (p. 462). They are positively geotropic, but their response to the action of gravity is only sufficient to cause their direction of growth, in uniformly moist soil, to deviate but little from the horizontal. As in the case of primary roots, their hydrotropic irritability is much greater than their geotropic, so that their direction of growth may be considerably affected by hydrotropism. They curve from relatively dry into relatively moist soil, or from dry soil into a saturated atmosphere; the curvature may be even such that their direction of growth is vertically upwards.

The plagiotropism of dorsiventral organs, such as shoots and leaves, is a more complicated phenomenon. It is the resultant expression of the effect of light and of gravity upon them, promoted, in many cases, by their own weight. In some cases light, and in others gravity, is the determining factor, as is clearly shewn by the fact that some of these organs assume a vertical direction of growth in darkness (p. 441 and 469), whereas others remain plagiotropic. The nature of the effect produced by light, appears, so far as we know it, to be in all cases the same: it induces epinasty and diaheliotropism (p. 450), that is, it affects not only the direction of growth but also the direction of the opposed surfaces of the organ. As regards the effect of gravity, we see that it is not uniform like that of light, for some of these organs grow erect when gravity is the sole external directive influence acting upon them, whereas others continue to grow horizontally. Plagiotropism is induced by gravity only in the latter case, in organs, namely, which possess that peculiar irritability to its action which we know as Diageotropism (p. 470), in virtue of which these organs tend to direct their morphologically superior surface upwards at right angles to the vertical, a

position which entails a horizontal direction of the axis of growth. The degree of the plagiotropism induced by light depends, in the first instance, upon the relative irritability of the organ to light and to gravity, and further upon the angle of incidence and the intensity of the rays.

In endeavouring to illustrate the foregoing considerations by reference to examples, we will begin with the case in which the organs grow fully exposed to light, so that the rays may be regarded as falling vertically downwards upon them.

In the case of diageotropic dorsiventral organs, as examples of which we may mention the runners of *Fragaria lucida*, by the lateral branches of Conifers and other trees (p. 470), and by some leaves, the angle of deviation from the vertical, under the assumed conditions of illumination, is either a right angle or is greater than a right angle, so that the direction of growth is either horizontal or obliquely descending. The horizontal direction of growth is to be attributed to an equality between diageotropism and diaheliotropism on the one hand, and photo-epinasty on the other: the obliquely descending direction, to the preponderance of photo-epinasty over diageotropism and diaheliotropism. A striking instance of the latter is afforded by F. Darwin's observation, that a cherry-leaf, exposed to light falling vertically downwards upon it, curved downwards epinastically.

The angle of deviation of negatively geotropic dorsiventral organs is, in some instances, lateral branches for example, less than a right angle, so that the direction of growth is obliquely ascending; in others, as the shoots of *Polygonum aviculare* (p. 450), the angle of deviation is a right angle, so that the direction of growth is horizontal; in others, again, as the shoots of *Lysimachia Nummularia* (p. 450), the angle of deviation is greater than a right angle, so that the direction of growth is obliquely descending. In the first case, the direction of growth is the resultant effect of the antagonistic operation of negative geotropism on the one hand, and of photo-epinasty and diaheliotropism on the other; in the second case, diaheliotropism co-operates with

either negative geotropism or with photo-epinasty, with whichever of the two opposing forces is the weaker, to produce equilibrium; in the third case, photo-epinasty is more powerful than negative geotropism and diaheliotropism combined.

The relative sensitiveness of an organ to light and to gravity is indicated by any change of the direction of growth which may take place when an organ, previously growing in darkness, is exposed to light. We have seen that in these dorsiventral organs the relation of the dark-position and the light-position is not the same in all cases, and we may therefore conclude that the relative sensitiveness to gravity and to light is not the same in all cases. But the angle between the two directions of growth cannot always be taken as an accurate measure of the relative sensitiveness. For instance, a diageotropic dorsiventral organ which, when exposed to light falling vertically downwards upon its morphologically superior surface, grows obliquely downwards, is clearly more sensitive to light than to gravity. But the degree of its deviation from the horizontal cannot be taken as a measure of this relative sensitiveness, for the effect of light upon it is probably twofold, photo-epinastic and diaheliotropic, and the tendency of the former to produce downward curvature, that is, to increase the obliquity of the direction of growth, is opposed by that of the latter to maintain the superior surface horizontal. Similarly, in the case of a negatively geotropic dorsiventral organ, the angle of deviation from the vertical is only a measure of the relative sensitiveness to gravity and to light when the epinastic and diaheliotropic effects of light co-operate. This is only the case, in vertical light, when the angle of deviation is less than a right angle; when, under these circumstances, the direction of growth is obliquely descending, the angle of deviation below the horizontal is a measure only of the epinastic effect of light as opposed to negative geotropism and to diaheliotropism.

With regard, now, to the relation between the plagiotropic effect of light and the angle of incidence of the rays, it is clear that only that portion of the plagiotropic effect which

is due to diaheliotropism is to be considered, for we know that photo-epinasty is not affected by the direction of the incident light. The most marked plagiotropic effect will be produced when photo-epinasty and diaheliotropism co-operate, and when the deviation of the organ takes place downwards in a vertical plane. This will be produced when the median plane of the organ, that is the longitudinal plane passing through its dorsal and ventral surfaces, is vertical, and when the incident rays lie also in a vertical plane. The most effective angle of incidence of the rays in this plane is that in which they fall upon the apex of the organ, at angles between the vertical and the horizontal, the plagiotropic effect increasing as the direction of the incident rays approaches the horizontal. For instance, when a dorsiventral organ is placed with its apex pointing vertically upwards, and light falls vertically upon it, it will tend plagiotropically towards the horizontal, and if its photo-epinasty is sufficient to overcome the diaheliotropic and geotropic effects, its direction of growth may be obliquely descending. Again, when a dorsiventral organ is placed horizontally, with its morphologically superior surface uppermost, and light falls horizontally on its apex, it will tend downwards in consequence of photo-epinasty and diaheliotropism, provided that they can overcome the geotropic effect, until the long axis of the organ is directed vertically downwards, until, that is, the highest possible degree of plagiotropism is attained. An illustration of this is afforded by F. Darwin's observations on the leaves of *Ranunculus Ficaria*, to which allusion was made in a previous lecture (p. 448).

When, however, the rays of light do not fall upon the organ in a vertical plane, parallel to its own median plane, but in planes more or less inclined to this, the plagiotropic effect gradually diminishes as the plane of incidence is more and more removed from the vertical towards the horizontal, until, when the plane of incidence is horizontal, that is, when the rays of light fall upon the flanks of the organ, no plagiotropic effect is produced. Under these circumstances the organ simply twists round its long axis in consequence of

diaheliotropism, though it may at the same time curve laterally away from the light in consequence of photo-epinasty. Its plagiotropism, that is, the angle of deviation of its long axis from the vertical, is clearly not affected.

The manifestation of sensitiveness to light by these organs, is, as we have seen, affected by the intensity of the light. The light falling upon the organs must be of a certain intensity in order that any perceptible plagiotropic effect may be induced. For instance, we know that when negatively geotropic dorsiventral organs grow in faint light, the effect of gravity asserts itself by an upward curvature (p. 441). But it does not follow that the most intense light produces the greatest effect; on the contrary, different organs seem to be most sensible to light of different degrees of intensity. For instance, the fixed light-position of most leaves, when fully exposed to light, is such that their surfaces are horizontal, the morphologically superior surface being directed upwards; the significance of this is, that it is in this position that the superior surface of the leaf is perpendicular to the direction of incidence of light of the appropriate intensity, which appears to be, according to Wiesner (p. 447), the brightest diffuse daylight. In some cases, as we have seen (p. 445), leaves assume, either by curvature or by torsion round their long axes, a vertical position under the same conditions of illumination; this position is doubtless also determined by the direction of incidence of the light of that degree of intensity to which the leaves are most sensitive. A striking instance of this is afforded by the Compass-plants, alluded to in a previous lecture (p. 446), in which, when fully exposed to light, the surfaces of the leaves are vertical, this position being determined by the oblique or horizontal rays of the morning and evening sun. These plants with vertical leaves, in fact, exhibit diaheliotropic irritability in a very high degree, so much so, indeed, that their response to the directive influence of light may entirely obliterate that to the action of gravity. The leaves are, as a matter of fact, negatively geotropic; but, when the plants grow exposed to light, it seems to be a matter of little importance what the direction

of the long axis is, whether it be horizontal or vertical, so long as the vertical position of the surfaces is secured.

We have now fully discussed the various influences which determine the position and the direction of growth of shoots, roots, and leaves, in general, and it now only remains to consider some special cases.

In speaking of the direction of growth of plant-organs, we have tacitly assumed, so far, that the rigidity of the organ is sufficiently great to prevent any very considerable modification of the direction of its growth in consequence merely of its own weight. But it not infrequently happens that the stems of plants are not sufficiently rigid to support their own weight and that of their foliage. When this is the case the stem may simply trail along the ground, or it may in some way attach itself to external objects and thus grow upwards into the air. The mode of attachment, in the latter case, is different in different plants. Some, such as the Brambles, are simply hooked on by the prickles with which their stems are provided (hook-climbers); others attach themselves by means of tendrils (tendrill-climbers), or by leaf-stalks which act like tendrils (leaf-climbers); others again, like the Ivy, attach themselves by roots (root-climbers); others, finally, have twining stems. It is to these last that we will specially direct our attention with the view of ascertaining the various factors which determine this peculiar mode of growth.

A twining shoot, at its first development is straight, but, after it has come to consist of two or three internodes, its apex hangs over on one side, and it then exhibits in a marked manner that circumnutation which we have discussed in a previous lecture (p. 363). This hanging-over of the apex is due to the fact that the shoot is now no longer able to maintain itself in a vertical position. The twining shoot at this stage exhibits, in fact, that excessive elongation of its internodes which is so often to be found in etiolated plants, and it is for this reason that Sachs has termed these twining shoots "normally etiolated shoots" (p. 385). If, now, the shoot comes into contact with or more or less nearly vertical support of appropriate thickness, it twines round it.

What, now, are the causes of this twining? It is clear, since von Mohl and Palm found that shoots will not twine round a horizontal support, an observation confirmed by Schwendener's, that when a shoot and its support are rotated on a clinostat no twining takes place, that the negative geotropism of the shoots is an important factor in producing twining. But the negative geotropism of these shoots cannot, however, be the sole cause of their twining, for then any excessively elongated etiolated shoot might twine. The circumnutation of the shoot, for instance, may contribute to the twining, and it is possible to conceive, as von Mohl did, that the shoot is sensitive to contact.

With regard to the possible connexion between circumnutation and twining, it must be pointed out that in all cases the direction of twining is the same as that of circumnutation. In consequence of this, circumnutation has come to be regarded as the primary cause of twining, but its mode of action has been differently regarded by various observers. Palm first suggested a view with regard to its mode of action which Darwin subsequently stated with great precision. He says, "When a revolving shoot meets with a support, its motion is necessarily arrested at the point of contact, but the free projecting part goes on revolving. As this continues, higher and higher points are brought into contact with the support and are arrested; and so onwards to the extremity; and thus the shoot winds round its support." And again: "If a man swings a rope round his head, and the end of it hits a stick, it will coil round the stick according to the direction of the swinging movement; so it is with a twining plant, a line of growth travelling round the free part of the shoot causing it to bend towards the opposite side, and this replaces the momentum of the free end of the rope." This very simple explanation is, however, insufficient. In the first place, in the circumnutation of the end of a shoot no momentum is acquired which might be compared to the centrifugal force in the swinging rope; secondly, the axis of circumnutation does not necessarily coincide with the axis of twining, as is the case in the swinging rope; thirdly, the

number of cycles of circumnutation performed in a given time is not the same, as in the case of the rope, as the number of turns round the support, but the former is much larger than the latter. Darwin himself noticed this last difficulty, and he accounts for it by assuming that it is due to the retarding effect of contact with the support on the circumnutation of the part of the shoot touching it.

According to Dutrochet, the twining of climbing stems is due to an "internal and vital force the action of which is revolving round the central axis of the stem." This finds its expression in that that portion of the stem which forms the outer side of the spiral described grows more actively than that which forms the inner side, the difference of growth never being compensated; the result is necessarily the formation of a spiral. He points out that this difference is not due to the contact of the inner side of the spiral with the support, for he had observed that spirals were in many cases formed by twining stems which were not in contact with a support. There is, in fact, in these stems, a natural tendency to grow spirally. Nevertheless, he admits that the support has some influence in inducing twining, for in most cases no spiral is formed unless the stem is in contact with a support. But even admitting the universality of Dutrochet's assumed natural tendency, his view is no explanation but a mere statement of fact.

De Vries regards the prevention of circumnutation as the cause of the spiral growth of twining stems. Thus, for instance, when any point of the overhanging free end of a stem is held fast, let us say the highest point of the curvature, the normal circumnutation is arrested. The free end now endeavours to nutate round an axis which is a straight line produced through the axis of the stem at the fixed point. It raises itself until its plane of curvature is above the horizontal. The described curve may, at this moment, be regarded as a portion of a spiral, the axis of which is vertical, which has the same direction as the circumnutation, and the apex continues to travel upward in this spiral. When, as is usually the case in nature, the apex itself is the fixed point,

or in other words, is the part which comes into contact with the support, the turns of the spiral which it describes will encircle the support provided it be of appropriate thickness. The spiral growth is promoted by torsion due to internal causes (p. 353), and may be either promoted or hindered by torsion due to external causes of which the weight of the terminal bud, of the leaves, and friction against the support are the most important.

In his paper on the subject, which affords much valuable information as to the mechanism of the process, Schwendener attributes twining to circumnutation and to an antidromous torsion, that is, a torsion in an opposite direction to that of circumnutation, which causes the nutating stem to present constantly its concavity to the support.

Again, Baranetzki attributes twining to what he terms the asymmetrical circumnutation of the apex of the stem, that is, to circumnutation round an axis which is inclined to the vertical. His mode of regarding the process would seem to approach that of de Vries. His views concerning the influence of geotropism are worthy of note. He finds, like Schwendener, that a stem will not twine whilst it is being rotated on a clinostat; he considers that this is due to an arrest of its circumnutation, for he finds that under these circumstances the nutation is of the kind which is termed undulating (p. 368). It is on this ground that he concludes, as mentioned in a previous lecture (p. 361), that circumnutation is not spontaneous, but is induced by gravity.

It will be seen that in nearly all these suggested explanations twining is referred to negative geotropism, to circumnutation, and to torsion, in various combinations. But we have seen that stems which do not twine exhibit negative geotropism, circumnutate, and may undergo torsion. The question of the ultimate difference between stems which do and those which do not twine, still seems to remain unanswered. If twining simply depends upon these factors, why cannot we induce any flexible stem, for instance excessively elongated etiolated stems, to twine?

Of all these various attempts at explanations of twining

Dutrochet's is the only one which suggests that twining stems possess properties which are peculiar to themselves, and are not possessed by stems which do not twine. He attributes to them, namely, an inherent tendency to grow spirally. But, even admitting this, this assumption does not explain the twining of these stems round supports. For it is clear that every stem which exhibits torsion must have been growing spirally; that is, its apex has been circumnutating and at the same time a twisting round its own axis has been taking place, conditions which necessitate a spiral direction of growth. We must, to be consistent, admit that every stem which exhibits torsion has an inherent tendency to grow spirally. And yet it is not true that all stems which undergo torsion are capable of twining. It is the confusion of a spiral direction of growth with twining round a support which makes all these explanations unsatisfactory. All stems which twine grow spirally, but the converse is not true, that all stems which grow spirally twine. It is true that, as de Vries pointed out, anything which interferes with the circumnutation of a twining stem induces spiral growth, but this is not true only of the stems of twining plants, it is true of all circumnutating stems whatsoever.

Von Mohl recognised this difficulty, and met it by assuming that twining stems must be endowed with irritability. This view was contradicted by all subsequent observers, until, quite recently, Kohl reasserted it, as already mentioned above, and he has proved it in various ways. His most striking observation is perhaps this, that a stem of *Calystegia* will twine round a perfectly loose string. It is clear that the string cannot mechanically interfere with the circumnutation so as to cause the stem to grow spirally round it; and yet the stem was concave at all the points of contact. It is impossible to explain this otherwise than Kohl has done, that is, by assuming that the stem is irritable, like a tendril, though perhaps in a less degree, and that, as in the case of a tendril, the concavity at each point of contact is the result of the contact upon the irritable organ. When we remember that the stem of one twining plant, *Cuscuta*

(p. 491), is on all hands admitted to be irritable, it is not surprising that irritability should be found to exist in others also.

But it may be objected that, as has been frequently observed, the stems of twining plants form spirals when they are not in contact with a support. If, however, we clearly distinguish between spiral growth and twining, this objection will be at once perceived not to be a real one. It is not at all surprising that a flexible shoot should, in consequence of its negative geotropism, of its own weight, of its spontaneous torsion, and of its circumnutation, assume a spiral growth in its endeavours to grow upwards. Schwendener has rightly pointed out that spiral growth under these conditions has nothing whatever to do with twining. He mentions other cases of other organs which exhibit spiral growth, such as tendrils which have not grasped a support, and the stalks of the female flowers of *Vallisneria*. Sachs also mentions cases of this kind, such as primary roots of *Vicia Faba* and shoots of *Enteromorpha mesenterica*, which he had found to have grown spirally. Moreover, as was pointed out above, all organs which exhibit torsion must have grown spirally, though in this case the axis of the spiral is the longitudinal axis of the organ. The fact that twining stems may form spirals independently of a support, does not affect the view that the twining round a support is due to irritability to contact.

Another objection to the assumption of irritability to contact in climbing stems might be based upon Schwendener's and Baranetski's observations (see p. 510), that a stem will not twine when it is rotated horizontally, together with its support, on a clinostat, and that, under these circumstances, one or more of the last-formed turns round the support will become unwound. But this objection is by no means fatal, and the fact is capable of a simple explanation. When the stem is rotating on the clinostat, each side of it in turn tends, in virtue of its negative geotropism, to grow so as to produce an upward curvature, the resultant effect being to cause the stem to grow straight horizontally. Under

these circumstances there is a conflict between the geotropic effect and the tendency to twine induced by contact with the support. Of these the former is clearly the more powerful, so much so that internodes which have already twined, but which are still growing, unroll themselves and straighten themselves out. The fact that stems will not twine round supports which are inclined at a considerable angle to the vertical is to be explained in the same way; it is the result of the preponderance of the geotropic effect over the effect of contact. With tendrils this is not so; their irritability to contact is so great that they twine round supports in any position.

The view that the twining of stems depends upon their irritability receives indirect support from some observations of Darwin's, which shew that the nature of the support is of some importance in determining twining. He found, for instance, that when a plant of *Hibbertia dentata* was surrounded by branched twigs, its shoots did not twine around them, but immediately did so when the plant was surrounded with thin upright sticks. Again, he observed that the stem of *Solanum Dulcamara* will only twine round thin and flexible supports. It is clear that if the twining of stems depended on purely mechanical conditions, the nature of the support, provided it fulfil the necessary requirements as to thickness, ought not to influence the twining. These observations of Darwin's are only intelligible on the assumption that twining stems are sensitive.

The conclusion to be drawn as to the process of twining appears, then, to be this. By its circumnutation a twining stem is brought into contact with a support; the effect of contact is to cause a concavity of the stem at the point of contact; this concavity causes fresh portions of the stem to touch the support, and thus, supposing that its position and its thickness are appropriate, the stem twines round it. It is not improbable that the spirals formed by the free ends of twining stems which have outgrown their supports is due to some extent, as in the case of tendrils, to a conduction of the stimulus from the parts below which are in contact with the support.

It has been incidentally mentioned that twining can only take place when the support is of appropriate thickness. In illustration we may cite Darwin's general observation, that the English twiners, excepting the Honeysuckle (*Lonicera Periclymenum*), never twine round trees, whereas tropical twiners can ascend thick trees. In one particular case, that of *Phaseolus*, he found that the stem could twine round a support four inches in diameter but failed with a support nine inches in diameter. There appears to be no limit of thinness, for, as we have seen, stems will twine round thin strings or wires, but when the support, assumed to be vertical, is very thin, the spiral is long drawn out, so that the stem is nearly straight, clearly because, under these circumstances, negative geotropism can most fully assert itself. The thicker the support, the more do the turns of the stem round the support approach the horizontal. When the support is of such a thickness that the stem, in order to embrace it, would have to twine horizontally, twining no longer takes place, for it is prevented by negative geotropism. But the limit of thickness is not the same in all cases; one stem can twine, whereas another cannot, round a support of a given thickness. This appears, according to Schwendener, to depend on the length of the still growing portion of the stem; the longer it is, the less need it approach the horizontal in growing round the support, but this view is rendered improbable by Darwin's observation that the long circumnutating shoots of *Ceropegia Gardnerii* failed to twine round a support six inches in diameter.

Allusion has been incidentally made to the torsion exhibited by twining stems, and as this torsion has been regarded by some as an important factor in the process of twining, we may now devote a short time to a consideration of it. Von Mohl, for instance, considered that the circumnutation of twining stems, and therefore indirectly their twining also, was due to torsion.

We must first clearly understand what torsion means; it means a twisting of the organ about its own axis. This is always exhibited sooner or later by twining stems, but it

is not essential to twining. When a young internode twines round a smooth support of appropriate thickness, it may do so just in the same way as it performs its circumnutation, that is, that any one side may always face the same point of the compass (see Fig. 41, p. 364). Under these circumstances a line drawn longitudinally down any one side remains all the time parallel to the axis of the stem. But, sooner or later, the internode begins to twist on its own axis, so that a longitudinal line on any one side no longer remains parallel to the axis, but describes a spiral about it. There are two sets of influences at work to produce torsion, the internal and the external. The internal cause, which is by no means peculiar to twining internodes, is that more prolonged growth of the peripheral as compared with the central tissues to which we have alluded in a previous lecture (p. 353), and it tends to cause a twisting of the internode round its own axis in the same direction as that of twining, to produce, that is, *homodromous* torsion. The external causes are various; the negative geotropism of the internode, the weight of the terminal bud or of the leaves, the alteration in position of the leaves, as Dutrochet and Wiesner point out, in the taking up by them of the most favourable fixed light-position, and lastly, the friction of the stem against the support. With regard to the nature of the torsion produced by these external causes, it depends upon circumstances, in most cases, whether it is homodromous or *antidromous*, that is, with or against the direction of twining. The effect of the last-named cause, the friction against the support, is constant; in all cases it produces antidromous torsion. Von Mohl first observed, namely, that when a stem twines round a smooth cylindrical support the torsion is not well marked, whereas when the support is rough it is considerable, an observation which has been confirmed by all subsequent researches. The torsion which a twining stem exhibits is the algebraical sum of the action of these various causes; it will depend upon the conditions under which it has been growing whether its torsion is homodromous or antidromous. In some cases, as Léon has observed, successive internodes

may exhibit different torsion, some being homodromously and others antidromously twisted. Torsion is then clearly not the cause, nor is it a necessary accompaniment, of twining, but it arises in twining stems from causes most of which also produce it in stems which do not twine, the only cause peculiar to twining plants being the friction against the support.

We have now to consider the direction of twining. It was pointed out in a previous lecture (p. 363), that whereas some stems circumnutate in the direction of the sun, others circumnutate in the opposite direction; and since, as we have seen, the direction of twining of a stem is the same as that of its circumnutation, there are two modes of twining as there are of circumnutation. The direction of twining



Fig. 54 (after Payer). *A*, Hop twining with the sun; *B*, Convolvulus twining against the sun.

is not, however, always constant throughout a Natural Order, nor throughout a genus, nor even in individuals of the same species as Darwin found in *Loasa aurantiaca*. The direction of twining may even be reversed in successive internodes of the same stem: this occurs, according to Darwin, occasionally in *Loasa aurantiaca*, and habitually in *Scyphanthus elegans*.

Finally, in order to complete the subject, we have to enquire into the influence of light upon climbing stems. In the first place, with regard to the tonic influence of light, Sachs has ascertained that *Phaseolus multiflorus* and *Ipomœa purpurea* can twine in continuous darkness, whereas *Dioscorea Batatas* (Duchartre, de Vries) and *Mandevillea suaveolens* (Duchartre) cannot twine under these circumstances. With regard to the directive influence of light, von Mohl concluded that twining stems are positively heliotropic, but less markedly so than other stems. Wiesner detected slight positive heliotropism in the stems of species of *Convolvulus*, *Ipomœa*, and *Calystegia*, but not in *Phaseolus multiflorus* nor in *Cuscuta*. Darwin observed the same in *Ipomœa jucunda* and in *Lonicera brachypoda*: the circumnutating apex of the former described the semicircle towards the light in one hour, and the semicircle away from the light in four hours and a half; the apex of the latter described the corresponding semicircles in 2 hrs. 37 min. and 5 hrs. 23 min. respectively. Baranetzky's observations agree in the main with the foregoing, but he found that the internodes were positively heliotropic only when young; when older they became negatively heliotropic.

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LECTURE XX.

IRRITABILITY (*continued*).

II. *The Irritability of Mature Organs.*

HITHERTO we have confined our attention to the manifestation of irritability by growing organs, but now we turn to the study of the phenomena of irritability presented by organs which are not growing.

The various movements which we have to consider under this head will be taken in the following order: first, movements which involve the locomotion of entire organisms: secondly, the streaming movement of protoplasm, and the contraction of contractile vacuoles; and finally the movements of cellular organs.

The simplest case of locomotion is afforded by the amœboid movement exhibited, among plants, by the zoospores of some Algæ and of the Myxomycetes, and by the plasmodia of the Myxomycetes, which are naked masses of protoplasm. Here there are no specialised motile organs, but any part of the protoplasm may be protruded as a *pseudopodium* into which the remainder of the protoplasm gradually flows, and thus locomotion is effected. In other cases a portion of the protoplasm is differentiated as a motile organ in the form of one or more delicate filaments known as *cilia* (see p. 1), by the lashing movement of which the organism revolves on its own axis and at the same time travels forward. Ciliary movement is exhibited by the majority of zoospores, by antherozoids

(excepting those of the Florideæ and of certain Fungi, which are better termed *spermatia*), and in some cases by plants, such as Volvox, Pandorina, etc., and some Bacteria during a longer or shorter period of their life. As a rule the ciliated zoospores possess no cell-wall, but in some cases it is present (p. 1): permanently motile plants, such as Volvox, etc., possess cell-walls.

Locomotion is also exhibited by Diatoms, Desmids and Oscillatorias, but the mode in which it is effected is not fully understood. According to some observers (M. Schultze, Engelmann) the movement of Diatoms and Oscillatorias is effected by means of the layer of mucilaginous substance which invests the organism and which they believe to be of a protoplasmic nature; Schultze even went so far as to suggest that filaments of protoplasm are protruded through the Diatom-frustule, along the median line (*raphe*) which act as pseudopodia or temporary cilia. According to others (Nägeli, Dippel, Borscow, Mereschkowsky, Hansgirg) the movement is the result of osmotic processes taking place between the cells and the surrounding water. The nature of the movement throws no light upon the subject; the Oscillatorias revolve on their own axes whilst moving forward, and this has been found to be true of Diatoms in certain cases at least. It is admitted on all hands that these organisms can creep over solid bodies, but it has been denied by Cohn and others, that they can swim: Nägeli, Pfitzer, and others have, however, observed it. The power of creeping rather suggests the existence of something like pseudopodia, whereas the swimming seems to support the osmotic theory. It must be stated, however, that nothing like pseudopodia has ever been detected, and that the protoplasmic nature of the mucilaginous investing layer has not been established.

With regard to Desmids, a remarkable form of locomotion has been described by Stahl in *Closterium moniliforme*: the elongated cell attaches itself at one end, then swings itself over and attaches itself by the other: each time this is repeated the organism moves the length of its body. It is probable, from Stahl's observations, that Desmids can swim.

We come now to the consideration of the streaming movement of protoplasm, which is commonly designated by the terms *Circulation* and *Rotation*. This streaming movement of the protoplasm is made apparent by the granules of foreign substances which are carried along in the current. These terms have been more especially applied to the streaming of the protoplasm of cells enclosed by cell-walls. The difference between them is only superficial, and depends upon the distribution of the protoplasm within the cell. When (as in Fig. 3, p. 13) the protoplasm is not confined to the peripheral layer (primordial utricle), and there is a more or less nearly central mass, investing the nucleus, connected by delicate strands, varying from time to time in position and number, with the primordial utricle, the streaming movement can be detected not merely in the peripheral layer, but in the strands in various directions (indicated by the arrows), and is termed *Circulation*. When, as in the internodal cells of *Chara*, the protoplasm constitutes only a primordial utricle, the streaming movement follows the contour of the cell, down one side, across the end, up the other side, etc. This is what is termed *Rotation*. It is not, however, the whole primordial utricle which moves, but an internal layer only, consisting of relatively fluid protoplasm; the external layer, in which the chlorophyll-corpuscles are imbedded, remains stationary. This moving layer constitutes a hollow cylinder, each half of which is moving in the opposite direction to the other, as is well seen when the longitudinal line of contact of the two halves is brought into view; the direction of the current on one side of this line is exactly opposite to that on the other. In some cases (*Chara*, *Nitella*) this longitudinal line, which is termed the *indifferent line*, is clearly marked out by the absence of chlorophyll-corpuscles, in the external resting layer, along its course. With regard to the occurrence of the streaming movement of the protoplasm in plant-cells, it may be pointed out that it is not confined to a few exceptional cases, but that it probably exists, at least for a time, in all plant-cells. This is true particularly of the *Circulation*, which has been most frequently observed in young cells especially in connexion with the

formative processes. From the nature of the case, Rotation can only be observed in full-grown cells. Nor is the streaming movement confined to protoplasm enclosed in a cell-wall; it is strikingly exhibited by the plasmodia of the Myxomycetes.

The last kind of movement to be considered under this head is that of pulsating vacuoles. These are small more or less nearly spherical cavities which make their appearance in the protoplasm, and then suddenly disappear. In the course of their relatively slow expansion (diastole) they become filled with cell-sap, which is forced out on the sudden contraction (systole).

Nothing is certainly known as to the physiological significance of the pulsating vacuoles. It seems obvious to suggest, as Cohn has done, since in *Gonium* and *Chlamydomonas* the contractile vacuole apparently communicates with the permanent vacuole, that they assist in the distribution of nutriment or of oxygen. The fact that pulsating vacuoles have been exclusively found in motile organisms, such as *Volvox*, *Gonium*, *Eudorina*, the plasmodia of Myxomycetes, the zoospores of many Algæ (*Chætophora*, *Ulothrix*, etc.) and of some Fungi (some sp. of *Cystopus*, Myxomycetes), seems to suggest, as Engelmann has pointed out, some possible connexion between the vacuoles and locomotion.

Before entering upon the consideration of the movements of cellular organs, it will be convenient to discuss the relation of the movements already described to external conditions. It was pointed out in a previous lecture (p. 297) that they can only be performed within certain limits of temperature. A second essential condition, in the case, at least, of aërobiotic plants, is the presence of free oxygen; it has been already mentioned (p. 297) that motile anaërobiotic plants continue to move in the absence of free oxygen.

In the majority of cases, exposure to light is not an essential condition of these protoplasmic movements. Sachs and others have observed, for instance, that the streaming of the protoplasm in plant-cells continues in prolonged darkness, and that it occurs in the cells of etiolated plants. The effect of

continuous darkness on zoospores appears to be that it prolongs their period of motility: instead of coming to rest and germinating, they continue to swim about until they die. Strasburger observed that the zoospores of *Ulothrix zonata* continued to move for about three days, and those of *Hæmatococcus lacustris* for over a fortnight, in darkness. But there is a case to which allusion was made in a previous lecture (p. 299), in which the tonic influence of light is an essential condition, namely, the movement of Engelmann's *Bacterium photometricum*. This is a case of very great interest. We have here, namely, a motile organism which can only move in the presence of light, or in other words, when it is in a phototonic condition, a condition which we have found to be essential to the growth of leaves (p. 380). When the Bacteria are exposed to light, movement does not at once begin, but there is a "latent period," which is the shorter, the more intense the light. Similarly when the Bacteria are placed in darkness, the movement does not cease abruptly, but gradually becomes less and less active: exposure to light produces a well-marked after-effect, the duration of which is the longer, the longer, and especially the more intense, the previous illumination. When exposed for some time to bright light of constant intensity, the Bacteria come to rest, especially in the absence of an adequate supply of free oxygen: when they have come to rest, they can be readily stimulated to renewed movement by a sudden and considerable variation in the intensity of the light, provided that the period of rest has not been longer than a few minutes; when, however, the Bacteria have been at rest, exposed to light, for some hours, they are no longer irritable by variations in the intensity of the light. Engelmann has ascertained that, of the rays of the spectrum, the dark ultra-red are those which are most active in inducing the phototonic condition; next in order come the orange, yellow, blue, and visible red. The only other case which at all resembles this of the Bacterium, is that of the Oscillatorias, which, according to Famintzin, move less actively in darkness than in light. On the other hand, instances are on record of a diminution of motility in consequence of exposure to light; this has been observed

by Pringsheim with regard to the streaming movement of protoplasm in the cells of *Spirogyra*, *Nitella*, and of the hairs of *Tradescantia*, and by Hofmeister and Baranetzky in the case of the plasmodia of *Myxomycetes*.

These movements are also affected by other conditions. They are affected, for instance, by the amount of water of imbibition; thus the movements of zoospores are retarded by increasing the concentration of the solution in which they are swimming; in the case of the streaming movement of the protoplasm there appears to be, according to Velten, a certain optimum proportion of water at which the movements are most active, any increase or diminution of which tends to diminish the activity of the movement. Mechanical stimuli also affect these movements; according to Strasburger the movements of zoospores are temporarily arrested by vibration; and pressure and concussion tend to arrest the streaming, as well as the amœboid, movement of protoplasm, and to cause rounding-off of the protoplasm, an effect which is also produced by electrical stimuli, though apparently in some cases a weak stimulus gives rise to an acceleration of movement. The movements are also affected by various chemical substances. Strasburger found that zoospores are at once killed by morphia, strychnia, curare, chloroform, salicylic acid, etc. The streaming and the amœboid movement of protoplasm is arrested by chloroform and ether (Kühne); and by dilute alkalies (Dutrochet), but it is not clear that the latter is a direct effect; the alkali may operate by modifying the proportion of water of imbibition.

The direction of these different movements is influenced in a striking manner by various external agents. Of the effects thus produced, the most remarkable are perhaps those which are due to the direction and intensity of the incident rays of light. With regard to the influence of the *direction* of the incident rays, it has been observed (Strasburger, Stahl) that the zoospores of various plants (*Ulothrix*, *Hæmatococcus*, *Botrydium*, *Polyphagus Euglenæ*, *Chytridium vorax*) when exposed to oblique illumination place their long axes parallel to the direction of the incident rays, and this the more

readily the smaller the zoospores. This taking up of a definite position by the organism with reference to the direction of the incident rays Strasburger terms *Phototaxis*. Phototaxis has also been observed in certain Desmids; by Braun in *Penium curtum*, and by Stahl in a species of *Pleurotænium*, in *Closterium moniliforme*, and others. These Desmids place themselves with their long axes parallel to the direction of the incident rays when the light is moderately intense, and in *Penium* and *Pleurotænium* it is always the younger half which is directed towards the source of light, but in *Closterium* Stahl observed a periodical reversal of position such that, for a time, one end is directed towards the source of light, and then the body is swung over like a pendulum, so that the other end comes to be directed towards the source of light. When, however, the light is intense, these Desmids, according to Stahl, place their long axes perpendicularly to the direction of the incident rays. Another instance of phototaxis is afforded by the changes of position of chlorophyll-corpuscles under the influence of light, to which allusion was made in a previous lecture (p. 299). Thus Frank and Stahl have observed that when delicate structures like Fern-prothallia, Moss-leaves, or *Vaucheria* filaments, are exposed to diffuse daylight falling upon them in one direction only, the chlorophyll-corpuscles collect on the cell-walls which are perpendicular to the direction of the incident rays (see Fig. 36, *B*, p. 300). Stahl has also observed that the chlorophyll-band of *Mesocarpus*, when the light is moderately intense, is perpendicular to the direction of the incident rays.

With regard, now, to the *intensity* of the incident rays it appears that zoospores move towards the source of light when its intensity is below a certain degree, and move from it when its intensity is above this critical degree. This critical intensity is by no means the same in all cases, nor even in all zoospores of the same kind, nor in the same zoospore at different times. It depends, obviously, upon the sensitiveness of the zoospore, and this is readily affected by various conditions. It is affected, in the first place, by temperature. Thus, supposing that at a certain medium temperature, zoospores

move towards light of a given intensity; if the temperature be lowered several degrees, the intensity of the light remaining the same, the zoospores will now move away from the source of light, that is, their sensitiveness to light is now greater. Again, supposing that at a certain medium temperature zoospores move away from light of a given, and considerable, intensity; if now the temperature be raised several degrees, the zoospores will move towards the source of light, that is, at the higher temperature they are less sensitive to light.

Strasburger gives, amongst others, the following illustration of the relation of sensitiveness to temperature in the case of the zoospores of *Hæmatococcus lacustris*; the light was throughout of the same intensity.

16° - 18° C. - zoospores moved towards light,
 4° C. - „ „ away from light.

It may be mentioned here that the distribution of the zoospores in a vessel of water is affected, as Sachs has shewn, by differences of temperature in different parts of the liquid, which give rise to currents which are strong enough to carry the zoospores along. Sachs was able, with emulsions of oil, etc., to reproduce many of the phenomena presented by zoospores. It is quite clear, however, that the distribution of the zoospores under the influence of light, is to be attributed only in a small degree to these currents in the water; it is mainly due to their own sensitiveness to light.

In the second place, the sensitiveness of zoospores to light is affected by the supply of free oxygen. Strasburger observed that when zoospores are kept in a closed vessel for some hours their sensitiveness diminishes, that is, that at the end of the time they move towards light from which, at the beginning, they moved away. Finally, it appears that the sensitiveness of zoospores increases with their age; that when they are young, they move towards light, from which, when they are older, they move away.

The position of the chlorophyll-bodies in the cells of plants is also affected by the intensity of the light falling upon them. Under the influence of light of moderate intensity, the chlorophyll-corpuscles are collected on the cell-walls which are perpendicular to the direction of incident rays (epistrophe, see p. 300, Fig. 36, *B*), so that their flat

surfaces are exposed to the light : when the light is intense, they are collected on the cell-walls which are parallel to the direction of the incident rays (light-apostrophe), so that they present their edges to the incident rays. Stahl has observed much the same thing in the case of the chlorophyll-band of *Mesocarpus*. When the light is only moderately intense, the chlorophyll-band presents its flat surface to the incident rays, as mentioned above ; when the light is intense, it presents its edge to the incident rays.

Phenomena of this kind have also been observed in the case of the plasmodia of *Myxomycetes*. All observers agree that the plasmodia move away from intense light, but it is not clear whether, under any circumstances they move towards the light. Baranetzky asserts, with reference to the plasmodia of *Aethalium* and *Didymium*, that they always move away from the light, and the more markedly so the more intense the light, an assertion which is confirmed by Stahl, although Hofmeister states that rather fluid plasmodia move towards light at least in certain stages of their development. Strasburger mentions some experiments in which plasmodia of *Aethalium* came to the surface of a mass of spent tan in faint light ; but there is no ground for concluding that, in these experiments, the faint light determined the direction of the movement of the plasmodia, for *Aethalium*-plasmodia come readily to the surface of tan in complete darkness.

With regard to the distribution of phototactic influence in the spectrum, it appears, from the observations of Cohn and of Strasburger on zoospores, from those of Baranetzky on plasmodia, and from those of Sachs on chlorophyll-corpuscles, that this influence is confined to the rays of high refrangibility.

The influence of other external agents in determining the direction of movement has been chiefly studied in the case of the plasmodia of *Myxomycetes*. Hofmeister and Rosanoff appear to have been the first to investigate the subject, and they concluded from their observations that the plasmodia of *Aethalium septicum* are negatively geotropic. This view

was supported by Baranetzky, who made the further remarkable observation that by a lowering of the temperature and exposure to light the negative geotropism is converted into positive. Strasburger, Pfeffer, and Stahl, however, failed to detect any indication of geotropic irritability in the plasmodia. Strasburger and Stahl shew, on the contrary, that the apparently geotropic phenomena are due to altogether different causes; either to the direction of the current of water by which the plasmodia were moistened during the experiment, or to differences of moisture in the neighbourhood. Strasburger and Stahl have conclusively proved that the plasmodia are negatively rheotropic, that is, when a stream of water is allowed to trickle over them, they move in a direction opposite to that of the stream; a result which has also been obtained by Jönsson. Stahl has further ascertained that the plasmodia are positively hydrotropic during the greater part of their existence, that is, that they move towards the most moist spot in their neighbourhood. When, however, they are about to form sporangia, they become negatively hydrotropic, and move away from moisture. It is on this account, as Stahl points out, and not on account of negative geotropism, that plasmodia which are about to produce spores come to the surface of the substratum or even climb up on various objects such as plants, etc. Further it has been ascertained that plasmodia are thermotropic. Stahl observed that when a strip of blotting paper, with a plasmodium on it, was placed on the adjacent margins of two vessels containing water, the one at 7° C., the other at 30° C., the plasmodium moved towards the vessel containing water at the higher temperature. This observation has been confirmed by Wortmann, who has further ascertained that at relatively high temperatures the plasmodium is negatively thermotropic. On repeating Stahl's experiment, the water in the cooler vessel being at 15° – 20° C., and in the warmer at 40° C., he found that the plasmodium moved away from the water on both sides. He determined the maximum temperature for positive thermotropism to be 36° C.

The direction of movement can also be affected by chemical means. It is known that zoospores, plasmodia, and *Bacterium termo* (see Fig. 35, p. 256) move towards free oxygen, and it has been further ascertained that various substances exercise an attractive or a repellent influence. Stahl has observed, in the case of plasmodia, that sodium chloride, potassium nitrate, glycerin, sugar, etc., have the effect of repelling the plasmodia of *Aethalium*, whereas watery extract of tan attracts them. He has, however, found that the nature of the effect depends upon the concentration of the solution with which the experiment is made. When the water with which a plasmodium is supplied is suddenly replaced by a dilute (0.25—2 per cent.) solution of sugar, the plasmodium at once retires from it. After some days the plasmodium gradually adapts itself to the new conditions and spreads itself out in the solution. If now the solution of sugar be replaced by a more dilute solution or by water, the plasmodium will again retire.

The most interesting observations of this kind, inasmuch as they have a direct bearing upon an important function of plants, are those of Pfeffer. He finds that the direction of movement of ciliated organisms, such as antherozoids, zoospores of *Saprolegnia*, motile *Schizomycetes*, is affected by presenting to them solutions of certain substances which have a specific attraction for these organisms. With regard to antherozoids, Strasburger had pointed out that in Ferns and in *Marchantia*, they are attracted by the substance which is extruded from the neck of the archegonium. Pfeffer found that malic acid (in combination) is the specific attractive substance for the antherozoids of Ferns and *Selaginella*, and cane-sugar for those of the Mosses, but he failed to ascertain what the specific substances were for those of the Liverworts, of *Marsilia*, and of *Chara*. Extract of meat exercises an attractive influence on the zoospores of *Saprolegnia*, and any nutritive solution attracts the motile *Schizomycetes*.

The experiments were made by introducing capillary tubes filled with the solution into water in which the antherozoids etc. were swimming,

and observing the movement of the organisms towards the tubes or even their entrance into them.

The strength and nature of the stimulating effect varies with the concentration of the solution. Pfeffer ascertained that the weakest solution of malic acid which perceptibly affected the antherozoids was one of 0.001 per cent., the antherozoids being in water. When the antherozoids are swimming in dilute solution of malic acid or of a malate, the solution in the capillary tube must be relatively much higher in order that the antherozoids may be attracted to it. Thus when the antherozoids were swimming in a solution containing 0.0005 per cent. of malic acid, the weakest attractive solution in the tube had to contain 0.015 per cent. of malic acid; and when the liquid in which the antherozoids were swimming contained 0.01 per cent. of malic acid, the weakest solution which attracted them to the tube was one containing 0.3 per cent. malic acid. Clearly the presence of malic acid in the liquid diminished the irritability of the antherozoids. As the strength of the solution is increased, the attraction which it exercises on the antherozoids also increases, but the more highly concentrated solution comes to exercise a repellent effect in virtue, simply, of its concentration. But it appears that a strong solution of a malate exercises a specific repellent effect quite independently of that due to its concentration; that an increase of the stimulus beyond a certain point induces a reversed result. Pfeffer did not determine exactly the concentration at which this reversal takes place, but he found that a solution of a malate, containing 10 per cent., or even 5 per cent., of malic acid had a marked repellent effect, whereas a solution containing 15.5 per cent. of nitre, and 0.5 of malic acid was attractive.

Further, a strongly acid or an alkaline reaction exercises a repellent influence on antherozoids. A solution containing 0.01 per cent. of free malic acid attracted apparently to the same extent as one containing the same proportion of acid in combination with sodium; a solution, however, which contains 0.1 per cent. of free acid repelled, whereas one containing that proportion of acid combined with sodium strongly

attracted. An alkaline solution, however weak, always repelled.

In concluding our study of these various forms of movements and their relation to external agents we may briefly consider their physiological significance, and compare them with other phenomena with which we have already become acquainted. In the case of motile organisms, their power of locomotion and their irritability to external agents enable them to seek a habitat in which the conditions of their life are the most favourable. By means of zoospores the distribution of the plants producing them is ensured. The production of motile and irritable antherozoids by plants of a more or less aquatic habit is essential to ensure the fertilisation of the oospheres; in some such plants, such as the Florideæ, the antherozoids (spermatia) are neither motile nor irritable, and in these the fertilisation of the female organ is left entirely to chance. To this latter point we shall subsequently recur. The streaming movement of the protoplasm is doubtless connected with its nutrition, a view which is supported by the fact that this movement can, in some cases, only be detected when the formative processes (*e.g.* the formation of a wall after division) are most active.

These movements which we are considering are spontaneous, given the necessary external conditions, and are thus comparable to the spontaneous movement of growing organs which we have already studied (p. 360). We see, further, that these spontaneously moving masses of protoplasm are affected by external agents much in the same way as the spontaneously moving growing organs. We find, for example, that the direction of movement of zoospores is determined by the direction of the incident rays of light, just as is the direction of growth of radial organs (p. 428). When exposed to light, the zoospores place themselves so that their long axes are parallel to the direction of the incident rays; this is precisely what radial organs tend to do under the same circumstances. According to circumstances the zoospores move either towards or away from the source of light; similarly, growing radial organs direct their apices towards or

away from the source of light. Positive and negative phototaxis find their parallels in positive and negative heliotropism. But there is a difference between the two cases, that the positive or negative character of the phototaxis depends entirely upon the intensity of the light, whereas the character of the heliotropism of growing radial organs is not so determined. The positive or negative heliotropism of a growing radial organ is a specific property which is not altered by external conditions; a negatively heliotropic root, for example, cannot be made positively heliotropic by any variation in the intensity of the light to which it may be exposed; nor can a positively heliotropic shoot be made negatively heliotropic, though, as we have learned (pp. 425, 429, 443) exposure to intense unilateral illumination may cause a radial shoot to become dorsiventral and at the same time diaheliotropic. It is true that the direction of movement of these masses of protoplasm does not appear to be affected by the action of gravity as is the direction of growth of growing organs, but, on the other hand, we find them exhibiting in a striking manner the phenomena of thermotropism, hydrotropism, and rheotropism.

We pass now to the consideration of the movements of mature cellular organs. The irritability of mature organs is manifested in essentially the same manner as that of growing organs, and the nature of the response is essentially the same in both cases. But it is convenient to treat of them separately, inasmuch as the result is different. When a growing organ, namely, performs a movement in consequence of stimulation, the movement is irreversible; when, for instance, a root or a shoot curves geotropically, the curvature is rendered permanent by deposition of substance. When, however, a mature organ performs a movement in consequence of stimulation, the position which it takes up is not thus rendered permanent; when the action of the stimulus has ceased, the organ resumes its normal position, and is again susceptible of stimulation, and the movements may be repeated an indefinite number of times. The movements of mature organs have, on this account, been designated as "movements of variation"

by Pfeffer, and a distinction between these and those of growing organs has also been drawn by de Vries who, designating the movements of variation by the equivalent term "allassotonic," speaks of those of growing organs as "auxotonic."

The movements of variation are most commonly exhibited by foliar organs. In the case of foliage-leaves the movement is effected by means of a special motile organ, the *pulvinus*, which is situated at the insertion of the leaf. This is a swelling consisting of a mass of rather small-celled parenchymatous tissue covered by the epidermis and traversed by a delicate fibrovascular bundle. The fibrovascular bundle may be central so that there is an equal thickness of parenchymatous tissue above and below it, as in *Oxalis Acetosella*, or excentric, as in *Mimosa pudica*, where there is more parenchymatous tissue below than above the bundle, the proportion being as 6 : 7. In some cases, as in *Oxalis Acetosella*, the walls of the parenchymatous cells of the pulvinus are all of uniform thickness, whereas in *Mimosa pudica* the cells of the upper half of the pulvinus have rather thicker walls than those of the lower. There are also intercellular spaces in the parenchymatous tissue of the pulvinus, which are largest in the neighbourhood of the fibrovascular bundle, but diminish in size in the outer layers of the tissue, until, in the most external, they are altogether absent. The structure of the whole motile portion of motile floral leaves, such as petals, stamens, or styles, is essentially the same as that of the pulvinus, as is also that of the tentacles of *Drosera*, except that in some cases, as in the staminal filaments of *Berberis* and *Mahonia*, the intercellular spaces are absent (Morren, Unger), and the tentacles of *Drosera* (see Fig. 33, p. 248). According to Unger and Pfeffer, intercellular spaces are present in the staminal filaments of the *Cynareæ*.

Of these movements of variation some are spontaneous. The most marked instance of spontaneous movement is afforded by the two lateral leaflets of the trifoliate leaf of *Desmodium (Hedysarum) gyrans*, known familiarly as the Telegraph-plant, first observed by Lady Morrison, and first

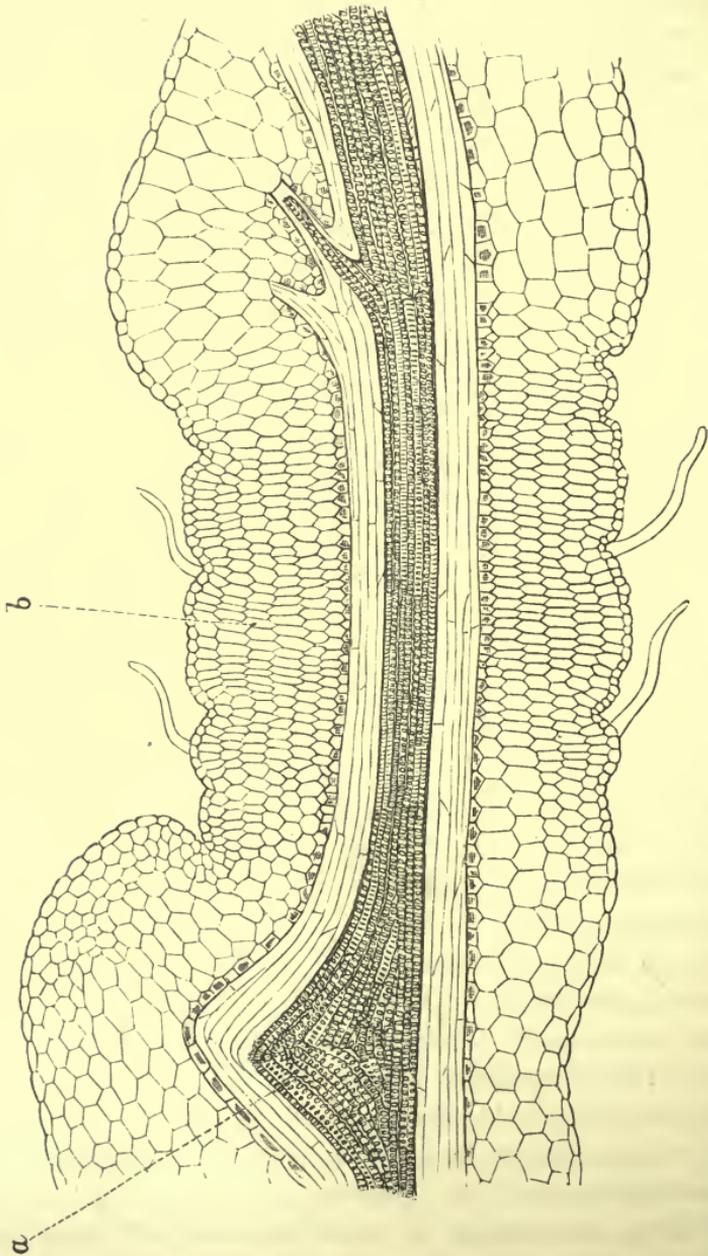


FIG. 55 (after Gardiner). Longitudinal section of pulvinus of *Mimosa pudica*
a, fibrovascular bundle; *b*, parenchymatous tissue of upper half.

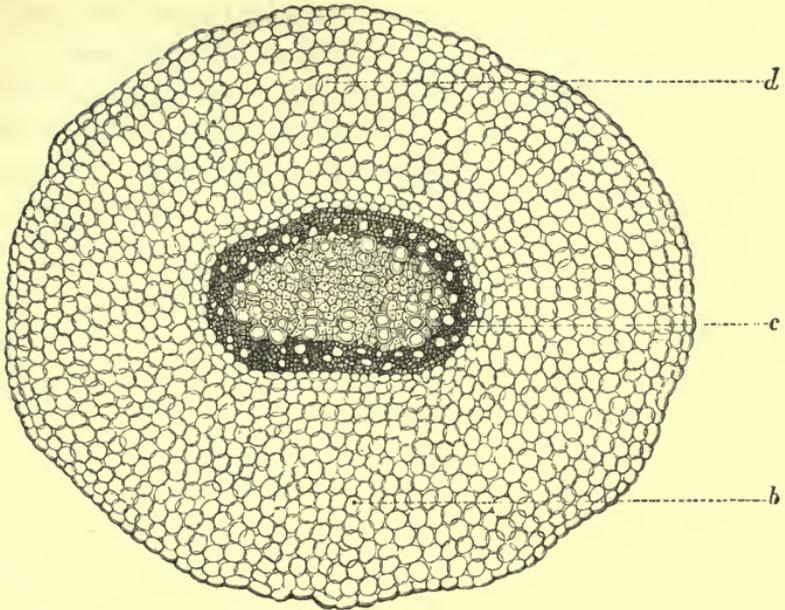


FIG. 56 (after Gardiner). Transverse section of pulvinus of *Mimosa pudica*; *b*, parenchyma of lower half; *c*, fibrovascular bundle; *d*, parenchyma of upper half.

described by Pohl in 1779. The lateral leaflets are inserted by means of a relatively long pulvinus on opposite sides of the main petiole just below the large terminal leaflet. The leaflets move upwards and downwards, changing their position sometimes by as much as 180° . At the same time they twist



FIG. 57 (after Duchartre). Leaf of *Hedysarum* (*Desmodium*) *gyrans*.

somewhat on their own axes so that the figure described by the apex is an irregular oval or ellipse. The rapidity of the movement varies with the temperature; but at a moderately high temperature (30° — 40° C.) the cycle is completed in about two minutes. In *Averrhoa bilimbi* (Lynch) the spontaneous movements of the leaflets are very striking. Some instances of spontaneous movement of floral organs are also known, and although it has not been definitely ascertained whether they belong to the category of movements of variation; or whether they are due to growth, like the opening and closing of flowers (pp. 378—400), it seems probable that the former is the case. A well-marked case is that of the labellum of *Megaclinium falcatum*, an African Orchid, described by Morren: the labellum consists of a limb and a claw, and the former oscillates upwards and downwards on the latter. Another, again, is the movement of the gynostemium of *Stylidium adnatum*. From the researches of Kabsch it appeared that the movement of this organ was induced and not spontaneous, but Gad's more recent and complete observations leave no doubt as to its spontaneity. The object of the movement is the scattering of the pollen, and it accordingly begins when the anthers are about to open. The gynostemium bends over on to the surface of the labellum, a reduced segment of the quinquepetalous corolla, which bears a viscid projecting gland: to this the gynostemium adheres until the moment arrives when the internal tensions which tend to straighten it are strong enough to free it from the adhesive surface; the gynostemium is then released with such violence that it swings over to the other side of the flower, at the same time scattering the pollen; it then slowly curves back again on to the gland of the labellum, and is then in position for a repetition of the movement. No case of spontaneous movement of stamens is certainly known, but Morren fancied he observed something of the kind in *Sparmannia* and *Cereus*.

The foliage-leaves of many plants, particularly of those belonging to the Leguminosæ and Oxalidaceæ, possess the power of spontaneous movement; for instance, the terminal

leaflet of *Hedysarum*, leaves of *Mimosa pudica*, of *Trifolium incarnatum* and *pratense*, of *Oxalis Acetosella*, and others. But the movements are not to be readily observed under ordinary conditions, inasmuch as they are masked by the movements which these leaves execute, as will be subsequently described, under the influence of those variations in the intensity of light which normally take place in the course of the twenty-four hours. The spontaneous movements can only be made manifest, either by keeping the plant for some time in darkness, or by exposing it continuously, as de Candolle, Bert, and Pfeffer have done, to artificial light of uniform intensity. Again, it appears from Darwin's researches, that the cotyledons of many plants belonging to these Natural Orders possess pulvini, and it is therefore probable that they too perform spontaneous periodic movements of variation.

As illustrations of these spontaneous movements the following observations of Pfeffer's may be given. When exposed to continuous illumination a terminal leaflet of *Trifolium pratense* executed movements through from 30° to 120° in periods of from $1\frac{1}{2}$ to 4 hours. The terminal leaflet of *Hedysarum* (*Desmodium*) performs more rapid but less extensive movements: it has been observed to move through 8° in from 10 to 30 seconds.

The performance of spontaneous movements of variation is dependent upon a combination of favourable external conditions. These conditions are, a suitable temperature, exposure to light, a supply of free oxygen, and a supply of water. With regard to the relation between the activity of movement and the temperature, it is doubtless essentially the same as in the case of all other functions: that there are, namely, minimum and maximum temperatures at which the movement is arrested, and between these an optimum temperature at which it is most active. For example, according to Kabsch, the lateral leaflets of *Desmodium* do not move at temperatures below 22° C.; at 28° to 30° C. the cycle of movement occupies about four minutes; at 35° C. it occupies from 85 to 90 seconds: at higher temperatures, probably, though the observations were not made, the movement would be less active, and finally would be arrested.

With regard to the action of light, it is true that, as mentioned above, the spontaneous movements are exhibited when the plant is kept in darkness, but, if the period be prolonged, the movements cease altogether, as Sachs and others have ascertained. Clearly, the tonic influence of light, the state of phototonus, is essential to the movement of these leaves, just as it is essential, as a rule, to the growth of leaves (p. 380). Long continued drought also leads to the arrest of the spontaneous movements. The effect of prolonged exposure to extremes of heat and cold, to darkness, and to drought, has been investigated by Sachs in the case of *Mimosa pudica*. Under all these circumstances the spontaneous movements are arrested, a state of complete immotility being induced.

Leaving, now, the spontaneous movements of variation, we pass to the consideration of those which are induced by the action of stimuli, and we will begin with those induced by variations in the intensity of light. It may be stated generally that a marked diminution in the intensity causes what is termed a movement of closing, and a marked increase, a movement of opening, that is, the assumption of a position in which the leaves are fully expanded. This may be well seen in the case of the Sensitive Plant (*Mimosa pudica*); when it is removed into darkness its leaflets close, and when it is again brought into the light its leaflets open. The effect is not, however, immediate in either case; in this, as in all other cases of the action of stimuli, there is a latent period, a time, that is, which intervenes between the action of the stimulus and the first indication of its effect. In the Sensitive Plant this period is relatively short, and it is on this account that this plant is especially suitable for the purpose of experiment. A peculiar effect of an increase in the intensity of light on the position of leaves was first observed by Cohn, and subsequently studied by Batalin and by Pfeffer, in the case of *Oxalis Acetosella*. When a plant with expanded leaves is brought from diffuse daylight into bright sunlight, its leaves fall down, just as they do when the plant is placed in darkness, and they retain that

position so long as the sunlight continues to fall upon them ; their position being quite independent of the direction of the incident rays. This matter has not been fully investigated, but, as Pfeffer points out, it suggests that there is a certain optimum intensity of light under which the leaves are fully expanded, and that any increase beyond this acts like a diminution in causing them to close.

With regard to the particular rays of the spectrum which determine these movements, it appears, from the observations of Sachs and of Bert, that the highly refrangible rays are those which are especially concerned. When a plant with its leaves fully expanded, is exposed to yellow light, the leaves soon close ; whereas if, under the same circumstances, the plant be exposed to blue light its leaves will remain expanded. Yellow light acts like darkness : blue light like daylight.

In consequence of their sensitiveness to variations in the intensity of light, motile leaves perform periodic movements in accordance with the normal variations which take place within the twenty-four hours. When darkness comes on they close, and when it again becomes light they unfold. The movement of closing is termed the "sleep" or *nyctitropic* movement, and recalls those exhibited by some growing floral and foliage leaves. The closed condition is what is known as the nocturnal position, the expanded, as the diurnal position. The normal alternation of day and night thus impresses on these motile organs a daily periodicity of movement, just as it impresses on growing organs a daily periodicity of growth (p. 400).

Periodic movements occur generally in the orders Leguminosæ and Oxalidaceæ, and they have been observed in various plants belonging to other orders ; in *Phyllanthus Niruri* (Euphorbiaceæ), *Porlieria hygrometrica*, (Zygophyllaceæ), among Dicotyledons ; in *Thalia dealbata* and *Maranta arundinacea* (Cannaceæ), *Strepthium floribundum* (Gramineæ), among Monocotyledons ; and in *Marsilea quadrifolia* among Vascular Cryptogams. (See Darwin.)

The sleep-movement has in all cases this result, that the upper surface of the leaf, instead of being horizontal, is brought more or less nearly into a vertical plane, but the direction of the movement is different in different cases.

Among the Oxalidaceæ the sleep-movement consists in the downward sinking of the leaflets, the leaflets becoming at the same time somewhat folded on themselves in the genus *Oxalis*; in *Averrhoa* the leaves simply hang vertically downwards. Among the Leguminosæ the leaflets, in some cases, simply sink vertically downwards (Phaseoleæ); in others, they sink down whilst the main petiole rises (terminal leaflet of *Desmodium*, *Acacia Farnesiana*); in others, they sink downwards and twist on their axes so that their upper surfaces are in contact beneath the main petiole (*Cassia*); in others, again, they rise and bend backwards towards the insertion of the petiole (*Coronilla rosea*); in others, they rise, and the main petiole rises also (*Lotus*, *Cytisus*, *Trigonella*, *Medicago*), whereas in *Mimosa pudica* the leaflets rise and bend forwards, whilst the main petiole falls; in some, finally, the leaflet (*Melilotus*) or the whole leaf (*Lupinus*) turns through an angle of 90° so that its surfaces are vertical. The sleep-movement of the leaflet of *Phyllanthus Niruri* resembles that of *Cassia*: the leaves of *Porlieria hygrometrica* sink downwards: those of *Thalia dealbata* and *Maranta arundinacea* (Cannaceæ) rise up: in the Grass *Strepium floribundum*, the leaves on the upright shoots rise up at night, whereas those on the horizontal shoots twist through an angle of nearly 90° so that the tips point towards the apex of the shoot the surfaces being vertical: in *Marsilea* the leaflets rise up, the two upper leaflets being embraced by the two lower. (See Darwin.)

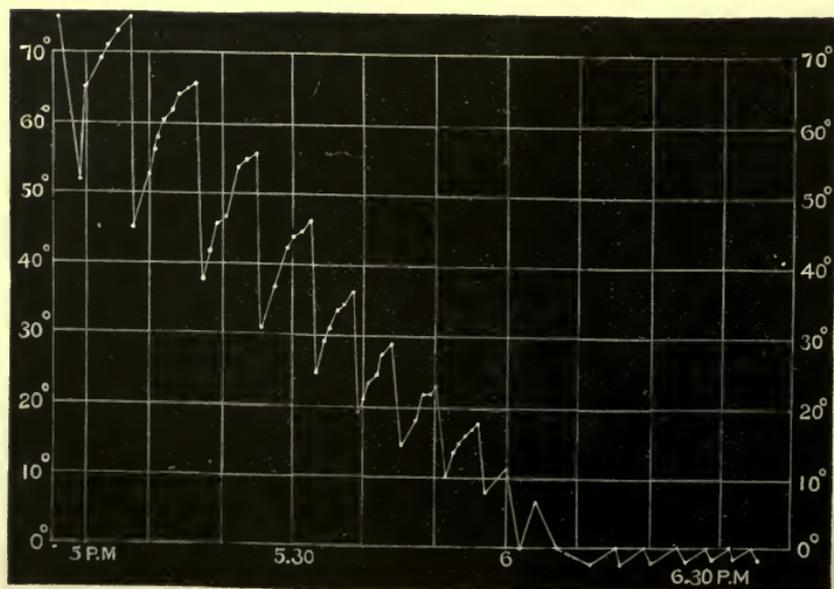


FIG. 58 (after Darwin). Tracing of the nyctitropic movement of a leaflet of *Averrhoa bilimbi*.

The accompanying tracing illustrates the downward sleep-movement of a leaflet of *Averrhoa bilimbi*. It will be seen that the fall is not continuous, but that it is interrupted by rises, so that the lines traced is a zig-zag. These secondary rises are due to the spontaneous movements of the leaflet.

Inasmuch as the movements which depend upon the alternation of day and night have been more especially studied in the Sensitive Plant (*Mimosa pudica*), it will be well to describe them as they occur in this plant. The leaf is bipinnate: the primary petiole is articulated to the stem by a pulvinus, as are also the secondary petioles to the primary, and the leaflets to the secondary petioles. Beginning, now, the observation of the changes in position of the leaf, we find that in the middle of the day the primary petiole of a vigorous and fully developed leaf, makes an acute angle, not much smaller than a right angle, with the internode above its insertion; at the same time the secondary petioles are widely divaricated and the leaflets are fully expanded. In the course of the afternoon the main petiole slowly sinks, so that the angle which it makes with the internode above its insertion increases to a right angle or even to an obtuse angle. As darkness comes on the leaflets fold upwards and forwards in pairs, and the secondary petioles approach each other so as to become nearly parallel; this is followed by a sudden fall of the main petiole so that it now makes a large obtuse angle with the internode above its insertion. This is the nocturnal position. It was thought that the leaf retained this position throughout the hours of darkness, but the researches of Bert, Millardet, and Pfeffer have shewn that this is not the case. After having sunk during the first hours of the night, the primary petiole slowly rises until it forms a highly acute angle with the internode above its insertion; at the same time the secondary petioles gradually separate and expand. With the morning light, the leaflets open, and the main petiole sinks down during some hours until it gains the nearly horizontal direction in which it remains during the middle of the day, and which is characteristic of the diurnal position of the leaf.

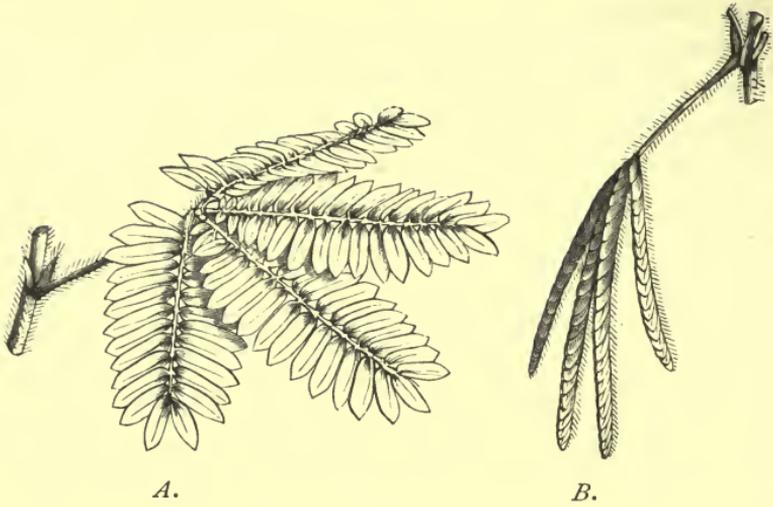


FIG. 59 (after Duchartre). *A*, leaf of *Mimosa pudica* in the diurnal position; *B*, in the nocturnal position.



FIG. 60 (after Darwin). *A*, Leaves of *Hedysarum (Desmodium) gyrans*, in the diurnal position; *B*, in the nocturnal position.

It will be observed that the primary petiole has a complete daily period of this kind, that from dawn to evening it sinks, and rises from evening to dawn. Millardet has shewn that this periodicity of movement of the primary petiole stands in direct relation to the daily periodicity of tension in the plant (p. 406), just as is the case with the daily period of growth in length (see p. 408). He finds, namely, that the maximum tension occurs just before dawn, and the minimum early in the evening, the tension decreasing during the day, and increasing during the night. The time of maximum tension coincides with the most elevated position of the primary petiole; and as the tension diminishes during the day, so the primary petiole sinks downwards. There is, however, an apparent discrepancy in that whereas the tension begins to increase early in the evening, the primary petiole sinks rapidly during the first hours of the night. This discrepancy is, as Pfeffer has clearly shewn, only apparent and not real. The rapid fall of the primary petiole at this period is due to the increased mechanical moment of the secondary petioles and their leaflets when they have assumed their nocturnal position, in consequence of which the primary petiole is bent downwards. When the secondary petioles are removed, the primary petiole does not perform this downward movement, but begins to rise as the tension increases. When the leaf is entire the primary petiole is only able to raise the weight of the secondary petioles and leaflets when the tension has increased considerably above the minimum, and its rise is then assisted by the gradual separation of the secondary petioles which is also a result of the increased tension. This relation between the tension of the tissues and the daily movement of the leaves has only been investigated in the case of the Sensitive Plant, but it doubtless exists in all cases.

The daily periodicity of movement thus induced by the normal variations in the intensity of light during the twenty-four hours, makes itself apparent for a time after the plant has ceased to be exposed to them, either, by being kept in darkness or by being exposed to continuous light. Thus

Sachs observed, in the case of *Mimosa*, that the daily period persisted for four days in darkness, and similar observations have been made by Bert. The movements, however, gradually become irregular, owing to the manifestation of the spontaneous movements. When the plant is kept in darkness the leaves eventually become rigid, but when continuously illuminated the spontaneous movements continue without any apparent diminution of amplitude.

We are now in a position to consider the fact, to which allusion was made above, that the spontaneous movements are, as a rule, either arrested or much diminished in amplitude under normal conditions of illumination. The daily periodicity of movement is, as it were, so forcibly impressed on the plant that it leads to the more or less complete obliteration of the spontaneous movement. The reason why the lateral leaflets of *Desmodium gyrans* continue their movements actively at all times is that they are apparently not sensitive to variations in the intensity of light, for, as Darwin points out, they do not sleep.

Variations of temperature act as stimuli, though not very powerfully, in inducing movements. Pfeffer remarked that a sudden change from a temperature of 18° to 20° C. to one of 30° to 31° C. caused the leaflets of *Oxalis Acetosella* to sink through 80° in the course of half-an-hour. So marked a result was, however, only attained when the effect of the variation of temperature coincided with the phase of the daily period, that is, when it was made in the afternoon or evening. When made in the morning the variation of temperature produced a much smaller fall, usually not more than 10° or 15°. The same effect was produced by a gradual rise of temperature. According to Millardet a rise of temperature causes the main petiole of *Mimosa* to rise, and a fall causes it to sink: the effect of a variation of temperature in either direction on the leaflets is to cause them to close.

Some of these motile leaves or leaflets, such as those of the Oxalidaceæ and the Leguminosæ, notably those of the Sensitive Plant, are sensitive to mechanical, electrical, or

chemical stimuli. Not all motile leaves, however, are thus sensitive, as is clearly seen in the case of the lateral leaflets of *Desmodium*. The effect of such a stimulus is to cause the leaves or leaflets to take up a position closely resembling the nocturnal position, though, as we shall see, the mechanism in the two cases is different. Some organs which do not exhibit spontaneous movement, and are not affected by variations in the intensity of light, are sensitive to stimuli of this kind: instances of this are afforded by the stamens of the *Cynareæ*, of *Berberis*, of the *Cistineæ*, of *Sparmannia*, the style of *Goldfussia anisophylla*, the lobes of the stigma of *Mimulus*, *Martynia*, *Bignonia*, and others, the tentacles on the leaf of *Drosera*, the blade of the leaf of *Dionæa*, of *Aldrovanda*, and of *Pinguicula*. The effect of stimulation on the stamens of the *Cynareæ* is to cause them to shorten (Pfeffer): the stamens of *Berberis* rise up from their nearly horizontal position so that the anther comes into contact with the stigma: the effect of a stimulus on those of *Sparmannia* and of the *Cistineæ* is, on the contrary to cause them to bend outwards and downwards towards the petals: in both cases the stamens slowly regain their original position (Morren). Stimulation causes the curved style of *Goldfussia anisophylla* to straighten itself, or even to bend over in the opposite direction (Morren). The stigmas of *Mimulus*, *Martynia*, *Bignonia*, etc., are bilabiate, and the effect of stimulation is that the two lips close together. The marginal tentacles of *Drosera* curve inwards towards the centre of the leaf on being stimulated: the two halves of the leaf-blade of *Dionæa muscipula* fold upwards and meet, as do also those of the leaf of *Aldrovanda vesiculosa*: the margin of the leaf of *Pinguicula* curves inwards.

The nature and the degree of the sensitiveness are by no means the same in all these cases. In most *Oxalidaceæ* and *Leguminosæ* movement can only be induced by violent shaking, whereas, in some, such as *Mimosa pudica* and *Oxalis sensitiva*, a touch suffices. A very slight touch also suffices to induce movement in the sensitive floral organs, and in the leaves of *Dionæa* and *Aldrovanda*. In the other insectivorous plants

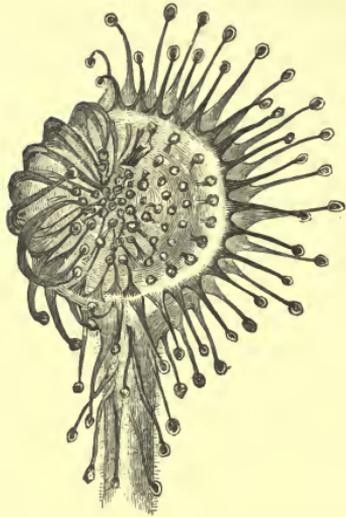


FIG. 61 (after Darwin). Surface-view of leaf of *Drosera rotundifolia* with marginal tentacles of one side inflected.

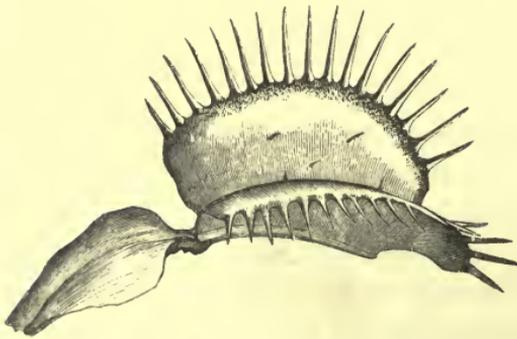


FIG. 62 (after Darwin). Leaf of *Dionaea muscipula* open.



FIG. 63 (after Kurtz). Portion of a transverse section of the leaf-blade of *Dionaea muscipula*, with a sensitive hair on the inner surface of one lateral half of the blade.

a single touch is not sufficient, as appears from Darwin's observations. Thus, a tentacle of *Drosera* requires to be touched several times before any movement occurs, and reacts better under the continued contact of some small body; the incurving of the margin of the leaf of *Pinguicula* is only induced by placing small objects on it. These organs are remarkable for their ready reaction to chemical stimuli. The tentacles of *Drosera*, for instance, are caused to inflect much more rapidly when the bodies placed on the leaves are such that they contain some nitrogenous substance which can be absorbed by the plant, such as pieces of raw meat, of hard-boiled eggs, fragments of insects. For example, a small piece of raw meat placed on the gland of a tentacle caused inflexion in five or six minutes, whilst with a piece of cinder the shortest time of inflexion was 3 hours and 40 minutes. Drops of nitrogenous liquids, such as milk, solution of albumen, of urea, infusion of raw meat, or of peas or cabbages, cause rapid and well-marked inflexion; this effect is produced also in a remarkable degree by dilute solution of salts of ammonia applied either to the glands of the marginal tentacles or to the disc of the leaf-blade. In some cases the application of a nitrogenous substance caused an incurvation of the margin of the blade as well as inflexion of the tentacles. Similarly, the application of organic nitrogenous substances, such as pieces of meat and fragments of insects, or drops of nitrogenous liquids caused more rapid and more marked incurvation of the margins of the leaf of *Pinguicula* than when other substances were employed. And not only do these nitrogenous substances give rise to more active movements, but the new position induced by them is maintained for a much longer time than when other substances are employed. Ammonia gas is one of the most powerful chemical irritants; exposure to it induces movement in all irritable motile organs.

In many of these organs it can be clearly observed that the stimulus is transmitted from one part to another. Thus if the terminal pair of leaflets of a pinna of the leaf of the Sensitive Plant be irritated, not only will they fold up, but

each of the other pairs of leaflets of the same pinna will fold up in succession: if the stimulus is sufficiently strong its effect may extend to other pinnæ causing their leaflets to fold up, or even to the main petiole which then sinks downwards. Stimulation of one leaf, if sufficiently powerful, will cause movement in another. In the case of *Drosera*, Darwin ascertained that stimulation of the central tentacles of a leaf eventually causes the inflexion of the marginal tentacles, and that the stimulus travels more readily longitudinally than transversely through the leaf. Morren observed also in *Sparmannia africana* that stimulation of one stamen causes the others to move. In *Dionæa* the stimulation of one half of the lamina causes both halves to close.

In some cases the irritability to contact is especially localised in particular parts of the organ. Thus, in *Mimosa pudica*, no movement ensues if the upper side of the pulvinus of the primary petioles is touched, but only when the sensitive hairs on the under side of the pulvini are touched; and, in the leaflets, it is the upper surface which is sensitive; in more general terms, that side is sensitive towards which the movement consequent on stimulation takes place. In *Drosera* the irritability of the tentacles is localised in the terminal gland; tentacles deprived of their glands are not irritable, as Darwin ascertained. In *Dionæa* movement only ensues when the irritable hairs on the upper surface are touched.

We have now to consider the conditions of irritability. In the first place, a supply of free oxygen is essential. Dutrochet observed that the leaves of *Mimosa pudica* lose their irritability *in vacuo*, an observation which Kabsch confirmed and extended to the stamens of *Berberis* and *Helianthemum*. Kabsch also ascertained that these stamens lose their irritability in an atmosphere of nitrogen, hydrogen, or carbon dioxide. Darwin observed that an atmosphere of carbon dioxide had a paralysing effect on the tentacles of *Drosera*. Secondly, the temperature must be suitable. According to Sachs the leaves of *Mimosa* lose their irritability when kept for some hours in air at a temperature of 15° C., and within

half-an-hour in air at 45° C. Thirdly, in the case of motile organs containing chlorophyll, such as foliage-leaves, exposure to light is essential. From the observations of Sachs, and Bert, it appears that the leaves of *Mimosa* cease to be irritable when kept in darkness for two or three days, the leaflets losing it earlier than the petioles; irritable stamens, on the contrary retain their irritability in darkness. The irritability of motile leaves, like that of growing leaves (p. 380), is clearly dependent upon phototonus. It appears, from Bert's observations on the Sensitive Plant, that the rays of low refrangibility (red-yellow) are those which are most favourable to the phototonic condition, whereas green light causes a loss of irritability almost as rapidly as darkness. He exposed plants to white, red, yellow, green, violet, and blue light, and he found that at the end of twelve days the plants in the green light had entirely lost their sensitiveness, whereas all the others were highly sensitive and remained so for many weeks. With regard to the relative value of the other colours Bert's results are not definite inasmuch as the glasses which he used were by no means monochromatic. Lastly, a supply of water is necessary. Sachs observed that a *Mimosa* left unwatered for a considerable time lost its irritability, and Darwin mentions that the leaves of a plant of *Porlieria hygrometrica* left unwatered ceased to perform their daily periodic movements, the leaflets remaining partially or completely closed during the day.

Irritability is also temporarily destroyed when the motile organs are exposed to the action of chloroform or ether, and this appears to be true, so far as the observations go, of other anæsthetics. This has been observed in the case of *Mimosa* by Bert and by Pfeffer, and in the case of the stamens of *Berberis*, *Mahonia*, the *Cynareæ* and *Cistineæ*, the stigmas of *Mimulus*, *Martynia*, etc., by Heckel. Heckel also ascertained that a solution of morphia (1·0 per cent.) acts on the stamens of *Berberis*. After exposure to ether Darwin found the leaf of *Dionæa muscipula* did not move when the sensitive hairs were touched, but it did so when the tip of it was cut off. It appears that the sensitiveness of the leaf was much

diminished since so powerful a stimulus was needed to make it close.

Bert seems to be mistaken in asserting that under the influence of chloroform a stimulated leaf of *Mimosa* is arrested in the position, which it assumes on stimulation, for Pfeffer, on repeating the experiment, found that under these circumstances, the primary petiole slowly rises although the leaf may have become quite insensible to touch under the influence of chloroform.

Another means by which irritability is diminished or abolished is repeated stimulation. This has been observed by Bert and by Pfeffer in the case of *Mimosa pudica*. When the primary petiole is first stimulated it sinks, and then rises, although the stimulation is continued, quite as rapidly as under normal conditions. The pulvinus is, however, now insensible, and a fall of the petiole on stimulation can only be induced after a period of rest of from five to fifteen minutes. The interval between the stimuli, in order that the condition of fatigue may be thus induced, must be very short, the shorter the more irritable the condition of the plant: with imperfectly irritable plants Pfeffer found that the interval might be as long as two minutes. If, however, a sufficient time be allowed to elapse between each stimulation to permit the leaf to regain its irritable condition, it appears that stimulation an indefinite number of times will be followed by movement.

The effect of anæsthetics or of repeated stimulation in destroying irritability are purely local. When one leaf of a *Mimosa* is exposed to the action of chloroform or ether, that leaf alone is affected, the other leaves remaining irritable, and this is true also of the repeated stimulation of one leaf. Burdon-Sanderson states that when in consequence of repeated stimulation any one of the sensitive hairs on the leaf of *Dionæa* has lost its irritability, the movements of the leaf may be induced by stimulation of another hair.

In some cases not only is irritability destroyed by these conditions but, as mentioned above, the organ passes into a completely immotile state under prolonged exposure to them.

This has been ascertained with regard to extremes of heat and cold, darkness, and drought in the case of *Mimosa pudica*. The position of the immotile leaf is peculiar and is worthy of note. It somewhat resembles the diurnal position; but the main petiole is horizontal, instead of being directed obliquely upwards, and the leaflets are incompletely expanded, but the secondary petioles are divaricated. The first effect upon the leaf is that it loses its irritability to mechanical stimulation; then its daily periodic movement ceases; and finally its spontaneous movement is arrested. The evidence as to the effect of anæsthetics is somewhat conflicting. Bert states that the spontaneous movements of *Mimosa* are not arrested by chloroform or ether, but it appears that by "spontaneous movements" he means the periodic movements induced by the daily variations in the intensity of light. Heckel found that the spontaneous movements of the stamens of *Ruta* were not arrested by chloroform, but it is not clear that the movement of these stamens belongs to the category of movements of variation; it is more probably a movement of growth. On the other hand Kabsch states that he observed an arrest of the movement of the lateral leaflets of *Hedysarum* under the influence of chloroform.

The foregoing are not, however, all the manifestations of irritability exhibited by motile organs. Motile foliage-leaves are sensitive also to those influences which determine the position of growing leaves, namely, to the direction of the incident rays of light and to gravity. With regard to the former, it has long been known that the motile leaves of many Leguminosæ and Oxalidaceæ when exposed to light of moderate intensity place themselves so that their upper surfaces are perpendicular to the direction of the incident rays. We have here then additional instances of *Diaheliotropism*. When, however, these leaves are exposed to bright sunlight they assume such a position that their surfaces are parallel to the direction of the incident rays. This movement has long been known as the "diurnal sleep" of leaves, and Darwin terms it *Paraheliotropism*. This position, however, differs widely from the nocturnal position. Thus, according

to Darwin, under the influence of bright sunlight the leaflets of *Robinia* rise up, instead of sinking down as they do at night: the leaflets of *Amphicarpæa monoica* twist so as to turn their edges to the sun, whereas at night they sink down vertically; those of *Mimosa albida* twist in a similar manner instead of enfolding each other as they do at night. These cases are clearly analogous to those of the leaves of the Compass-plants and others which, under the influence of full exposure to bright sunlight, assume, in the course of their growth, a position such that their surfaces are in a vertical plane (p. 446).

The sensitiveness of motile leaves to the action of gravity can be readily observed by hanging a plant possessing them upside down in the dark. If this be done with *Mimosa pudica*, for instance, it will be seen that the primary petioles raise themselves so as to form an acute angle with the internodes which, in the normal position, are below them. The primary petioles are clearly negatively geotropic. This upward movement is accompanied usually by a twisting either of the primary or of the secondary petioles which brings the leaflets into such a position that their normally upper surfaces are again directed towards the zenith. The leaf-blade of *Mimosa* appears, then, to be diageotropic. Pfeffer, however, does not accept this view, but regards the twisting which brings the leaf-blade into its normal position with reference to the vertical as a purely mechanical phenomenon. The normal position of the leaf-surfaces is the position of stable equilibrium of the leaf; when the leaf is reversed it is brought into a position of unstable equilibrium, and the result is twisting until the position of stable equilibrium is again obtained. He observed in the case of a leaf of *Phaseolus* that, the plant lying horizontally, there is no torsion of the petiole when the lamina is cut off, but that torsion at once ensues when the lamina is replaced by a piece of paper of about the same weight. The views held with regard to the diageotropism of motile leaves stand in the same relation to each other as those respecting that of growing dorsiventral organs (p. 473), and all that can be said is

that more experimental evidence must be forthcoming before it is possible to decide between them.

In conclusion, the general mechanism of the movements of variation may be briefly alluded to. The fundamental fact to be apprehended is this, that all these movements depend upon variations in the turgidity of the cells of the motile organs. When the organ simply shortens, as in the case of the stamens of the *Cynareæ*, it is because the turgidity of all the cells has diminished. When the organ performs an up and down movement, as is the case, for instance, in motile foliage-leaves, it is because the relative turgidity of the upper and lower halves of the pulvinus varies; when the organ moves up, the lower half of the pulvinus is more turgid than the upper, and conversely, when it moves down, the upper is more turgid than the lower. The details of the mechanism will form the subject of the next lecture.

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LECTURE XXI.

IRRITABILITY (*continued*).

The Mechanism of the Movements.

WE have now concluded our description of the movements of plants, whether spontaneous or induced, whether performed by mature or by growing organs. In the course of the description the mechanism of the movements has been incidentally alluded to, but now it will be fully discussed, though some portion of this lecture will be devoted to the consideration of the biological significance of the movements and of the peculiar forms of irritability of which they are the expression.

With regard to the mechanism of the movements of locomotion of motile organisms, with which we will begin, all that can be said is that whether the movement be amoeboid or ciliary, it depends upon that fundamental property of protoplasm which was mentioned in the first lecture, namely *contractility*. What contractility really is we do not know; all that we know are the manifestations of it. It must be borne in mind that our conception of this property of protoplasm, and the very name we give it, is based upon the phenomena presented by the most highly differentiated contractile protoplasm, the striated muscular fibre of animals. The fibre, on stimulation, shortens, and at the same time thickens to about an equal extent; hence it is said to contract. But it must not be assumed that the effect of stimulation upon all forms of contractile protoplasm will be precisely this, nor must we limit the term contraction

merely to this particular phenomenon. The throwing out of a pseudopodium by an amœboid zoospore, the formation of a protuberance of the ectoplasm into which the more fluid endoplasm is, as it were, sucked, is a phenomenon of contraction. So is also the lashing of a cilium whether, as some suppose, the contraction takes place in the cilium itself, or, as others suggest, in the cell bearing it.

Little as we know about the mechanism of the locomotory movements of ciliated or amœboid organisms, we know even less as to the mechanism of the streaming-movement of protoplasm. It appears to be allied to the amœboid movement, and, like that, to be a manifestation of contractility.

The phenomena presented by contractile vacuoles are of great physiological interest, though their mechanism is imperfectly understood. With regard to the sudden systole, it is not clear whether it is due to an active contraction of the protoplasm, or merely to elastic recoil; but it seems probable that the former is the case, for Cohn has observed that the vacuoles of *Gonium* and *Chlamydomonas* remain as clear spaces when the zoospores are mounted in glycerin, under conditions, that is, which render any pressure of the contained liquid on the wall impossible.

We come now to the movements of organs consisting of one or more cells clothed with a cell-wall. The structure of the cell or cells concerned in the movement is that which has already been described more than once: there is, namely, an extensible and elastic cell-wall, lined by a layer of protoplasm, enclosing a vacuole filled with cell-sap, and we have to ascertain how a movement can be performed by such an organ.

We will begin with instances of movement which admit of direct observation, and will then pass to others which, from the nature of the case, cannot be so readily investigated. Such instances are afforded by the movements performed by mature organs in response to a mechanical or electrical stimulus. It was pointed out in the last lecture (p. 545) that the effect of stimulation on the stamens of the

Cynaræ is to cause shortening of the filament. The movement of the filament on stimulation bears a superficial resemblance to the contraction of a muscular fibre, but it is in reality an altogether different process. The contraction of a muscular fibre is accompanied, as mentioned above, by a thickening, so that the total bulk of the fibre is not perceptibly altered; but the shortening of the staminal filament is, as Pfeffer has clearly shewn, unaccompanied by any appreciable thickening, so that the bulk of the filament is considerably diminished, and is not due, as Unger thought, merely to a change in form of the cells. Pfeffer has ascertained that the diminution in bulk of the filament as a whole is the result of the diminution in volume of its constituent parenchymatous cells. Each cell, on stimulation, parts with a portion of the water which it contains, so that from being turgid it becomes flaccid; and, inasmuch as the cells are scarcely at all expanded in the tangential direction, the effect of the loss of water is to cause them to shorten. The escape of water, on shortening, from the parenchymatous cells into the intercellular spaces, is not infrequently manifested by the appearance of a drop of water at the cut surface of a filament, an effect which is always produced when the intercellular spaces of the filament have been previously injected with water. The mechanism of the movement is then this: when the filament is at rest the cells are turgid, and their elastic cell-walls are on the stretch; on stimulation the escape of water from the cells is rendered possible, and the cells consequently become relatively flaccid and shorten.

In the other cases of movement induced by mechanical or electrical stimulation, one side only of the organ is affected; the result is that, instead of a shortening of the whole organ, an up or down movement is performed; but the mechanism is essentially the same. Thus, in the case of the stamens of *Berberis*, it is the upper or inner surface of the filament which alone is irritable, and it is the corresponding half of it which loses its turgidity on stimulation. The mechanism of the movement is briefly this: the turgidity of the cells of the inner longitudinal half of the filament

being suddenly abolished, there is nothing to oppose the pressure exercised by the turgid cells of the outer longitudinal half, consequently the filament moves upwards and inwards. In this case also there is evidence that the irritable cells give up water on stimulation, for a drop of water appears at the cut surface of a filament, though, inasmuch as there are no intercellular spaces it is not clear how exactly the water travels.

The mechanism of the movements of the leaf of *Mimosa pudica* on stimulation is essentially the same as that of the stamens of *Berberis*. With regard first to the movement of the primary petiole. From his observation that when he removed the lower half of the pulvinus the petiole remained directed almost vertically downwards, Lindsay concluded that the depression of the petiole on stimulation is due to an increase of the pressure of the upper half. This conclusion, which was held also by Dutrochet and by Burnett and Mayo, was shewn by Brücke to be erroneous. It is clear that if Lindsay's view be correct, stimulation of the pulvinus must be accompanied by an increased turgidity of its cells, and therefore also by an increased rigidity of the whole organ. Brücke's observations, however, clearly prove that this is not the case. He found, namely, that, on stimulation, the rigidity of the pulvinus is markedly diminished, that stimulation induces flaccidity and not turgidity, and that therefore the fall of the petiole which follows on stimulation of its pulvinus is due, not to an increase of the downward pressure of the upper half of the organ, but to the abolition of the turgidity, and with it the upward pressure, of the lower half of the organ.

Brücke's method of estimating the rigidity of the pulvini has been so universally adopted in experiments with *Mimosa* that it is important to describe it. The plant is placed in such a position that the petiole to be observed is horizontal, and then the angle is measured which the petiole makes with the internode below its insertion. The plant is then turned upside down, the petiole under observation is again brought into a horizontal position, and the angle which it now makes with the same internode is measured. Inasmuch as the pulvinus is not perfectly rigid the two angles are not the same; the difference between them indicates

the extent to which the pulvinus is flaccid, so that calling the angles respectively a and a_1 , a_1 being greater than a , the flaccidity of the pulvinus is represented by $a_1 - a$. If now the same measurements be made after stimulation, it will be found that the difference between the two angles, which we may now term β and β_1 respectively, is greater than that between a and a_1 , that is, that the flaccidity of the pulvinus has increased. The following is an example of Brücke's observations.

$$\begin{array}{r} a_1 = 150^\circ \\ a = 136^\circ \\ \hline a_1 - a = 14^\circ \end{array} \qquad \begin{array}{r} \beta_1 = 120^\circ \\ \beta = 80^\circ \\ \hline \beta_1 - \beta = 40^\circ \end{array}$$

With regard to the nature of the changes induced in the cells of the lower half of the pulvinus, Lindsay observed that, on stimulation, this portion of the organ assumes a deeper colour. Brücke suggested that this change of colour is due to a replacement of the air in the intercellular spaces by water which has been driven out of the irritable cells, a view which is fully confirmed by Pfeffer who has further observed that, on stimulating the pulvinus of a petiole which has been cut off short, an escape of water at the cut surface may be observed under appropriate conditions. Further evidence, if any is needed, that currents of water are set in motion in the pulvinus in consequence of stimulation, is afforded by the electrical phenomena, described in a previous lecture (p. 324), to which stimulation gives rise. There can be little doubt that the positive variation of the normal current is due to electrical disturbances set up by the travelling of the water through the tissue.

The mechanism of the induced movements of the primary petiole of *Mimosa* is then this, that, on stimulation, the parenchymatous cells of the lower, irritable, half of the pulvinus give up water, so that they become flaccid and no longer exercise an upward pressure; consequently the petiole sinks down, partly under the downward pressure of the still relatively turgid cells of the upper half of the pulvinus, and partly under the weight of the secondary petioles and leaflets. This is also, *mutatis mutandis*, the mechanism of the induced movements of the secondary petioles and of the leaflets, and probably not of these only but of all induced

movements of motile organs whatsoever. Thus, in the case of the leaf of *Dionæa*, there is evidence that stimulation sets up currents of water. It was mentioned, when we were discussing the electrical phenomena presented by plants, that stimulation of the leaf of *Dionæa* is followed by a well-marked positive variation of the normal electrical condition of the upper and lower surfaces of the leaf, which indicates that currents of water are travelling from the upper towards the lower surface. It is worthy of note that this electrical disturbance is not dependent upon the actual movement, but only on stimulation: it is well marked when the stimulated leaf is mechanically prevented from moving.

Such being the effect on the motile organ of the action of a stimulus, the process of recovery must consist in the restoration of the turgidity of the flaccid cells by the absorption of water, accompanied by a gradual assumption of the position occupied before stimulation. The process of recovery is slow and gradual, as may be easily observed by stimulating a leaf of *Mimosa* and noting the time which elapses before it regains its original position. In the case of the primary petiole it will be observed that the upward movement begins almost immediately after the fall on stimulation, and that the time occupied in regaining the normal position is about twenty or twenty-five minutes.

In endeavouring to penetrate into the intimate mechanism of the movements of variation, the question which at once arises is as to how exactly the sudden abolition of the turgidity of the irritable cells which stimulation induces is brought about, and here we find ourselves face to face with the real difficulty of the subject. Let us call to mind what the factors of the turgid condition are, and then endeavour to determine which of them is affected on stimulation. The factors, as we learned in a previous lecture (p. 42), are three: the osmotically active substances in the cell-sap: the elasticity of the cell-wall: the resistance to the escape of the cell-sap offered by the layer of protoplasm lining the cell-wall.

Taking, now, these factors one by one, if we assume that the stimulus affects the first of them, we must conceive, as

Pfeffer suggests, that the osmotically active substances are destroyed, or that they are converted into substances of lower osmotic activity, and that the attraction by which the water is held in the vacuole being thus diminished, a portion of the water of the cell-sap is forced out by the pressure of the elastic cell-wall. Such a conception is not, however, easy of comprehension. The escape of liquid from a cell by filtration under pressure has surely nothing to do with the osmotic properties of the liquid. Were the escape of the liquid from the cell due to osmosis, were it attracted into other cells, then such a change in the quantity or quality of the osmotically active substances would render possible the removal of a portion of it. But this is not so. The liquid, in most cases at least, escapes by filtration under pressure into the inter-cellular spaces which contain air. The retention of the liquid in the vacuole, or its escape from it, whatever the osmotic properties of the liquid may be, is simply dependent on the relation between the pressure of the elastic cell-wall on the one hand, and the resistance to filtration under pressure offered by the primordial utricle on the other. It is easy to understand that, owing to the high osmotic activity of substances in the cell-sap, so much water may be absorbed into a cell that the pressure of the cell-wall may exceed the resistance to filtration offered by the primordial utricle, and so an escape of a portion of the cell-sap takes place; this occurs, as a matter of fact, in the parenchymatous cells of roots when absorption is active (p. 94); but it is not possible to realise how a diminution in the attraction of the cell-sap for water can bring about this result. This conception involves the further assumption that the liquid which escapes from the cells of a stimulated motile organ is pure water, an assumption which is not justified by the evidence. Pfeffer makes it on the ground that a stamen injected with water and lying in water regains its turgid irritable condition on being stimulated, arguing that had any osmotically active substances been given out by the cells on shortening they must have been removed by the surrounding water, and that, had they been so removed, the recovery of turgidity would

have been impossible. There is, on the face of it, no reason whatever to believe that when a portion of the cell-sap of a cell is forced out of it by pressure, that that portion should consist of pure water, and as to the fact which Pfeffer brings forward in support of his view, it may be equally well accounted for by the assumption that osmotically active substances may have been formed in sufficient quantity in the cells to make good the loss and to restore the cells to their turgid condition. In fact, there is some reason to believe that one of the effects of stimulation is to lead to the formation of osmotically active substances. From these considerations it is clear that the case has not been made out in favour of the view that the effect of stimulation on a motile organ is to destroy the osmotically active substances in the sap of its cells, or to diminish their osmotic activity.

If we assume, now, that the effect of stimulation is to lead to an increase of the pressure of the cell-wall upon the cell-contents, it is clear that can only be brought about by an increase in the rigidity of the cell-wall. Such a suggestion is, in itself, improbable, and it is at once put out of the question by Pfeffer's observation that, in the case of the stamens of the *Cynareæ*, the extensibility of the cell-walls is the same in both the expanded and contracted states of the filament.

Since the action of the stimulus is not to be traced either to the liquid cell-contents or to the cell-wall, we can only assume that it is the protoplasm which is affected, an assumption which, considering that the irritability of protoplasm is a well-established fact, is by no means hazardous. We have then to ascertain if any changes are induced in the protoplasm of the cells of a motile organ by stimulation, and, if so, what the nature of these changes may be.

No visible changes have been described as taking place in the protoplasm of the cells of any of the motile organs which we have been considering, but such changes have been described as taking place in the cells of the tentacles of *Drosera*. Attention was first drawn to this subject by Darwin, who designated by the term "aggregation" the changes induced in these cells by mechanical or chemical

stimulation, and who described it as follows: "the cells, instead of being filled with homogeneous purple fluid, now contain variously shaped masses of purple matter, suspended in a colourless or almost colourless fluid." Darwin came to the conclusion that the "masses of purple matter" consist of protoplasm, a view which, though rejected by Cohn, who considered that these bodies consisted of cell-sap, was re-asserted by F. Darwin. Schimper's observations, and those of Gardiner, place it beyond doubt that Cohn's view is the correct one. From Gardiner's observations it appears that the process of aggregation takes place in the following manner: the colourless protoplasm swells up very considerably by taking up water from the cell-sap, and, in consequence of this removal of a portion of its water, the tint of the cell-sap becomes deeper: then the rate of rotation of the protoplasm becomes much more rapid, with wave-like elevations making their appearance on the internal free surface of the endoplasm; this leads to a churning up, as it were, of the cell-sap, which becomes distributed in drops of various form throughout the protoplasm, these drops subsequently becoming rounded as the rate of rotation diminishes. This change in the condition of the protoplasm of its cells is accompanied, as Darwin ascertained, by flaccidity of the tentacle, so that probably water escapes from the cells in the process of aggregation.

Gardiner has observed in the stalk-cells of the tentacle of *Drosera* and in the mesophyll-cells of *Dionæa* a spindle-shaped or acicular body which he terms the *plastoid* or *rhabdoid*. It appears to be protoplasmic, and, in the resting state of the cells, it stretches diagonally across the cell, its two ends being embedded in the protoplasm. When the tentacle is stimulated, this body tends to become spherical. This change in form of the rhabdoid does not take place when the cell is plasmolysed. It is not clear what the significance of this body is, but it clearly affords an indication of the state of the protoplasm. From the behaviour of the rhabdoid it appears that stimulation induces a change in the protoplasm which leads to a diminished turgidity; but that this change is not induced when the turgidity of the cell is diminished by plasmolysis, for then the rhabdoid does not change its form.

The tentacles of *Drosera* afford us, then, an instance of a loss of turgidity which is brought about by changes in the protoplasm of the cells. But we have yet to determine

whether or not there exists any relation between these changes in the protoplasm of the stalk-cells and the movement of the tentacle, that is, whether or not the occurrence of aggregation in the stalk-cells is an essential condition of the inflexion of the tentacle. Darwin, it is true, states definitely that aggregation may take place without inflexion; but naturally no movement can take place, except a shortening like that of the filaments of the *Cynarææ*, if all the cells of the tentacle undergo aggregation simultaneously. He does not, however, express himself definitely as to the possibility of inflexion without aggregation, though he incidentally mentions, when speaking of the action of acids on the tentacles, that they caused the tentacles to bend without causing true aggregation. Much importance cannot be attached to this observation, inasmuch as most of the acids used proved to be highly poisonous to the plant. From Gardiner's observations it appears that the inflexion of the tentacle on stimulation is due to the occurrence of aggregation in the cells of the concave side, that is, to the abolition of their turgidity.

Without going so far as to assert that a process of aggregation, identical with that induced in the cells of the tentacles of *Drosera*, takes place in the cells of every motile organ when it is stimulated, we may reasonably infer that the protoplasm in the cells of these organs undergoes some molecular change, and in view of the mechanism of the movements, it seems probable that the effect of this molecular change is to diminish the resistance which the protoplasm offers to the escape of the cell-sap by filtration under pressure. It is a further question, and one which it is at present impossible to decide, whether or not the protoplasm, whilst thus becoming permeable, actually contracts upon its contents, like the wall of a contractile vacuole. It is not necessary, for the purpose of explaining the sudden loss of turgidity in the stimulated cells, to assume that the water is forced out by an active contraction of the primordial utricle, for the pressure of the stretched elastic cell-wall is sufficient for the purpose. But it is worth while to bear in mind that

such a contraction may take place. Sachs has drawn attention to a case which tends to establish the possibility of a simultaneous increase of the permeability and a contraction of the protoplasm, namely, the cells of *Spirogyra*. As a preliminary to conjugation the primordial utricle of one of these cells contracts away from the cell-wall, and, since it now encloses a much smaller space than it did before contraction, it is clear that, during contraction, a portion of the cell-sap must have escaped through it.

But whether or not it be admitted that the protoplasm of the cells of a motile organ actually contracts, in the strict sense of the word, in response to a stimulus, we cannot but regard the change, whatever it may be, which the protoplasm undergoes, as a manifestation of that fundamental property of protoplasm which, in the first lecture, we termed contractility. It is, like the contraction of muscular fibre, a molecular change accompanied by electrical and thermal phenomena which indicate an evolution of energy on the explosive decomposition of some complex substance; for we learned in a previous lecture (p. 324) that when the pulvinus of *Mimosa* or the leaf of *Dionæa* is stimulated, there is a distinct negative variation of the normal electrical current as there is when a striated muscle is stimulated; and again (p. 312) that the movement of the petiole of *Mimosa* is accompanied by a rise of temperature, just as is the contraction of a muscular fibre.

We will now briefly consider the recovery of the turgid condition of the cell from this point of view. The first step will be the restitution of that condition of the protoplasm in which it prevents the escape of the cell-sap by filtration under the pressure of the cell-wall, the next, the absorption of water into the vacuole. It is not improbable that, in the chemical decomposition to which we have alluded as taking place in the cell on stimulation, osmotically active substances, such as organic acids, are formed which promote the absorption of water in the process of recovery. Whether or not the protoplasm actively expands, or is simply passively distended in consequence of the absorption of water, is a question which

cannot at present be decided, any more than the question, alluded to above, as to whether or not the protoplasm actively contracts on stimulation. In any case the protoplasm is not wholly passive in the process of recovery. The restoration of its resistance to the filtration of the cell-sap under pressure is, like the loss of it, an active process, and is doubtless dependent upon molecular changes, of a nutritive nature, going on within it.

Taking all these facts and inferences into consideration, we come to the conclusion that the variations of turgidity upon which movement in response to a stimulus depends, are to be attributed to molecular changes in the protoplasm of the cells. We may accept Cohn's dictum that "the living protoplasmic substance, the primordial utricle, is the essentially contractile portion of the cell," but we are not justified in following him when he compares the motile cells of the filaments of the *Cynareæ* to unstriated muscular fibres, and says that "now we know plants which (so to speak) actually possess muscles." We do not know whether or not the protoplasm of these motile cells contracts actively like a muscular fibre; all that the facts before us tend to establish is that the state of aggregation of the protoplasm varies so as to lead to corresponding variations in its resistance to the escape of the cell-sap by filtration under pressure. This being so, it will be perhaps well, in speaking of these phenomena, to use, not the term contractility, but the term motility, suggested in a previous lecture (p. 372).

We may now take up the consideration of the daily periodic movements of motile organs, taking *Mimosa pudica* as our illustrative case. With regard to the primary petiole, we learned in the previous lecture (p. 543) that it has no proper nyctitropic movement, that the fall at night is not the response to the diminution in the intensity of the light, but is the mechanical effect of the nyctitropic change in position of the secondary petioles and leaflets. It might be thought that the fall of the primary petiole in the evening is to be ascribed to the stimulating influence of the diminution in the intensity of the light, inasmuch as the position then assumed bears a

superficial resemblance to that which they take up when stimulated mechanically, but Brücke's observations shew that the condition of the pulvinus is entirely different in the two cases. In the first place, when the petiole has sunk in the evening, it is still irritable and will sink still lower on stimulation, and secondly, the rigidity of the pulvinus is well-marked, whereas, when the petiole has sunk in consequence of stimulation, it will not sink lower on further stimulation, and the rigidity of the pulvinus is much diminished. But we also learned in the last lecture that the primary petiole has a daily periodic movement, and we will now endeavour to understand the mechanism of it. Brücke ascertained that the rigidity of the pulvinus is less during the day than during the night, and it might be concluded from this that the gradual fall of the petiole during the afternoon is simply to be attributed to the diminished rigidity, and the rise during the night to the increased rigidity of the pulvinus. But Pfeffer's observations on the pulvinus of *Phaseolus*, and we may infer that what is true in this case holds good in the case of *Mimosa*, shew that this is not the case. He found, namely, that when either the upper or the lower half of the pulvinus was removed, the petiole rose during the night and sank during the day-time. The significance of these facts is this, that, the fall of the petiole during the day is due to the diminishing turgidity of the cells of the lower half of the pulvinus and to the increasing turgidity of those of the upper half; and conversely, that the rise of the petiole during the night is due to the increasing turgidity of the cells of the lower half of the pulvinus and to the diminishing turgidity of those of the upper half. Inasmuch as the rigidity of the pulvinus is less during the day-time than it is at night, we conclude that the turgidity in the lower half of the pulvinus during the day is less than the gain in the upper half, and conversely, that the gain of turgidity in the lower half during the night is more considerable than the loss in the upper half. Clearly, then, the daily periodic movement of the petiole is not due to uniform variations taking place simultaneously in all the cells of the pulvinus, but to variations of an opposite nature

taking place simultaneously in the cells of its two opposed halves.

The nyctitropic movement of the leaflets of *Mimosa* has been described (p. 541) as a folding upwards and forwards in pairs at night. The state of the pulvinus of the leaflet in the nocturnal position differs from that of the pulvinus of the primary petiole, in that the former has lost its power of movement on stimulation whereas the latter retains it. The cells of the upper irritable half of the pulvinus of the leaflet pass at night into just the same condition as that which is induced by a stimulus; they are flaccid. Whether or not this flaccidity of the cells of the upper half of the pulvinus is accompanied by an increase in the turgidity of the cells of the lower half, we do not know; but in any case the mechanism of the movement is this, that, in the absence of any opposition from the upper half of the pulvinus, the leaflet is raised by the upward pressure of the turgid cells of the lower half. A further peculiarity in the behaviour of the pulvinus of the leaflet is this, that this relative condition of the two opposed halves is maintained until morning, when the turgidity of the cells of the upper half is restored.

The mechanism of the daily periodic movements of motile organs may be briefly stated as variations in the relative degree of turgidity of the two opposed halves of the pulvinus, variations which, in accordance with the conclusions previously arrived at, we ascribe to variations in the molecular structure of the protoplasm of the cells. These variations, moreover, are rhythmical, and are induced by the normal alternation of day and night. In endeavouring to explain the influence of the alternation of day and night in inducing these variations, we must be careful not to regard the effect as immediate. For instance, we must not attempt to explain the movements of the leaflets of *Mimosa* by assuming that the nocturnal flaccidity of the cells of the upper half of the pulvinus is the direct effect of darkness, and that the diurnal turgidity of these cells is the direct effect of light, on their protoplasm. It is the leaflet as a whole which is affected by the variations in the intensity of light to which it is highly

sensitive, and its response to these variations is that it performs movements of opening or closing according to circumstances, the active mechanism of these movements being, as we have seen, variations in the turgidity of the cells of the upper half of the pulvinus. When the variations in the intensity of light occur periodically, as they do under normal conditions, the response of the leaflet becomes rhythmical; the movements of opening and closing are performed at definite intervals. And so deeply does this rhythm become impressed upon the leaflet, that it will continue, as we have seen, to perform its daily periodic movements for some days when kept in darkness.

What is true of the leaflet is true, in the main, of the primary petiole. Because the cells of the upper half of the pulvinus gain in turgidity during the day and lose during the night, and the cells of the lower half lose during the day and gain during the night, we are not justified in assuming that the protoplasm of the cells of the upper half reacts differently from the protoplasm of the cells of the lower half to variations in the intensity of light, as we must assume if we regard the protoplasm as being directly affected by the variations. Such an assumption is altogether inadmissible. It is the leaf as a whole which is affected, and its response to the variations in the intensity of light is such that it sinks downwards during the day and rises during the night, the downward movement being effected by the concomitant increase of turgidity in the cells of the upper half of the pulvinus and decrease in those of the lower half, the upward movement by the concomitant decrease in the turgidity in the cells of the upper half and increase in those of the lower.

It is, from the nature of the case, impossible to ascertain by direct investigation what, precisely, the mechanism of the spontaneous movements of motile organs may be, but we may reasonably infer that it essentially consists, like that of induced movements, in variations in the turgidity in the cells of one or both halves of the pulvinus, and that these variations are likewise dependent upon molecular changes in the protoplasm.

We have now to consider the effect of various external conditions in abolishing the irritability or in arresting the movements of motile organs. It was pointed out in the last lecture (p. 548) that motile organs which are irritable to touch do not respond by a movement to stimulation when they have been exposed to the vapour of chloroform or ether, or when they have been fatigued by repeated stimulation. The condition of the organs under these circumstances is probably the same: their cells, as Pfeffer has shewn, are fully turgid; so that the reason why stimulation is not followed by movement is probably the same in both. From Bert's observation that the daily periodic movements, and probably also the spontaneous movements, of the leaf of *Mimosa* are not arrested by anæsthetics, it is clear that the absence of movement on stimulation is not to be attributed to any interference with the motility of the protoplasm of the organs, but to an abolition of their irritability. Now the manifestation of irritability depends, as we have seen (p. 371), in the presence of readily decomposable substance, and secondly, upon the decomposition of this substance. In the case of the fatigued organ, the loss of irritability is to be attributed to the absence of this readily decomposable substance; in the case of the chloroformed organ, to an inhibition of its decomposition. This mode of regarding the effect of anæsthetics is supported by Darwin's observation, which was mentioned in the last lecture, that, after exposure to the vapour of ether, the leaf of *Dionæa muscipula* did not close when the sensitive hairs were touched, but did so under the stronger stimulus of cutting off the tip of the leaf.

It would appear, though the data are scanty, that the loss of the power of movement which, as we have seen, is induced when the supply of free oxygen to the motile organ is cut off, is due to the same cause as the effect of anæsthetics. Thus Kabsch observed that a leaf of *Mimosa* *in vacuo*, which did not move when touched, moved under the stronger stimulus of an electric shock.

It was further stated in the last lecture that the movements of motile organs are arrested by such conditions as drought,

extremes of heat and cold, and, in the case of organs containing chlorophyll, long-continued darkness, and that in the case of *Mimosa pudica*, the first effect upon the leaves is to deprive them of their irritability to stimulation; then the daily periodic movements cease, and finally the spontaneous movements. The position which the leaves assume when all movement is at an end, indicates that the pulvini are in a state of imperfect turgidity, though unfortunately we have no determinations by Brücke's method of the rigidity of the pulvini in the immotile condition. In accordance with our views as to the intimate mechanism of the movements of these organs, we attribute the immotile condition of the pulvini to a destruction of the motility of the protoplasm.

We now leave the mature motile organs, and pass to the consideration of the mechanism of the movements of growing organs, of the "auxotonic" movements, to use de Vries' term. The mechanism of growth we have learned to be this (p. 334), that the cell is expanded by the hydrostatic pressure of the cell-sap, and that this expansion is rendered permanent by deposition of substance. In view of the facts with which we have already become acquainted, there can be no doubt as to the importance of the absorption of water in bringing about the expansion of the cell. But it is a question whether or not this simply mechanical explanation of the expansion of growing cells is really adequate; for it is quite possible that the protoplasm takes an active part in producing it. The importance of this consideration will become apparent in the following discussions.

We will begin by considering the influence of light upon growing organs. We have learned (p. 380) that this influence is two-fold. In the case of most leaves, growth is altogether arrested by prolonged exposure to darkness, and the power of growth is restored on exposure to light; this we term the *phototonic* influence of light. In the case of all growing organs, growth is more rapid in darkness than in light; this effect of light in retarding growth we term the *paratonic* influence of light.

What, now, is the nature of the phototonic influence of

light? We have no reason to suppose that the arrest of the growth of the cells of a young leaf when kept in darkness is due to any diminution in the quantity, or to a change in the properties, of the osmotically active substances present in the cell-sap; on the contrary, all that we know on the matter goes to prove that these substances are more abundantly present in darkness than in light. Nor is there any ground for assuming that long-continued darkness induces an increase in the rigidity of the cell-wall. We must assume that it is the protoplasm of the cells which is affected, and when we recall the behaviour of mature motile organs under the same conditions, and the cessation of the movement of *Bacterium photometricum* in darkness (p. 298), we see that this assumption is not groundless. What exactly the nature of the effect produced on the protoplasm is, we cannot decide, as we have no information as to the state of turgidity or flaccidity of the cells in question. All that we can say is that the arrest of growth induced by long-continued darkness is to be ascribed to the abolition of the motility of the protoplasm of the cells. The phototonic influence of light is, then, of this nature, that it restores the motility of the protoplasm; and it probably does so by rendering possible the performance of certain nutritive processes.

Now as to the paratonic influence of light. In dealing with this subject we must have this view clearly in our minds, that the paratonic effect of light on plant-organs is not to be attributed to the action of light upon the individual cells of the organ, but to its action on the organ as a whole; the change induced in the individual cells is the expression of the response of the organ as a whole to the action of light. Thus, we may make the general statement that the effect of exposure to light is to diminish the turgidity of turgid organs. This loss of turgidity by the organ as a whole is of course due to a loss of turgidity by its constituent cells. But in endeavouring to account for this fact we must not say that the organ has become less turgid because exposure to light has diminished the turgidity of its cells, but rather this, that the loss of turgidity by its constituent cells is the response of the organ

as a whole to exposure to light. We shall illustrate this subject more fully when we have to consider the daily periodic movements of certain floral and foliage leaves.

We have now to enquire into the mechanism of this response: by what means does the organ thus respond to the stimulus of exposure to light? One of the most striking cases of the paratonic influence of light, an influence, be it said, which does not only affect growing organs, is afforded by the diminution in the tensions of the tissues induced by exposure to light, allusion to which was made in a previous lecture (p. 405). This diminution in the tissue-tensions is due, as was pointed out, mainly to a loss of water by the parenchymatous cells. Without again discussing whether this loss of water takes place in consequence of changes in the properties of the cell-wall, or of the cell-sap, or of the protoplasm, we will simply assume that it is the protoplasm which is directly concerned. Leaving out of the question the possibility that the expulsion of water from the cells is to some extent effected by an active contraction of the protoplasm, we will account for it in this way, that the permeability of the protoplasm is increased so that water is now forced out by filtration under the pressure of the elastic cell-wall. The retardation of the growth of an organ when exposed to light is due to a diminution in the turgidity of the growing cells brought about in the manner just described.

So far we have had the case of a multicellular organ in view; we will now briefly consider the case of a unicellular organ. We have learned, for instance, that the growth of a sporangiferous hypha of *Phycomyces* is retarded on exposure to light (p. 394). In the absence of any direct information as to the turgidity of the organ, we may assume, in view of the facts now before us, that it is diminished. Now diminution of turgidity means loss of water. It is clear, inasmuch as the whole plant consists of one continuous much-branched hypha, that water cannot be driven from the sporangiferous hypha into other parts of the plant. In this case it is a question not of redistribution of water in the plant, but of a loss of it. The loss is probably due, ultimately, to increased

activity of transpiration, for we have seen (p. 109) in how high a degree light promotes this process. But the question as to how light promotes transpiration has yet to be considered. It seems probable that the effect of light on transpiration is due in no small degree to changes in the properties of the protoplasm of the transpiring cells. It was pointed out at the time when we were studying this process that transpiration is something different from mere evaporation, that it is a process essentially dependent upon the life of the plant. The account which, from our point of view, we give of the effect of light in promoting transpiration is that the permeability of the protoplasm of the transpiring cell is increased, and that water is consequently more readily forced to the surface of the cell, where it is evaporated. This account is supported by the fact, to which attention was drawn at the appropriate time, that the transpiration of leaves is temporarily increased by violently shaking them, a fact which clearly points to the possibility of molecular change in the protoplasm of the transpiring cells.

Exposure to light acts, then, as a stimulus to the growing organ, in consequence of which the protoplasm of the cells undergoes a molecular change which leads to an increase of its permeability and thus induces a diminution in the turgidity of the cells. So long as the exposure continues the protoplasm remains in this condition, a result which we must attribute to an interference with the motility of the protoplasm. The stimulating effect of sudden exposure to light or of sudden withdrawal from its influence, in a word, of rapid variations in its intensity, is only manifested in a marked manner by organs possessing a high degree of irritability. Instances of these are afforded by the flowers and leaves of certain plants mentioned in a previous lecture (p. 400), which are excited by such variations to perform movements; movements closely resembling those performed by leaves provided with pulvini, which we have just been discussing. With regard to the mechanism of the movements of growing floral and foliage leaves, it is essentially the same as that of leaves which move by means of pulvini. Neither the movement of opening which follows on an increase in the intensity of light, nor the

movement of closing which follows on a decrease in the intensity, is due to antagonistic effects induced simultaneously in the cells of the two halves of the growing region by the direct action on them of the stimulus : it is the leaf as a whole which is stimulated, and its response to a sudden increase in the intensity of the light is that it opens, and to a sudden decrease, that it closes.

The manner in which temperature affects growth may next be considered. We have learned (p. 293) that there is for every growing organ a minimum temperature at which growth begins, an optimum at which it is most rapid, and a maximum at which it is arrested. Inasmuch as this relation to temperature has been established in the case of almost every vital process of plants, there can be little doubt that it is the protoplasm of the growing cells which is especially concerned. Though there can be no doubt that at different temperatures the actual process of growth, the building up of the cell-structure, takes place with different degrees of rapidity, yet the rate of growth at these temperatures must be dependent in the first instance upon the turgidity of the cells. Kraus has shewn that, at low temperatures, the tension of the tissues, or in other words, the turgidity of the parenchymatous cells, is very slight. This we attribute to the induction of a permeable condition of the protoplasm. If the organ be exposed for a long period to a low temperature, no variations in the tissue-tensions can be observed; the motility of the protoplasm is abolished. The same holds good apparently, though the observations are not so decisive, of the effect of excessively high temperatures. From these facts we can readily infer how it is that at extreme temperatures growth is arrested. As the temperature rises above the minimum, the turgidity of the parenchymatous cells, as estimated both by the tensions and by the actual amount of water which they contain, increases, and, accordingly, growth is resumed; the protoplasm resumes its normal condition. An optimum temperature for the turgidity of the cells has not been determined, but it cannot be doubted that there is one, inasmuch as it has been determined in the case of growth.

The periodic variations in the external conditions which are due to the regular alternation of day and night induce, as we have seen, a daily periodicity in the growth of plant-organs, which is conspicuously manifested by those growing foliar organs which perform movements of opening and closing. The daily period of growth closely corresponds with that of tissue-tensions and with that of the variation in bulk of plant-organs (see p. 408); there can, in fact, be no doubt that they are all due to the same cause, to a periodic variation in the turgidity of the cells. From our point of view this is the expression of periodic changes in the molecular state of the protoplasm of the cells, of such a nature that its permeability increases during the hours of the day, and decreases during the hours of the night: and so deeply does this periodicity become impressed upon the protoplasm, that, as we already know, the periodic changes continue for some considerable time after the plant has been placed in continuous darkness. The daily periodic movements of growing floral or foliage leaves are brought about in precisely the same manner as are those of leaves provided with pulvini; the regular recurrence in the evening of the stimulus of the diminution in the intensity of light which causes them to close, and in the morning, of the increase in the intensity of light which causes them to open, so impresses itself upon the plant, that the opening and closing movements of its leaves will go on for some time under perfectly constant external conditions.

The spontaneous variations in the rate of growth, like the induced variations, we attribute in the first instance to variations in the turgidity of the growing cells due to corresponding molecular changes in the protoplasm.

Leaving the variations in the rate of growth, we pass to the consideration of changes in the direction of growth, and we begin with the induced changes. In entering upon this subject we must bear in mind that, as has already been pointed out (pp. 432, 473, 481), the change is not due to a difference in the effect of the stimulus on the two sides of the organ; the organ, as a whole, is stimulated, and the change in the direction of its growth is its response to the stimulus.

We will first take the case of multicellular organs. The curvature of such an organ is due, in the first instance, to a difference in the turgidity of the cells of the two opposite halves of the growing region, those of the concave side being less turgid than those of the convex, this difference being due as well to a decrease in the turgidity of those of the concave side as to an increase in that of the cells of the convex side. The fact that the curvature is due to a difference in turgidity of the cells of the opposed halves of the growing region is established by the observations of de Vries, who found that an organ which has begun to curve, whether heliotropically or geotropically, or, as in the case of tendrils, in consequence of contact, is more or less straightened out on plasmolysis. The fact that the curvature is due as well to a decrease in the turgidity of the cells of the concave side as to an increase in that of the cells of the convex side is established by the general observation that, whereas the rate of growth of the convex side is more rapid than that of the organ when straight, the rate of growth of the concave side is less rapid. The slower growth of these cells may be due in part to compression, but it is mainly due to a definite diminution of turgidity.

This being the mechanism of curvature of multicellular growing organs, the question arises as to how the observed differences in turgidity are brought about. It is inconceivable that it should be due to differences in the rigidity of the cell-walls of the cells of the two halves of the organ. If it be suggested that curvature is due to an increased rigidity of the walls of the cells of the concave side, such an assumption must involve the further assumption that the rigidity of the walls of the cells of the convex side is diminished. Such changes in the physical properties of the cell-wall necessarily involve modifications of structure of the nature of growth. Such modifications of structure are, however, permanent. But we have seen that the incipient curvature is obliterated on plasmolysis, which would not be the case were the cell-walls of one side of the organ more rigid than those of the other. It must depend, then, either upon differences in the attraction

for water exercised by the cell-sap, or to changes in the protoplasm, in the cells.

The former of these alternatives is strongly supported by de Vries, who regards the differences in the turgidity of the cells of the two sides of the curving organ as being due to an increased formation of osmotically active substances in the cells of the convex side. But to this view there are certain fatal objections. In the first place, according to de Vries' own observations it appears that the osmotically active substances of the cell-sap are organic acids. From the point of view which he takes up with regard to the intimate mechanism of curvature it is to be expected that the cells of the convex side of the curving organ should contain a relatively large quantity of organic acids. As a matter of fact, however, it appears from Kraus' researches that, in the case of geotropic curvature, the absolute amount of organic acids in the cells of the convex side diminishes, instead of increasing, as curvature proceeds. In the second place, de Vries' view does not take into account the diminution of the turgidity of the cells of the concave side. It may be argued that the loss of water which these cells undergo is due to the increased osmotic attraction exercised by the sap of the cells of the convex side, in other words, to a redistribution of the water in the cells of the growing region. But de Vries' own observations prove that this is not the case. He found, namely, that the curvature of a tendril on stimulation is more rapid when its intercellular spaces are injected with water. Under such circumstances there can be no question of a redistribution of the water in the growing region. De Vries' explanation, to be complete, must include not only an increase in the amount of the osmotically active substances in the cells of the convex side, but also a diminution in the amount of these substances in the cells of the concave side, inasmuch as the latter fail to become turgid when water, as in the injection-experiment, is abundantly supplied to them. In view of these various facts it is impossible to consider that curvature is due to differences in the osmotic properties of the cell-sap of the cells of the opposed halves of the curving organ.

We are led to conclude that the difference in turgidity upon which curvature depends is brought about by changes in the protoplasm of the cells of the two sides. In accordance with what has been said with reference to other modifications of turgidity, we attribute the diminution of the turgidity of the cells of the concave side to an increased permeability of the protoplasm in consequence of which water is forced out of them. With regard to the expansion beyond the normal which the cells of the convex side undergo, this appears to be due to an increased motility of the protoplasm in consequence of which it yields more readily to the pressure of the cell-sap. We will defer the full discussion of this very important point for a few minutes.

Now as to the curvatures of unicellular organs. Inasmuch as there is no ground for the assumption that the rigidity of the cell-wall is increased on the concave and diminished on the convex side, and inasmuch as the pressure of the cell-sap must be the same at all points, it is clear that curvature must be due to changes in the properties of the protoplasm of the two opposite halves of the cell. Without pretending to say precisely what these changes may be, we may suggest that they consist in a modification of the motility of the protoplasm of one or both sides of the cell; the motility of the protoplasm of the concave side may be diminished, or that of the convex side increased, or, as is more probable, in view of the curvature of multicellular organs, both these effects may be simultaneously produced. In any case the result is that the protoplasm of one side yields less readily to the pressure of the cell-sap than the other.

The changes which the protoplasm of a unicellular organ undergoes in connexion with curvature are not such as affect the permeability of the protoplasm, for in this case the mechanism of curvature is in no wise dependent upon an escape of water. The consideration of these phenomena again raises the question as to whether or not a diminution in the turgidity of cells is not in all cases accompanied by a molecular change of the nature of a contraction in the protoplasm, and an increase in turgidity by an active expansion of the protoplasm.

This question cannot at present be definitely answered, but it may be pointed out that the excessive elongation of the cells of the convex side of a curving multicellular organ, and certain other phenomena to which attention was drawn when we were discussing the mechanics of growth (p. 335, small print), suggest that at least an active expansion of the protoplasm may take place.

The recent observations of Kohl on the heliotropic, geotropic, and hydrotropic curvatures of various organs (sporangiferous hyphæ of *Phycomyces*, root-hairs, roots, etc.) lend some support to these views as to the intimate mechanism of curvature. He finds that the protoplasm aggregates on the *concave* side of the curving cell, but it is not clear at present what the exact significance of this fact may be.

We will conclude our study of the mechanism of the movements of growing organs with a brief consideration of the spontaneous movements. The movement of nutation of multicellular organs is due, like the curvature induced by a stimulus, to an inequality in the turgidity of the cells on two opposite sides of the organ, an inequality which in this case also is to be attributed to molecular changes in the protoplasm of the cells, but occurring spontaneously.

With regard to the intimate mechanism of the movement of nutation of unicellular organs, we can only repeat what has been said with regard to their induced movements, that the movement is due to a difference in the condition of the protoplasm of the two opposite halves of the organ, of such a nature that the protoplasm of the one side yields less readily to the pressure of the cell-sap than does that of the other.

Transmission of Stimuli.

In speaking of the action of stimuli in inducing movements of plant-organs it has been mentioned incidentally that there is considerable evidence to shew that the stimulus is transmitted from one part of the organ to another. Thus, a transmission of the heliotropic stimulus appears to have been made out in the case of certain cotyledons (p. 438), and of geotropic (p. 468), hydrotropic (p. 479), and electrical

stimuli (p. 474) in the case of roots. There is no doubt whatever that the stimulus of contact is transmitted in tendrils (p. 487), and in irritable leaves, such as those of *Mimosa* (p. 547), and *Drosera* (p. 548). We have now to enquire into the means by which the transmission is effected.

This subject has been more especially investigated in the case of *Mimosa pudica*. Dutrochet came to the conclusion that the stimulus travels along the fibrovascular bundles. He found, namely, that when he had removed either the cortex or the pith, or both, of a portion of the stem, a stimulus was transmitted from a leaf above the wound to one below it, or from one below the wound to one above it, but that no such transmission took place when the fibrovascular tissue was cut through. In another experiment he removed the whole of the parenchymatous tissue of the pulvinus of a leaf, leaving only the fibrovascular bundle; stimulation of this leaf caused the other leaves on the stem to move. Clearly, then, the fibrovascular tissue transmits the stimulus, but we have yet to learn what the mode of transmission is. Sachs considers that it is due to a disturbance of the hydrostatic equilibrium in the plant. He regards the state of equilibrium to be of this nature, that the parenchymatous cells of the pulvinus are in a state of high tension so that water would escape from them were it not prevented by the counter hydrostatic pressure in the fibrovascular tissue. In support of this view he cites the fact that when an incision is made into the stem of a *Mimosa*, which extends to the fibrovascular tissue, it is immediately followed by a fall of the petiole of the nearest leaf. The incision has diminished the hydrostatic pressure in the fibrovascular tissue; consequently the cells of the pulvinus of the nearest leaf give up water and a movement ensues. When a movement of a leaf is induced by stimulation, the converse of this takes place. The irritated pulvinus forces water into the fibrovascular tissue, thereby causing a disturbance of hydrostatic equilibrium which is propagated to adjacent pulvini. Though we cannot accept this view of the intimate mechanism of the movement of a pulvinus, yet it is possible to imagine that if two pulvini were

connected by an open tube filled with water, the disturbance of the hydrostatic equilibrium due to the forcing of water into the tube in consequence of the stimulation of one pulvinus might be propagated to the other pulvinus and might act as a stimulus upon it, a conception which might be realised by means of the vessels of the wood. But Dutrochet clearly shewed, and in this he is confirmed by Pfeffer, that the vessels of the wood are, as a matter of fact, not concerned in the transmission of the stimulus. We have to believe, then, that a disturbance of the hydrostatic equilibrium can be propagated for a considerable distance in the plant through a series of closed cells. It is a question whether or not such a propagation is possible; but even assuming that it is, there is the question of fact to be decided, whether there is any ground for assuming that the forcing of water out of the parenchymatous cells of the pulvinus on stimulation necessarily affects the fluid-pressure in the fibrovascular tissue. It is admitted on all hands that the water which is expelled from the irritated cells of a pulvinus is driven into the intercellular spaces, so that we cannot assume that more than a portion, probably a very small portion, of it enters the fibrovascular tissue. There is, in fact, no direct proof that any water is forced into the fibrovascular tissue of the pulvinus.

It appears from these considerations that the theory which regards the transmission of a stimulus as a mere propagation of a disturbance of hydrostatic equilibrium is not satisfactorily established. This theory is altogether too purely mechanical to account for so remarkable a phenomenon in a living organism, and we must endeavour to establish for it some other explanation which, while borne out at least as fully by the facts, will be more in harmony with our conceptions of the organisation of living beings.

We learned in one of the earlier lectures (p. 23), that the protoplasm of adjacent cells is, in many cases and perhaps universally, continuous through the cell-walls. This important fact, for which we are indebted mainly to Gardiner's researches, may help us in our endeavour to ascertain the means by which the transmission of a stimulus may be

effected in a plant. It is a well-known fact in physiology that living protoplasm is capable of transmitting a stimulus ;

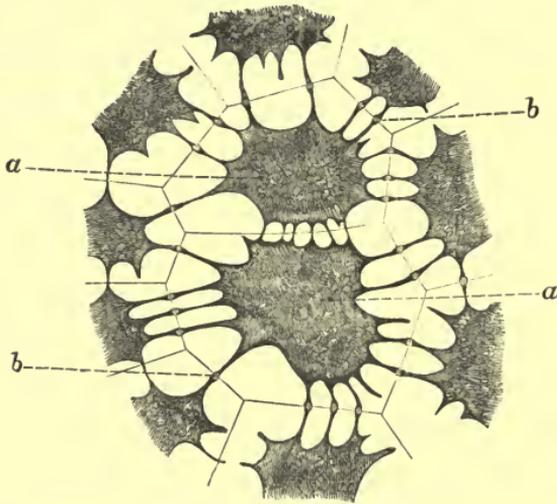


Fig. 64 (after Gardiner). Continuity of the protoplasm of adjacent cells of the endosperm of a Palm-seed (*Bentinckia*): *a*, contracted protoplasm of a cell; *b*, a group of delicate protoplasmic filaments, passing through a pit in the cell-wall.

in fact, the nerve-fibres of animals are simply protoplasm which has been specially modified for the performance of this very function. We may suggest, then, that a stimulus travels through a *Mimosa*-stem from cell to cell by means of the delicate filaments which place the protoplasm of the cells in direct communication.

The possibility of a vital, as distinguished from a mechanical, transmission of a stimulus from cell to cell had occurred to Pfeffer, but he believed that he had disproved it by the following experiment. He placed a leaf of a plant of *Mimosa* so that the middle portion of it was enclosed in a vessel containing chloroform-vapour in sufficient proportion to abolish the irritability of the pulvinus. Under these circumstances he found that a stimulation of the leaflets projecting beyond the vessel caused a movement in another leaf borne on the stem. The stimulus obviously travelled through that portion of the leaf which was exposed to the action of the chloroform. From this he infers that the transmission of the stimulus is not vital, for, had it been so, it could not have

traversed the chloroformed portion of the leaf. He assumes that since, as we know with regard to the pulvinus, the irritability of protoplasm is abolished by chloroform, the conductivity of protoplasm is similarly affected, an assumption for which there is no justification. This experiment, then, fails to overthrow the theory that the stimulus is transmitted from cell to cell by the protoplasm.

The theory which we substitute for what we may term the water-theory of the transmission of stimuli in *Mimosa* is briefly this: that stimuli are transmitted by means of the protoplasm from cell to cell in some portion of the fibrovascular tissue. It is possible to define the portion of the fibrovascular tissue in which the stimuli travel. Dutrochet found that a stimulus was transmitted from one leaf to another when the intermediate portion of the stem was cut away at some point so as to leave only the outer parts of the fibrovascular bundles intact, and he came to the conclusion that the stimulus travels in these remaining parts of the fibrovascular bundles through certain structures which he terms "tubes corpusculifères". Now the researches of Russow have shewn that the continuity of the protoplasm of adjacent cells is especially well-marked in the bast-parenchyma. It seems probable, therefore, that Dutrochet's "tubes corpusculifères" are the elongated bast-parenchyma cells of *Mimosa*.

But it will be objected that if the stimulus travels from cell to cell by means of the protoplasm, it ought to be transmitted equally well by the cortical or medullary parenchymatous tissues, for the protoplasm of these cells is probably also continuous. Gardiner has, in fact, shewn, that the protoplasm of the cortical parenchymatous cells of the pulvinus is continuous. But according to Dutrochet's observations, these tissues do not transmit a stimulus. In reply to this objection it may be pointed out that the conduction of a stimulus of a particular kind from one cell to another is not a necessary consequence of the continuity of the protoplasm. The conclusion from these facts is simply this, that the bast-parenchyma in the plant constitutes a system of tissue which possesses the property of conductivity in a high degree.

We will briefly discuss from this point of view the fact mentioned above that an incision into the stem of *Mimosa*, so soon as the fibrovascular tissue is touched, causes a movement in the nearest leaf. We can now account for this by attributing it to a stimulation of the protoplasm of the cells of the bast-parenchyma, the stimulus being transmitted in this tissue to the nearest leaf.

It must not, however, be assumed that the property of conductivity is confined to the bast-parenchyma. From Darwin's observations on *Drosera* and *Dionæa*, it appears that stimuli are transmitted through the parenchymatous cells of the leaf, and this must be also the case, as Cohn points out, in that of *Aldrovanda*, in the lamina of which no fibrovascular tissue is present. But Darwin has pointed out that in *Drosera* the rate of transmission of the stimulus is materially affected by the form of the cells and by the direction of their axes. A stimulus travels most rapidly in a tissue consisting of elongated cells, the direction of transmission being the same as that of the long axes of the cells. Clearly, in the case of *Mimosa*, the bast-parenchyma is, of all others, the tissue which meets the mechanical requirements of rapid transmission. It is not altogether clear why the rate of transmission of a stimulus should be thus dependent upon the form of the cells and the relation of their axes to the direction of transmission; but it may be, as Darwin suggests, that the transmission is retarded on passing through cell-walls. This suggestion at least enables us to account for the relatively great rapidity of transmission through a tissue consisting of elongated cells in the direction of their axes, for, under these circumstances the number of cell-walls to be traversed is the smallest possible.

Biological Significance of Plant-Movements.

In previous lectures we have described the phenomena of movement presented by plants, and in the present lecture we have endeavoured to explain the mechanism of movement. In order to conclude the subject we must enquire, though we

can only do so briefly and in the most general way, into the significance of movement in the economy of the plant. It is, in fact, only when we clearly apprehend that the various movements of plants have some bearing upon the well-being of the organism that we can approach the difficult subject of the mechanism of those movements with any hope of understanding it. It is only from this point of view that we can perceive the principle which alone can afford a clue to the mechanism of movement, the principle, namely, that all phenomena of movement induced by a stimulus are not the expression of the direct action of the stimulus on the cells by means of which the movement is performed, but are the response of the stimulated organ.

We will begin by discussing the most general of the phenomena of movement, the fact that growth is more rapid in darkness than in light. The question at once arises why this should be so; for it is possible to conceive that just the opposite should be the case, there being no *a priori* reason for the existing relation between light and the rate of growth. The answer is given by the following instance. A green plant requires to be exposed to light of a certain intensity in order that its metabolic processes may be carried on. If a seed of such a plant happens to germinate in a shady spot among bushes, the seedling will not receive light of sufficient intensity to enable it to carry on its processes of constructive metabolism, and the only means by which this can be attained is that its stem should grow rapidly in length so as to raise its leaves above the level of the surrounding bushes and expose them to the sunlight. Clearly, then, it is of great importance to the plant that, as we have seen, the growth of its stem should be rapid in feeble light. When once the apex of the stem has reached the light, there is no further need for rapid elongation; all that is then required is that its tissues should be well differentiated, so as to give rigidity to the stem and to ensure an adequate supply of water to the upper parts of the plant, and that its leaves should be fully developed. We now see the significance of the paratonic influence of light. The growth of the stem is retarded, and, at the same time, the

more perfect differentiation of the tissues, and the development of the leaves proceeds. This leads us to consider the relation of the growth of leaves to light. We have learned (p. 380), that in cases in which excessive elongation of the stem takes place in darkness, the leaves are imperfectly developed, and we found ourselves at a loss to explain, in any direct way, the fact of the rudimentary condition of the leaves. The explanation is that, under these circumstances, the development of the leaves would be of no advantage to the plant: it concentrates, as it were, all its efforts to the elongation of the stem to the end that light of sufficient intensity may ultimately be reached. We found also, in the case of plants in which, under similar circumstances, the stem does not become excessively elongated, the Onion for instance, the leaves become so. The significance of this is the same as that of the excessive elongation of the stem: the leaves elongate in search of light.

Another instance of precisely the same nature is afforded by climbing plants, whatever be the means by which their climbing is effected. The stems of these plants are not sufficiently rigid to enable them to support the leaves in the most favourable position as regards exposure to light. Consequently they attach themselves to supports and thus attain the required end. In some cases the attachment is of a mechanical nature, as in hook-climbers; in others existing parts of the plant possess special irritability, as in leaf-climbers and stem-climbers, or altogether new and irritable organs are developed, as in tendril-climbers.

It may perhaps be objected that it is not clear, from this point of view, why, as we have seen (p. 385), the shoot-organs of plants destitute of chlorophyll should grow more rapidly in darkness than in light. In reply to this objection it has to be pointed out that these plants have undoubtedly sprung from ancestors which contained chlorophyll: for instance, the Fungi have been derived from the Algæ. Now derivative forms retain, in a greater or less degree, the more general properties of their ancestors, even though these properties may be of comparatively little advantage to them, and the case before

us is an illustration of this general principle. But in some cases, at least, the excessive elongation in darkness of the shoot-organs of plants destitute of chlorophyll has an immediate significance. It was mentioned in a previous lecture (p. 393) that the spores of certain Fungi are not developed when the plant is kept continuously in darkness. The excessive elongation of the stalks of the fructifications of these Fungi in continuous darkness is the expression of the same tendency as the excessive elongation of the stems of normally green plants: it is the expression of the search after light, though the end to be attained is different in the two cases. In the one case light is essential to the development of the spores; in the other, to the performance of the processes of constructive metabolism.

We may now go on to discuss the significance of the various forms of changes in position. Beginning with the phenomena induced by light we will take as our first illustration the case of a positively heliotropic shoot. The effect of an obliquity in the incidence of the rays of light upon such an organ is to cause it to place its long axis in the direction of incidence of the rays, the apex being directed towards the source of light. Such a curvature of the stem necessarily alters the position of the leaves, the alteration being such that the upper surfaces of the leaves are placed perpendicularly to the direction of the incident rays. In this position the leaves are fully exposed to the incident light, and are under the most favourable conditions for the performance of their important metabolic processes.

But the position of leaves with regard to the direction of incidence of light is not altogether determined by the direction of growth of the stem which bears them; for we have seen (p. 445) that the fixed light-position of leaves is different in different plants. In endeavouring to explain the differences in the fixed light-positions of leaves, we must bear in mind that light not only promotes the constructive metabolic processes, but that, if intense, it also causes decomposition of chlorophyll (p. 265). It is important, therefore, that the position of a leaf should be such that whilst

it receives as much light as possible of an intensity sufficient for the performance of the constructive metabolic processes, it should receive as little light as possible of such an intensity as to lead to the decomposition of its chlorophyll. The fixed light-position of a leaf is then the position in which both these ends are as far as possible attained, the position being different in leaves of different organisation.

In connexion with this subject we will briefly consider the peculiarities of structure of leaves which are involved by the nature of the fixed light-position of leaves (see p. 384). A leaf which when fully exposed to light takes up such a position that its morphologically upper surface is directed towards the zenith, presents a well-marked difference in its internal structure between the upper and lower portions of its mesophyll. Towards the upper surface the mesophyll consists of elongated cells closely packed together, with scarcely any intercellular spaces, the long axes of the cells being perpendicular to the surface: this is the palisade-tissue. Towards the lower surface the mesophyll consists of irregularly shaped cells with large intercellular spaces: this is the spongy tissue (see Fig. 13, p. 70). Moreover there are but few stomata, if any, in the epidermis of the upper surface, whereas they are numerous in that of the lower. Such a leaf is manifestly dorsiventral. A leaf which when fully exposed to light takes up such a position that its surfaces lie in a vertical plane, does not exhibit this structure. At both surfaces of the leaf palisade-tissue is developed, usually to an equal extent, with a similar distribution of intercellular spaces, and stomata are present in the epidermis. Such a leaf is isobilateral. The difference in the anatomy of the two leaves is due to the fact that in the case of the horizontal leaf the one surface, the upper, is more directly exposed to light than the lower, whereas in the case of the vertical leaf both surfaces are equally exposed to light. Now the particular kind of tissue in which the processes of constructive metabolism can be most advantageously carried on is the spongy parenchyma: this kind of tissue most readily permits the entrance of light into the tissues.

This is proved by the fact that in leaves grown in feeble light the spongy tissue is well developed at the expense of the pallsade-tissue. But when a leaf is exposed to bright light, not only the constructive metabolic processes, but the decomposition of the chlorophyll has to be taken into consideration. The pallsade-tissue is to be regarded as a means of diminishing the intensity of the light as it penetrates into the leaf, and so of protecting, as it were, the chlorophyll of the subjacent spongy tissue. These considerations afford the explanation of the principal difference in structure between the horizontal and vertical leaf. It may be added that the different distribution of the stomata in the two cases is correlated with the differences of internal structure.

If it be enquired why the cells of the mesophyll of a leaf-surface exposed to bright light should assume the elongated form characteristic of the pallsade-tissue, and why these cells should be so placed in the leaf that their long axes should be, as they are, parallel to the direction of the incident rays, the answer is again, that it is for the protection of the chlorophyll. It was mentioned in previous lectures (p. 299, see Fig. 36) that under the influence of changes in the intensity of the incident light, the position of the chlorophyll-corpuscles in the cells is changed. The effect of bright light is to induce light-apostrophe, that is, a position of the corpuscles in which they present, not their flat surfaces, but their edges, to the incident rays. The assumption of this position can, obviously, be most readily carried out when the form of the cell is a hollow cylinder placed with its long axis parallel to the direction of the incident rays, conditions which are exactly fulfilled by the cells of the pallsade-parenchyma.

But to return from this digression. In a previous lecture we have spoken of leaves which when fully exposed to light, take up a horizontal position, as being diaheliotropic, and we may speak of those which, under similar circumstances, take up a position which is more or less inclined to the horizontal, as being paraheliotropic. The significance of the fixed light position, whatever it may be, is that it is the

position in which the leaf receives light of that intensity which is most favourable to the performance of its functions. That this is the case is proved by the changes in position which some motile leaves undergo under variations in the intensity of light. Thus, it has been mentioned (p. 552) that, when exposed to light of moderate intensity, the leaflets of *Robinia* are horizontal, but that when the light is intense they move upwards until they present their margins to the incident light. In light of moderate intensity, then, these leaves are diaheliotropic; in intense light, they are paraheliotropic.

We may now conveniently consider the nyctitropic movements of leaves whether growing or motile. These consist in the assumption by the leaf or leaflet, on a diminution in the intensity of light, of a position in which the surfaces are more or less nearly vertical, the apex being directed either upwards or downwards (see pp. 405, 539.) That this movement is not essentially connected with any relation between the function of the leaves and the intensity of the light, is shewn by the fact that a similar movement may be induced by a fall in the temperature of the air (p. 378). The significance of it probably is, as Darwin suggests, that it prevents the excessive lowering of the temperature of the organs by radiation during the night; clearly the radiation from a leaf with its surfaces vertical must be much less than when its surfaces are horizontal. In the case of floral leaves the movement has, in some instances, the further significance, that by the closure of the petals the essential floral organs are protected not only from cold, but also from becoming wetted by dew or rain.

With regard to geotropism and hydrotropism, it is so obviously to the advantage of the plant that its shoot should be negatively geotropic, and its root positively geotropic, and further, that its root should be positively hydrotropic, that the facts need only to be mentioned to be understood.

Finally, though it is not possible in most cases to see what advantage accrues to the plant from the spontaneous movements of its organs, for instance, the movements of

the lateral leaflets of *Desmodium*, or the nutations of growing organs, yet in some cases the advantage is clear. This is notably the case with regard to the circumnutation of tendrils and of the stems of twining plants; clearly the travelling of these organs over a considerable area must largely increase the chances of their coming into contact with a support. The same may be said with regard to the movements of those organs which are irritable to touch. It is not clear what advantage the power of movement on mechanical stimulation of the leaves of *Mimosa* brings to the plant; but it is clear in the case of irritable stamens: when an insect visits a flower with irritable stamens it causes them to move, and the result of their movement is a discharge of pollen some of which is conveyed by the insect to another flower of the same kind, and thus cross-fertilisation is ensured.

It is impossible, within the limits of these lectures, to discuss all the very numerous phenomena of movement with which we have become acquainted, from the standpoint of their biological significance; to do that thoroughly, a separate course of lectures would be required. But with the help of the examples just given of the way in which various kinds of irritability have been acquired, the elucidation of other cases may be advantageously undertaken by the student himself.

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LECTURE XXII.

REPRODUCTION.

So far we have been mainly occupied with the means by which the maintenance of the individual is attained. But we have incidentally learned that the period during which the life of the individual can be maintained is limited, though the length of life may be widely different in different cases. Thus some plants, *annuals*, do not survive a single season of growth; others, *biennials*, live through two seasons; and others, *perennials*, persist for a greater or smaller number of years. But in any case any given individual eventually ceases to exist. Inasmuch, however, as the various species of plants continue to exist, it is clear that new individuals must be constantly being produced, and it is the object of these concluding lectures to study the various modes in which these new individuals are produced, to study, in other words, the Reproduction of Plants.

In the first lecture (p. 6) it was pointed out that reproduction is one of the fundamental properties of living protoplasm. The protoplasm of an individual possesses the property of giving rise to a new individual, and this may be effected in either of two ways; in the one case by means of cells, not specially modified for the purpose, forming part of the body of the individual, *somatic cells* as we may term them; in the other, by means of specially modified cells, the *reproductive cells*, which are usually set free from the individual. The former process we term *vegetative reproduction*, the latter *spore-reproduction*.

The simplest mode of vegetative reproduction is that which obtains among unicellular plants of low organisation. When the cell which constitutes the body of the individual has attained by growth its limit of size, it gives rise, by some form of cell-division, to one or more new cells, which then grow, and, becoming separated from one another, constitute one or more new individuals similar to the original organism. Good examples of this are afforded by the lowly organised unicellular Algæ and Fungi. This mode of vegetative reproduction is merely a process of cell-division essentially the same as that which takes place in the growing members of multicellular plants, with this difference, however, that whereas in a multicellular plant the products of cell-division remain coherent and add to the number of the cells of which the plant consists, in a unicellular plant the products of division separate and thus come to constitute new individuals.

Vegetative reproduction also takes place to a greater or less extent in plants of higher organisation. In the simplest case, parts of the body, not specially modified, become separated from each other, and each may constitute a new individual. For instance, it commonly happens in Mosses that the main stem gradually dies away from behind forwards, so that the lateral branches become isolated, and each of these then comes to be an independent Moss-plant. In fact, under artificial conditions, almost any part of a plant may subserve vegetative reproduction. For instance, the stem, the leaves, the rhizoids, or the sporogonium, of a Moss may be induced by appropriate cultivation to give rise to filamentous protonema on which new Moss-plants are developed as lateral buds. Again, a great number of our garden-plants are propagated by means of "cuttings"; that is, a shoot is removed from a plant and is induced to develop roots and thus to constitute a complete plant. In the case of some of the Begonias artificial propagation is effected by inducing adventitious budding on portions of isolated leaves, each bud developing into a new plant.

In a great number of plants vegetative reproduction is effected by means of specially modified embryonic shoots or

buds. In Lichens, for instance, there are the *soredia*, which are minute buds containing both algal and fungal cells; these are formed in large numbers on the thallus, and each is capable of developing into a new thallus. Among the Algæ, there are the *gemmæ* of the Sphacelariæ, the "propagula" of some Florideæ, and in the Characeæ the *bulbils* or "starch-stars" of *Chara stelligera*, which are underground nodes, the *branches with naked base* and the *proembryonic branches* found by Pringsheim on old nodes of *Chara fragilis*. In the Mosses, small tuberous bulbils frequently occur on the rhizoids, and in many cases (*Bryum annotinum*, *Aulacomnion androgynum*, *Tetraphis pellucida*, etc.) stalked fusiform or lenticular gemmæ containing chlorophyll are produced on the shoots, either in the axils of the leaves or in a special receptacle at the summit of the stem. Gemmæ of this kind are also produced in large numbers in special receptacles on the thalloid stem of Marchantia (see fig. 49, p. 426) and Lunularia among the Liverworts, as well as by the prothallia of some Ferns. In many cases (*Nephrolepis tuberosa*, *Lycopodium*, *Lilium bulbiferum*, etc.), the buds borne on the shoot become swollen and filled with nutritive substances, constituting bulbils, which, when they fall off and germinate, give rise to new plants. In a few plants adventitious buds are formed which subserve vegetative propagation. In *Bryophyllum Calycinum* (Crassulaceæ) and many Ferns (*Nephrodium* (*Lastrea*) *Filix mas*, *Asplenium* (*Athyrium*) *Filix fœmina*, and other species of *Asplenium*), such buds are formed on the leaves. A curious case of this has been observed by Strasburger in *Cælebogyne ilicifolia*, *Funkia*, *Citrus*, and *Nothoscordum fragrans*. In these plants adventitious budding takes place from the cells of the tissue of the nucellus which leads to the appearance of one or more embryos in the embryo-sac. The most familiar instance of reproduction by means of buds is afforded by the bulbous plants. These plants are annuals, and each during its life produces at least one modified subterranean bud, termed a corm or a bulb, from which a new plant is developed in the succeeding year. Other organs may also be modified to subserve vegetative propagation. Thus, the Potato-plant

is propagated by means of tubers which are modified subterranean shoots bearing numerous buds; and the Dahlia, by means of its tuberous roots which give rise on germination to shoots.

Although vegetative reproduction is in many cases very effectual, yet all plants possess the property of reproducing themselves by means of spores.

A spore is a single cell, a statement to which the "multicellular" or better the "compound" spores of some Fungi are not real exceptions, for these are, in fact, spore-aggregates. It consists, in the majority of cases, of a nucleated mass of protoplasm, enclosing starch or oil as reserve nutritive material, surrounded by a cell-wall. In those cases in which the spore is capable of germination immediately on the completion of its development, the cell-wall is a single delicate membrane consisting of cellulose: but in those cases in which the spore may have to, or must necessarily, pass through a period of quiescence before germination, the wall is thick and may consist of two layers, an inner, the *endospore*, which is delicate and consists of cellulose, an outer, the *exospore*, which is thick and rigid, frequently dark-coloured and beset externally with spines or bosses, and which consists of cutin. In some plants, particularly among the Algæ and also in some Fungi (*Peronosporæ*, *Saprolegnieæ*, *Myxomycetes*, *Chytridiaceæ*), spores are produced which are for a time destitute of any cell-wall, and are further peculiar in that they are motile, on which account they are termed *zoospores*. They move, sometimes in an amœboid manner by the protrusion of pseudopodia, but more frequently by means of cilia (see p. 1). The zoospore eventually comes to rest, surrounds itself with a cell-wall, and then germinates. In any case, a spore is a cell which is capable, by itself, of giving rise to a new individual on germination.

The main point concerning the development of spores is that they are produced in one of two ways, either *asexually* or *sexually*. In the former case they are directly produced from the protoplasm of a single reproductive organ, to which we may apply the general term *Sporangium*; hence we speak

of the sporangium as being an *asexual reproductive organ*. In the latter case the spores are not formed from the protoplasm of a single reproductive organ, but from the fused protoplasm of two distinct reproductive organs. A reproductive organ which is incapable of producing spores from its own protoplasm is a *sexual reproductive organ*; and the fusion of the protoplasm of two such organs which leads to the formation of spores constitutes what is known as the *sexual process*.

The mode in which the sexual process is effected is by no means the same in all plants. Without entering at present into minute details, it may be pointed out that it is usually preceded by a process of cell-formation in one or both of the organs concerned. The cells thus formed are, like the spores, reproductive cells, but unlike the spores they are not capable, each by itself, of giving rise to a new individual; it is only when two of these imperfect reproductive cells, sexual reproductive cells, or *gametes*, as they are termed, coalesce, that a fertile cell, a sexually produced spore, is formed.

Before entering into detail with regard to these two modes of spore-formation, we may note the fact that a suppression of spore-formation, either sexual or asexual, may occur, and vegetative reproduction be substituted. For instance, you are aware that, in the case of Ferns, the fern-plant produces spores which give rise to prothallia on germination. Now Bower has ascertained in the Fern *Athyrium Filix fœmina* var. *clarissima*, that the sporangia do not produce spores, but that some of them grow out directly into prothallia; that there is a substitution of vegetative reproduction for reproduction by means of asexually produced spores, a substitution which is termed *apospory*. Again, you are aware that the fern-plant is normally developed from the sexually produced spore (oospore) formed by means of the sexual reproductive organs of the prothallium. Now Farlow, de Bary, and Sadebeck, have observed cases (*Pteris cretica*, *Aspidium Filix mas*, var. *cristatum*, *Aspidium falcatum*, *Todea africana*) in which the fern-plant is developed as a bud from the prothallium without the intervention of the sexual

reproductive organs. In this case there is a substitution of vegetative reproduction for reproduction by means of a sexually produced spore, a substitution which is a case of what is termed *vegetative apogamy*.

The asexual production of spores is common to nearly all families of plants. In the simplest case of spore-production, of which plants of low organisation, such as *Nostoc* and *Bacillus*, afford examples, the spore is formed from the entire protoplasm of a single cell of the plant, which surrounds itself with the characteristic thick cell-wall. In other plants, somewhat more highly organised in this respect, the protoplasm of a cell, not specially modified but which may be regarded as a rudimentary sporangium, undergoes division, each portion constituting a spore. Examples of this are afforded, among unicellular plants, by Yeast and *Protococcus*, and in multicellular plants by the *Confervoideæ*, the *Ulvaceæ* and some *Florideæ*. In still more highly organised plants special organs are differentiated for the production of spores, and in the majority of these plants the special organ is a sporangium, that is a capsule in the interior of which the spores are developed. In the *Fungi*, however (*e.g.* some *Mucorini* such as *Chætocladium*, the *Ustilagineæ*, the *Entomophthoreæ*, the *Peronosporæ*, the *Ascomycetes*, the *Uredineæ*, the *Basidiomycetes*), the spores are produced by abstriction from hyphæ which are termed variously *conidiophores* or *basidia*.

As instances of plants in which the asexual production of spores either does not take place or is rare, the following may be mentioned :

Algæ: *Zygnemææ*, *Desmidiææ*, *Fucaceææ*, *Characeææ*, some *Florideææ* (*e.g.* *Lemaneaceææ*).

Fungi: *Peronosporææ*; *Pythium vexans*, *Artotrogus*.

Saprolegniææ; *Ancylistes Closterii*, *Aplanes Braunii*.

Ascomycetes; *Ascobolus furfuraceus*, *Pyronema (Peziza) confluens*, *Gymnoascus*, *Eremascus*, *Sordaria (Hypocopra)*, *Collemaceææ* and other *Lichen-fungi*.

In many cases, in speaking of asexually produced spores, a prefix is added to the word "spore," or an altogether different term may be employed, in order to mark some

peculiarity in this mode of their origin, to indicate the order of their development, to assign them without periphrasis to a particular group of plants, etc. Thus, as has been already mentioned, *zoospores* are motile spores: *stylospores* are spores which are developed, not in sporangia, but by abstriction as described above: *tetraspores* is the name given to the asexually produced spores of the Florideæ to denote the fact that usually four spores are produced by the division of the mother-cell: the *uredospores* of the Uredineæ are those which are produced during the summer, whereas the *teleutospores* of these Fungi are those which are formed in the autumn at the close of the season of growth. The spores of the Fungi are sometimes spoken of generally as *conidia*, and the word *gonidia* is sometimes applied to the spores of the Algæ. Certain vascular plants, constituting the Rhizocarpæ (Hydropterideæ), the Ligulatæ, and the Phanerogams, produce spores of two kinds, and are therefore said to be *heterosporous*, therein differing from their allies the Ferns, Equisetums, and Lycopodiums, which produce spores of one kind only, and are therefore said to be *isosporous* or *homosporous*. The two kinds of spores differ in size, and also in that they give rise to different organisms on germination. On account of their difference in size they are distinguished as large spores or *macrospores* and small spores or *microspores*, and the organs producing them are termed respectively *macrosporangia* and *microsporangia*. In the Phanerogams these organs are more familiarly known by other names; in this group of plants the macrosporangium is termed the *ovule*, and the macrospore, the *embryo-sac*; the microsporangium the *pollen-sac*, and the microspore, the *pollen-grain*. In some of these plants there is the further peculiarity that the spore is not liberated from the sporangium, but germinates there: this is the case with regard to the microspores of *Salvinia* among the Rhizocarpæ, and with regard to the macrospores (embryo-sacs) of the Phanerogams. This peculiarity in the Phanerogams, leads, as we shall subsequently learn more fully, to the production of that structure, the seed, which is characteristic of these plants. The production of a seed constitutes, in fact,

the only real and constant distinction between Phanerogams and Cryptogams.

In plants of comparatively low organisation the organs which give rise to the asexually produced spores are usually not confined to a particular part of the plant, though an instance of this is afforded by the *pycnidia* of the Pyrenomycetous Ascomycetes, which are receptacles in which the stylospores are produced. In the Muscinæ the production of spores only takes place in the capsule, which always constitutes a considerable portion, and in some cases (*Riccia*) the whole, of the body of the individual. In the vascular plants (Pteridophyta, Phanerogams) the sporangia are, speaking generally, confined to the leaves. In many of the Pteridophyta the sporangiferous leaves do not differ in appearance from the foliage-leaves; but in others they differ more or less widely from them, as in the Equisetaceæ, Marsiliaceæ, some species of *Lycopodium* and *Selaginella*, and notably in Phanerogams. When the sporangiferous leaves differ widely from the foliage-leaves in size, form, or colour, they are usually aggregated together in groups on a branch, and such an aggregate of sporangiferous leaves constitutes what is known as a *flower*. In the Phanerogams the modification of the sporangiferous leaves is so great that they have received special names; those which bear the macrosporangia (ovules) are termed *carpels*, and those which bear the microsporangia (pollen-sacs) are termed *stamens*.

We pass now to the consideration of the sexual production of spores. This mode of spore-formation is known to take place in nearly all families of plants above the Proto-phyta; and in those in which, in spite of careful observation, it cannot be detected, its absence is to be ascribed, not, as in the case of the Proto-phyta, to the non-development of sexuality, but to sexual degeneration.

The following are plants or families of plants in which no sexual spore-formation has yet been discovered:

Algæ: Cyanophyceæ (Phycobromaceæ); Protococcaceæ; Sphacelariæ; Laminariæ.

Fungi: Schizomycetes; Saccharomycetes; Myxomycetes; some

Chytridiæ; probably many Mucorini; a few Peronosporæ (probably *Phytophthora infestans* and *Pythium intermedium*); some Ascomycetes and Uredinæ; Basidiomycetes.

In the plants just enumerated, not only are spores not formed sexually, but the existence of sexual organs is unknown; these plants, so far as we know, are entirely asexual and are reproduced only either vegetatively or by means of asexually produced spores. In many other cases, which we shall subsequently discuss, we meet with an absence of sexuality which is less complete; in these, namely, organs which are morphologically sexual organs make their appearance, but instead of producing sexual reproductive cells, they produce cells which are capable each by itself of giving rise to a new individual;—in a word, they are physiologically sporangia producing spores. This substitution of an asexual for a sexual production of spores, is another form of apogamy, and is distinguished as *parthenogenesis*.

The most satisfactory method of arriving at a comprehension of the sexuality of plants is to study, on the one hand, the development, and, on the other, the degeneration of sexuality, and this method we will now pursue. We will, in the first place, trace the development of sexuality in the plants containing chlorophyll, beginning with the simplest Algæ, and then we will consider the degeneration of sexuality with special reference to the Fungi.

It has been already mentioned that the protophytic Algæ only produce spores asexually, but in some forms a differentiation of these spores can be detected. In *Hæmatococcus*, for instance (see Lect. 1, p. 1), zoospores are produced, but the zoospores are not all precisely alike. In some cases the protoplasm of the cell divides only once or twice, the result being the formation of two or four relatively large zoospores, called *macrozoospores*; in others the protoplasm divides a greater number of times so that a considerable number of relatively small zoospores, called *microzoospores*, are produced. Functionally these zoospores are all alike; they all come to rest, and each constitutes a new *Hæmatococcus*.

Amongst the Confervoideæ, which are somewhat more highly organised than the protophytic Algæ, we find forms, of which *Ulothrix* may be taken as an example, which likewise produce macro- and microzoospores. The macrozoospores simply come to rest and germinate. The microzoospores may also behave in this way; but, as Dodel-Port observed, they not infrequently coalesce in pairs, producing by their coalescence a single cell of the nature of a spore which on germination gives rise to a new *Ulothrix*-filament.

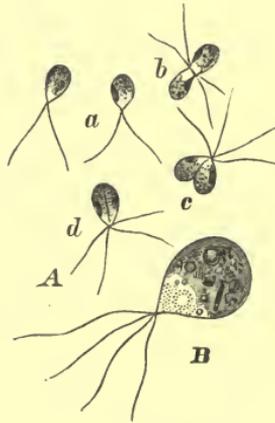


Fig. 65 (after Dodel-Port). *A* conjugating microzoospores of *Ulothrix*.
B macrozoospore of *Ulothrix*.

Comparing *Ulothrix* with *Hæmatococcus*, we see that in both plants the macrozoospores are asexual reproductive cells, that is, spores. This is true also of the microzoospores of *Hæmatococcus*, but only to a limited extent of the microzoospores of *Ulothrix*, for, instead of each germinating independently, they may coalesce in pairs, that is, go through a sexual process. The microzoospores of *Ulothrix* are reproductive cells which are intermediate between the altogether asexual microzoospores of plants like *Hæmatococcus* on the one hand, and the altogether sexual reproductive cells of the higher plants.

The coalescence in pairs of the microzoospores of *Ulothrix* is an instance of one of the simplest modes of the sexual

process. When, as in this case, the two coalescing cells are externally quite similar, the term *conjugation* is applied to the process; the coalescing cells are simply termed *gametes*, or, when as in this case they are ciliated and motile, *planogametes*; and the spore resulting from the coalescence is termed a *zygospore*. The cell in which the gametes are produced is termed a *gametangium*.

In some of the Siphonæ, such as *Acetabularia* and *Botrydium*, the asexually produced spores are ordinarily resting-spores, though an adventitious production of uniciliate zoospores may take place in *Botrydium*. On germination, the protoplasm of the resting-spore undergoes division to form a number of ciliated cells which are set free. In *Acetabularia* these cells are sexual, conjugating in pairs; they are planogametes, and the cell producing them a gametangium. This is true also in the case of *Botrydium* provided that the germinating resting-spore is young. When the resting-spore is old, the cells to which it gives rise on germination, as Rostafinski and Woronin point out, do not conjugate, but develop independently, though they are externally similar to the planogametes. We have, in fact, a case of parthenogenesis.

On reviewing the foregoing facts, we see that the entirely sexual planogametes of *Acetabularia* can be traced back, through *Botrydium* and *Ulothrix*, to the entirely asexual microzoospores of *Hæmatococcus*. We may conclude that all gametes are derivatives of the spore, and that all sexual reproductive organs are derivatives of the sporangium; in a word, that sexual has arisen out of asexual reproduction. To this point we shall again refer subsequently.

Up to this point we have had to deal with gametes which are externally similar, but in our further discussion of the subject we come now to gametes which are more or less dissimilar either in the size or form, or in the part which they take in the sexual process. These external differences are indications of a physiological difference which constitutes *sex*. Without entering at present into a discussion of the nature of sex, which we reserve for a future occasion, it may be

pointed out that a sexual difference probably exists even when the gametes are externally similar; that one of them is *male* and the other *female*. This is indicated by the fact that a planogamete of *Ulothrix* or *Acetabularia* will only conjugate with another derived from a different gametangium; and, in the case of *Dasycladus*, conjugation only takes place between planogametes derived from different individuals.

We will now trace the gradual external differentiation of the gametes. In *Ectocarpus siliculosus* and in *Scytosiphon*, Algæ belonging to the group of the Phæosporeæ, there are two kinds of reproductive organs, the unilocular and the multilocular, which both give rise to motile and externally similar reproductive cells. Those produced in the unilocular organ germinate independently; they are, in fact, zoospores, and the organ producing them, a sporangium. Those produced in the multilocular organs may germinate

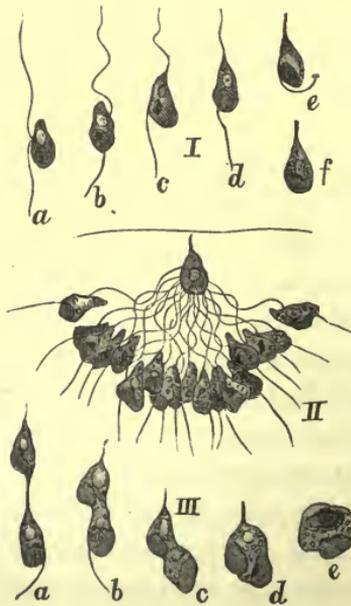


Fig. 66 (after Berthold). Process of conjugation in *Ectocarpus*. *I a-f* the female planogamete coming to rest. *II* the female planogamete at rest surrounded by male planogametes. *III a-e* the fusion of the female with a male planogamete.

independently, but they have been observed to conjugate in pairs. Thus, like the microzoospores of *Ulothrix*, they exhibit incomplete sexuality. The process of conjugation, as described by Berthold, indicates that, though externally similar, the planogametes are physiologically different. One of them, namely, comes to rest and withdraws its cilia; the other, remaining motile, approaches and coalesces with the former. The planogamete which is passive in the process is the female, the one which is active is the male.

In *Cutleria*, another of the *Phæosporeæ*, the sexual difference is more marked. To begin with, there are two kinds of gametangia which are obviously different from each other: the one consists of a large number of small cells, and produces a large number of small planogametes: the other consists of a relatively small number of large cells, and gives rise to a few large planogametes. The sexual process, as described by Falkenberg, consists in the coalescence of one of the small planogametes with one of the large ones. The large planogamete has but a short period of motility; it soon comes to rest, withdraws its cilia, and rounds itself off, the hyaline pointed end of the planogamete becoming the *receptive spot* of the resting-cell, the spot, that is, at which the small planogamete will coalesce with it. The large planogamete is clearly female, and the smaller one male.

In the *Fucaceæ* the sexual reproductive organs are very different from each other, and the gametes differ, not only in size, but in that the female cell is not, whereas the male cell is, a planogamete. The female gametes are, it is true, extruded from the organ producing them, but they are not motile. When the difference between the sexual organs and cells is so well-marked as this, special terms are employed. The female gamete is now called an *oosphere*, the male, an *antherozoid*: the organ producing the oosphere is termed an *oogonium*, and that producing the antherozoid, an *antheridium*. Inasmuch as the female gamete is wholly passive, the sexual process is termed *fertilisation*, the female gamete being said to be fertilised by the male. The product of the sexual process, the fertilised oosphere, is termed an *oospore*.

In such forms as *Coleochæte*, *Vaucheria*, *Oedogonium*, *Volvox*, *Sphæroplea*, and the *Characeæ*, the distinction of sex attains its fullest expression, in that the oosphere has lost every trace of its primitive planogamete character. In these *Algæ* it is not extruded from the oogonium, but is fertilised there by an antherozoid which makes its way into the organ. In *Vaucheria* and *Oedogonium* the oosphere presents, like the large planogamete of *Cutleria*, a well-defined receptive spot at which the entrance of the antherozoid into the oosphere takes place.

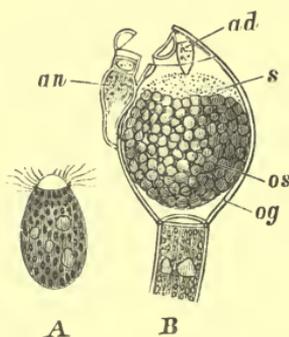


Fig. 67 (after Pringsheim). Reproduction of *Oedogonium*. *A* zoospore. *B* fertilisation. *og* oogonium. *os* oosphere. *an* antheridium (dwarf-male). *ad* antherozoid entering *s* the receptive spot of the oosphere.

This state of things, which is in fact the most perfect manifestation of sex which is attained among plants, obtains throughout the Mosses (*Muscineæ*) and the Vascular Cryptogams (*Pteridophyta*). In all these plants there is a female organ, the *archegonium*, in which, as in the oogonium of the *Algæ*, the female cell, the oosphere, is developed: the archegonium differs from the oogonium in this respect only, that whereas the former is usually multicellular, the latter is usually unicellular. The male cells in these plants are antherozoids, and the organ in which they are developed is termed an antheridium. The antheridium of these higher plants differs from that of the *Algæ* in that it is multicellular, whereas in the *Algæ* it is commonly unicellular, though to this there are exceptions, notably the *Characeæ*, in which group the antheridium is multicellular and of highly complex structure. In

connexion with the comparative structure of the antheridium it may be mentioned that, in the Muscineæ and the Vascular Cryptogams, each antherozoid is developed singly in a mother-cell. This is the case in some of the Algæ, such as the Characeæ, Coleochæte, and Oedogonium, but in the others, such as Volvox, Vaucheria, Sphæroplea, Fucus, the antherozoids are formed in considerable numbers from the protoplasm of one and the same cell.

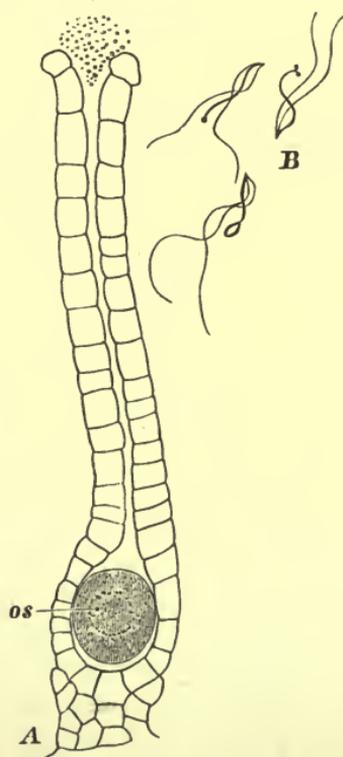


Fig. 68 (after Strasburger). (A) Archegonium of a Moss with antherozoids (B) :
os oosphere.

We have now completed the task of tracing the development of sexuality and the differentiation of the sexual cells from the first indications to the culminating point. Beginning with the entirely asexual microzoospores of *Hæmatococcus*, we have passed through the imperfectly sexual cells of *Ulothrix* and *Botrydium*, to the completely sexual planogametes of *Acetabularia*; and beginning again with the entirely similar planogametes of *Acetabularia*, we have passed

through the incompletely differentiated planogametes of *Ectocarpus* and *Cutleria* to the highly differentiated gametes of *Fucus* and the higher Algæ, the Muscineæ, and the Pteridophyta. In all these cases the product of the coalescence of the two sexual cells, whether externally different or similar, is a cell which, unlike the two cells which fuse to form it, is capable by itself of developing into a new individual; in a word, it is a sexually produced spore.

Before passing to the consideration of sexuality in the Fungi, we may conveniently discuss the peculiar modes of the sexual process which are characteristic of certain groups of plants which possess chlorophyll, namely, the Conjugatæ and the Florideæ among the Algæ, and the Phanerogams.

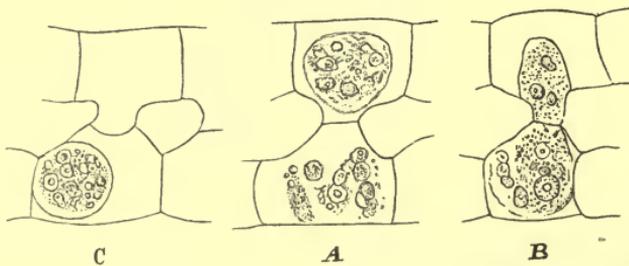


Fig. 69 (after Strasburger). Stages in the conjugation of *Spirogyra*.

The group of the Conjugatæ, including the *Zygnemeæ*, *Mesocarpeæ*, and *Desmidiæ*, is made up of plants which are either unicellular, or consist of filaments of similar cells. In all these plants the sexual process is of this kind, that the walls of two adjacent cells, whether they be isolated cells, or whether they form part of two contiguous filaments—or, rarely, when they form part of the same filament (*Rhynconema*)—grow out towards each other into protuberances which at length come into contact. The partition walls then undergo absorption, and thus a channel of communication is set up between the two cell-cavities (Fig. 69). The protoplasm of the two communicating cells fuses to form a spore, but this fusion does not take place in quite the same way in all cases. In the *Zygnemeæ* (Fig. 69), the protoplasm of one of the two cells contracts before that of the other, and travels through

the canal into the cavity of the other cell and then fuses with its contracted protoplasm. In the Mesocarpeæ and the Desmidiæ the protoplasm contracts simultaneously in both cells, and both the masses travel into the canal; so it is in the canal that the fusion takes place and the spore is formed.

The sexual process of the Diatomeæ differs from that of the allied Conjugatæ, in that the protoplasmic contents of the two conjugating cells escape from their respective cell-walls as a preliminary to fusion. It represents a mode of the sexual process which is intermediate in character between that of the typical Conjugatæ and the conjugation of planogametes.

In comparing these modes of the sexual process with those with which we have already become acquainted, we see at once that the two cells in question constitute rudimentary reproductive organs of the nature of gametangia, resembling in this respect the cells of a Ulothrix-filament. But whereas the protoplasm of the Ulothrix-cell undergoes division into a number of portions which are set free as, at least potential, planogametes, that of the cells of the Conjugatæ does not divide, but constitutes a single gamete. In speaking of the sexual process in the Conjugatæ, the process is termed conjugation, and the product a zygospore, on account of the general similarity of the gametes. But it must not be overlooked that this similarity is complete only in the Mesocarpeæ and in the Desmidiæ. In the case of the Zygnemeæ, it is clear that the gamete which is formed first and which takes the more active part in the process of conjugation must be regarded as a male cell, whereas the other, formed later and passive in the process of conjugation, must be regarded as a female cell.

In the Florideæ the sexual reproductive organs are differentiated, but it is only the male organ which produces sexual reproductive cells. In the simpler forms (Bangiaceæ) the male cells are developed several together from the protoplasm of a single mother-cell, whereas in the higher forms each mother-cell gives rise to only one male cell. The male-organ, or antheridium, may consist of a single mother-cell (*e.g.* *Batrachospermum*) or of a cluster or group of mother-cells. The male-cells differ from the antherozoids and gametes

already described in that they are not naked motile masses of protoplasm like these, but are enclosed in a cell-wall, and are not motile: they are sometimes spoken of as antherozoids, but it is convenient to distinguish them as *spermatia*. The female organ also is peculiar. It may consist of one or of many cells; but whatever its structure it always presents the following characteristic features: it is permanently closed: it exhibits a distinction into two parts, the one a filamentous receptive part, termed the *trichogyne*, and a more or less dilated portion, the *carpogonium*, the whole organ being termed a *procarpium*; and finally no female reproductive cell of the nature of an oosphere can be detected within it. The sexual process takes place in this manner. The spermatium (antherozoid) is brought passively into contact with the trichogyne; complete fusion takes place so that the contents of the spermatium pass into the trichogyne. When this has occurred the trichogyne withers and changes become apparent in the basal carpogonial portion of the procarpium. If it is unicellular it divides, and if multicellular one or more of its cells (*carpogenous cells*) divide, and by a process of budding a cluster of cells is produced, which frequently becomes invested by an upgrowth of tissue from the neighbouring vegetative cells of the plant. This fructification is termed a *cystocarp*. The cells thus produced are spores, that is to say, they are capable each by itself of giving rise to a new plant, and they are distinguished as *carpospores* to indicate the peculiarities connected with their production.

The sexual production of spores in the Floridæ is of special interest in that it affords us an example of a sexual process taking place, not as in the cases already considered between two sexual reproductive cells, but between a reproductive cell, the spermatium, on the one side and the undifferentiated protoplasm of a female organ on the other. It is, as we have seen, only as a consequence of fertilisation by the spermatium that a formation of reproductive cells takes place in the carpogonium; and the cells then formed are not female reproductive cells, but are spores. The significance of the facts is this, that in consequence of the fusion of the sperma-

tium with the trichogyne the carpogenous cell or cells are at once fertilised and stimulated to cell-formation, and accordingly they produce the carpospores, each of which is physiologically equivalent to a zygospore or an oospore, inasmuch as it is, like them, a sexually produced spore.

The peculiarities of the sexual process in some of the Florideæ are so striking as to merit brief mention.

In the Corallineæ, according to Solms-Laubach, the procarpia are produced several together in a conceptacle; it is, however, only the central procarpia of the group which are capable of being fertilised, and it is only the peripheral procarpia which produce carpospores; the former, in fact, are functionally only trichogynes, the latter only carpogonia. After the fertilisation of the central procarpia, the carpogonia of the whole of the procarpia fuse together to form one large cell from the periphery of which the carpospores are budded off; thus a number of procarpia eventually give rise to only one cystocarp.

This tendency to a physiological division of labour is more marked in *Dudresnaya* and a few other Florideæ. In these, some of the procarpia are altogether destitute of a trichogyne, whereas others possess one. The spermatia fertilise those procarpia which possess a trichogyne, but these procarpia do not produce carpospores. There grow out of them filaments which grow out towards the procarpia which have no trichogyne and fertilise them, and these then produce carpospores.

In the Phanerogams the sexual organs are essentially of the nature of the archegonia and antheridia mentioned above. In most of the Gymnosperms the female organ, though commonly termed a *corpusculum*, is in fact nothing more or less than an archegonium. In the Angiosperms the female organ is represented by a group of three cells, termed the *egg-apparatus*, one of the three cells being the oosphere and the other two the *synergidæ*. There is some ground for the view that these three cells represent three much reduced archegonia, only one of which is directly concerned in the sexual process. The male organ of the Phanerogams is a unicellular filament known as the *pollen-tube*. It is a male organ, the protoplasmic contents of which undergo imperfect differentiation into male gametes. Just before fertilisation takes place—the pollen-tube being already in close relation with the female organ—the apex of the pollen-tube contains protoplasm and a nucleus, which Strasburger has termed the *generative nucleus*. In most

cases the generative nucleus divides into two, and in some cases a second nuclear division takes place. At the time of fertilisation one of the nuclei thus produced escapes, together with a certain amount of protoplasm, through the mucilaginous apex of the pollen-tube. This gamete, as we may term it, enters the female organ, makes its way to the oosphere, and fertilises it.

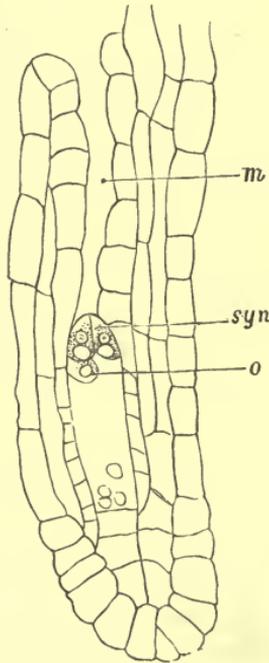


Fig. 70 (after Strasburger). Longitudinal section of the ovule of an Angiosperm (*Monotropa Hypopitys*). *m* micropyle. *syn* synergidæ. *o* oosphere.

In the Cupressineæ the mode of development is somewhat different, since in these plants one pollen-tube serves for the fertilisation of several female organs, and consequently several gametes have to be produced. The first division of the generative nucleus in the pollen-tube of the Cupressineæ is followed by an aggregation of protoplasm round each of the two new nuclei, so that two primordial cells are formed. Nucleus division is repeated in the primordial cell which is the nearer to the apex of the pollen-tube, without any corresponding cell-formation, so that several nuclei are to be found in the dilated apex of the pollen-tube; these, with a certain amount of protoplasm, escape as gametes through the mucilaginous apex of the pollen-tube, and each fertilises the oosphere of an archegonium.

Turning now to the Fungi, we find that in the lowest forms, the Zygomycetes, in which a sexual process has been observed (Chytridiaceæ, e.g. *Polyphagus Euglenæ*; the Mucorini; the Entomophthoræ), it is in the form of conjugation

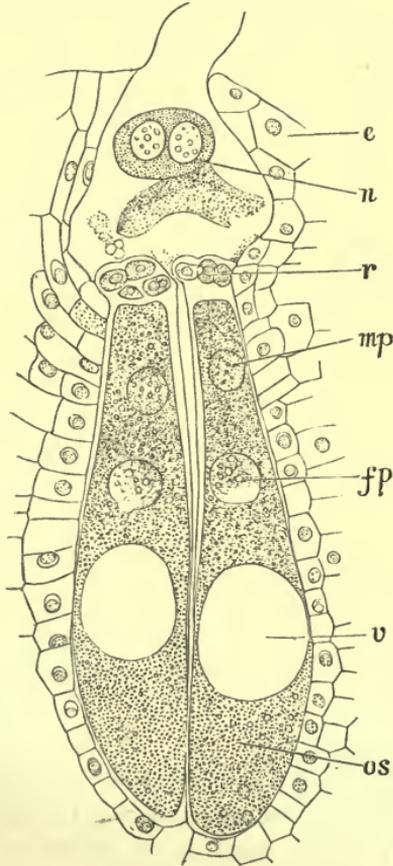


Fig. 71 (after Strasburger). Two corpuscula of *Juniperus virginiana* in process of fertilization. *e* endosperm. *os* oosphere. *v* vacuole of oosphere. *fp* female pronucleus. *mp* male pronucleus. *r* rosette or neck of corpusculum. *n* nucleus in dilated end of pollen-tube.

with the production of a zygospore. The conjugation is in nearly all cases of the kind described above in the Conjugatæ; that is, it consists in the coalescence of the protoplasmic contents of two externally similar sexual reproductive organs. Conjugation of planogametes is rare; it has been described by

Sorokin as occurring in two plants, Tetrachytrium and Haploctystis, which probably belong to the Chytridiaceæ.

It is of interest to note that in various Mucorini (*Absidia septata* and *capillata*, *Mucor fusiger*, Sporodinia, always in *Mucor tenuis*) and Entomophthorææ (*Entomophthora radicans*, and various species of *Empusa*) we have well-marked instances of sexual degeneration. Spores, exactly resembling the zygospores, are produced parthenogenetically by the reproductive organs. In some cases the reproductive organs are produced, and come into relation, but no fusion, no sexual process takes place, but each produces a zygospore independently. In other cases an isolated reproductive organ produces a single zygospore. These parthenogenetically produced spores are termed *azygospores*.

In Protomyces and the Ustilagineæ a peculiar mode of conjugation has been observed. Certain reproductive cells of an elongated form, termed *sporidia*, are produced, and these become connected in pairs by a transverse canal, so that they then resemble the letter H. No zygospore is formed, but the H-like body is its equivalent. The question of the sexual nature of this process is still under discussion, but it is made probable by the fact that in all fully investigated cases the sporidia are incapable of independent germination, a fact which, if fully established, would prove them to be sexual reproductive cells. But against this there is to be set Fisch's observation that the nuclei of the conjugating sporidia apparently do not fuse.

It is in the group of Fungi which we may term the Oomycetes, that the sexual process attains its highest development in the Fungi. In the Ancylisteæ, which may be regarded as the lowest form of this group, the sexual process shews but a slight advance on that obtaining among the Zygomycetes. It is true that the two sexual organs differ from each other in external appearance, the female organ, here termed an oogonium, being relatively large and expanded into a bulbous form, whereas the male organ, the antheridium, is filamentous and relatively small. In the sexual process the whole of the contents of the antheridium pass over as a gamete into the oogonium and fuse with the whole of its protoplasm, the product being an oospore. It may be incidentally mentioned

that a male organ of this kind is not uncommonly distinguished as a *pollinodium*.

In the Peronosporæ the sexual organs differ in size, the female organ (oogonium) being the larger, and, as in the Zygomycetes and in the Ancylisteæ, they are developed in close relation with each other. But there is this well-marked advance in sexuality that, as a preliminary to fertilisation, there is a process of cell-formation in both of the organs. In the pollinodium the protoplasm undergoes differentiation into a delicate hyaline peripheral layer, which de Bary has termed the *periplasm*, and a granular central mass, which he has termed the *gonoplasm*. In the oogonium, similarly, a layer of periplasm is differentiated from the granular central mass which is the oosphere. Just before fertilisation, the pollinodium puts out a small tubular protuberance which penetrates the wall of the oogonium and extends to the oosphere. The apex of this tube then opens and the gonoplasm of the pollinodium passes, as a gamete, through the tube and enters the oosphere, the product of the fusion being an oospore. (Fig. 72.)

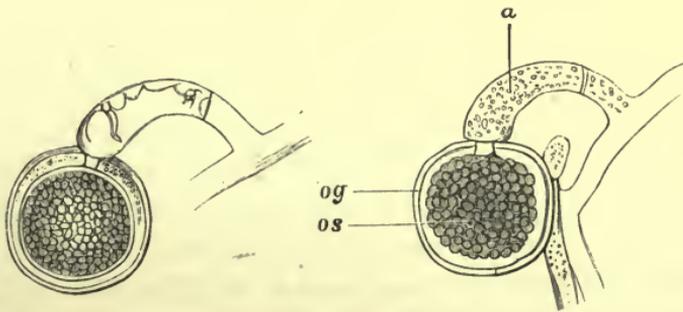


Fig. 72 (after de Bary). Sexual reproductive organs and fertilisation of *Pythium*. *a* antheridium. *og* oogonium. *os* oosphere. In the right-hand figure fertilisation is in progress: in the left-hand figure it is completed and the oospore is formed.

The sexual organs of the Saprolegnieæ closely resemble those of the Peronosporæ. In the oogonium a process of cell-formation takes place which results in the production of one or more oospheres; but there is this difference between this process and that which takes place in the oogonium of the

Peronosporæ, that there is no differentiation of the protoplasmic contents of the oogonium into periplasm and ooplasm, but the whole is employed in the formation of the oospheres. According to de Bary no differentiation takes place in the protoplasm of the pollinodium, whereas Pringsheim asserts that a formation of amœboid antherozoids takes place in *Achlya* and *Saprolegnia*. De Bary has been, in fact, unable to observe any actual sexual process in these plants, even in those cases in which the pollinodium throws out a tube which enters the oogonium, for it appears that the tube remains closed. Pringsheim, on the contrary, maintains that the oospheres are fertilised by the amœboid antherozoids. There is no doubt that in some cases the oospores are parthenogenetically developed, for in these cases (*e.g.* *Aphanomyces scaber*, *Saprolegnia hypogyna*) oogonia are developed without pollinodia in relation with them, and in many cases in which pollinodia are present they put forth no tube into their corresponding oogonia. There is therefore no *a priori* objection to de Bary's view that the oospores of the Saprolegniæ are always parthenogenetically developed. Assuming the correctness of de Bary's view, we have in the Saprolegniæ an instance of sexual degeneration in the group of the Oomycetes, corresponding to that which is afforded among the Zygomycetes by those forms which produce azygospores.

The genus *Monoblepharis*, described by Cornu, differs from the foregoing groups of the Oomycetes, and in fact from all other Fungi, in that the protoplasm of the male organ undergoes differentiation into ciliated antherozoids. A single oosphere is formed in the oogonium apparently from the whole of the protoplasm of the organ, and fertilisation is effected by the fusion of an antherozoid, which has entered through the ruptured apex of the oogonium, with the oosphere. We find in this genus a differentiation of the sexual cells which is as well-marked as it is in the higher Green Algæ, the Musciæ, or the Pteridophyta.

We pass now to the Ascomycetes. The simplest form of the sexual process in the plants of this group is that described by Eidam as occurring in *Eremascus albus*. The sexual organs

of this Ascomycete are two quite similar hyphal branches which are closely coiled round each other, and which coalesce, after the absorption of the intervening walls, at their apices. The product of coalescence is, in the first instance, a large rounded cell. So far the process and its product resemble those of the Mucorini, and were this all the process would be termed conjugation, and the product a zygospore. But the cell in question is not a zygospore; it does not, like a zygospore, germinate and give rise to a new plant. A process of cell-formation goes on within it, as a consequence of which eight free cells are produced, which, on being liberated, germinate. It is, in fact, these eight cells which are the spores; they are termed *ascospores*, and the large cell in which they are developed the *ascus*.

The peculiar nature of this mode of the sexual process demands a brief explanation. We have here a case in which no process of cell-formation takes place in either of the sexual organs as a preliminary to the sexual process. It is only when the protoplasmic contents of the two sexual organs have fused that cell-formation takes place; and inasmuch as the cells then formed consist of protoplasm derived from the two sexual organs, they are not sexual reproductive cells, but are sexually produced spores; each of them is, in fact, physiologically the equivalent of a zygospore or an oospore.

The sexual process is essentially of this nature in many Ascomycetes, though the sexual organs differ from each other externally, thus affording an indication of differentiation of sex which is wanting in Eremascus. In *Pyronema* (*Peziza*) *confluens*, according to the descriptions of De Bary, Tulasne, and Kihlmann, the sexual organs are hyphæ which are developed close together. One of these undergoes no special modification, and constitutes the male organ, the pollinodium; the other, which is the female organ, the *archicarp* or *carpogonium*, becomes somewhat dilated, and develops at its rounded free end a delicate tube which is a trichogyne. This trichogyne becomes closely applied to the pollinodium, and, in consequence of the absorption of the intervening cell-walls, complete fusion of the protoplasmic contents of the pollino-

dium with those of the trichogyne takes place. The effect of this fusion is soon manifested in the dilated basal portion, *ascogonium*, of the female organ. It increases in size and develops short tubular outgrowths, the *ascogenous hyphæ*, which give rise to numerous asci in which ascospores are eventually produced. Whilst this is going on, the female organ and its ascogenous hyphæ become surrounded by a dense upgrowth from the mycelium, the whole forming the characteristic fructification (*apothecium*).

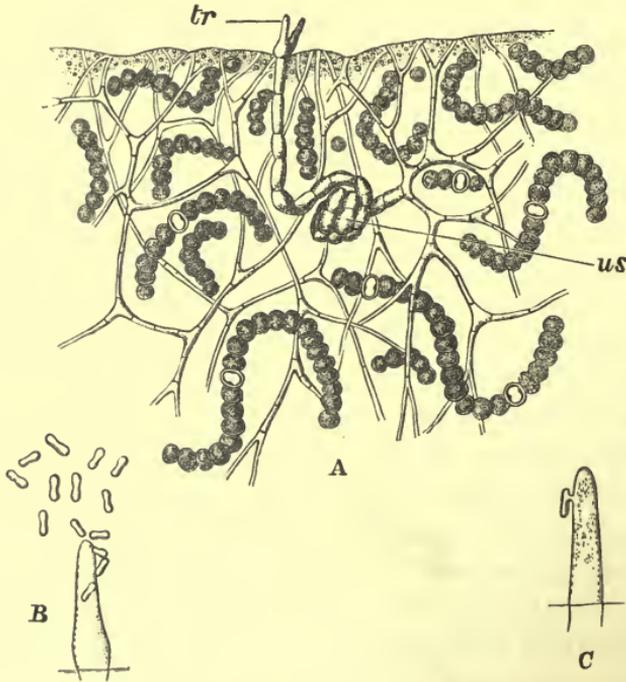


Fig. 73 (after Stahl). *A* section of the thallus of a Lichen (*Collema microphyllum*), shewing the ascogonium *us* and the projecting end of the trichogyne *tr*. *B* end of trichogyne surrounded by spermatia. *C* fusion of a spermatium with the terminal cell of the trichogyne.

But besides these sexual Ascomycetes in which there is no differentiation of sexual reproductive cells, there are others in which male reproductive cells are differentiated, though in no Ascomycete is there any differentiation of female reproductive cells. The differentiation of male reproductive cells takes place in certain Ascomycetes in which, unlike *Eremascus* and

Pyronema, the reproductive organs are not developed in close proximity to each other. In these Ascomycetes, which belong to the Discomycetous Lichens (*Collema*, *Synechoblastus*, *Leptogium*, *Physma*), and to the Pyrenomycetes (*Polystigma*), the antheridial filaments, termed *sterigmata*, are developed in special receptacles, the spermogonia. The male cells are formed by abstriction from the sterigmata; they are, like those of the Florideæ, non-motile cells provided with a cell-wall, and are likewise termed *spermatia*. The female organ is a multicellular hypha which forms a spirally wound basal portion (ascogonium) and is prolonged into a straight portion, a trichogyne (Fig. 73). Fertilisation is effected, as in the Florideæ, by the fusion of a spermatium with the trichogyne. The product of fertilisation is the same as in *Pyronema*: the fertilised ascogonium gives out hyphæ which bear asci, and these, together with sterile hyphæ derived from the mycelium, constitute a fructification.

It is of interest to note the close correspondence between the sexual process and the products of fertilisation of the Ascomycetes, on the one hand, and of the Florideæ, on the other. In both cases there is no cell-formation in the female organ which leads to the differentiation of one or more oospheres; and in both cases the product of the fertilisation of the female organ is a many-spored fructification, each spore (carpospore) being a sexually produced spore.

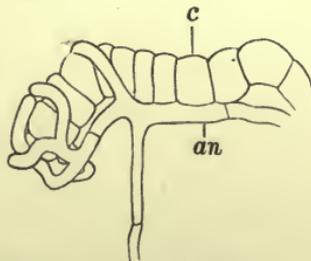


Fig. 74 (after Baranetzky). Sexual reproductive organs of *Ascobolus*.
an antheridium. *c* ascogonium.

In the Ascomycetes all stages of sexual degeneration are represented. Some members of the group (*e.g.* the *Erysiphææ*, *Ascobolus*, *Penicillium*, etc.,) possess distinct sexual organs

which more or less resemble those of *Pyronema*, but there is at present no evidence that a sexual process takes place between them. On the contrary, there is reason to believe that these Ascomycetes, though morphologically sexual, are not physiologically sexual. Still the ascogonium gives rise to asci and ascospores, but the ascospores must be regarded as being parthenogenetically produced. They are, then, not actually sexually produced spores, but they are homologous with them. In other forms (*Chætomium*, *Melanospora*) only one organ, the ascogonium has been found; it seems that the pollinodium has here disappeared. In these cases also the ascogonium produces asci and ascospores, and it is clear that these ascospores must be parthenogenetically developed. In others again (*Xylaria*), even the ascogonium is rudimentary (Woronin's hypha), and, finally, in others (*Claviceps*, *Cordiceps*, *Pleospora*) no trace even of an ascogonium can be found. But even in these cases asci and ascospores are produced, the asci springing from the vegetative mycelium. It is here a case, not of parthenogenesis, but of complete apogamy; the sexual production of spores is replaced by an altogether asexual process; but the mode of development of the spores resembles that of the sexually produced spores of the sexual forms.

In the remaining groups of the Fungi, the Uredineæ and the Basidiomycetes, no sexual process has been observed. In the Uredineæ, spermatia, like those of the Ascomycetes, are commonly produced, but no female organ has been discovered. However, the Uredineæ produce fructifications, termed *æcidia*, which somewhat resemble those of the Ascomycetes, but the spores (*æcidiospores*) are developed, not in asci, but by abstriction. It may be that we have in the *æcidium* a fructification which, though apparently produced independently of a female organ, corresponds to that of the Ascomycetes which is produced from the ascogonium in consequence of fertilisation; we know, in fact, that this is true of the fructification of the asexual Ascomycetes. But when we come to the fructification of the Basidiomycetes, such a correspondence cannot be traced. No kind of sexual organ has been discovered in the Basidiomycetes, in spite of the most careful and complete

observations, notably those of Brefeld, and it would appear that the fructifications on which the spores (basidiospores) of these plants are borne find their homologues, not in the sexually produced, but in the normally asexually produced fructifications of the other Fungi. The Basidiomycetes appear, in fact, to be altogether asexual. Not only are they destitute of sexual organs, but they lack even that trace of sexuality which is indicated in the asexual Ascomycetes, such as *Claviceps*, etc., by the production of fructifications resembling those which are the product of the sexual process in the sexual Ascomycetes. The fructifications of the Basidiomycetes are simply organs for the asexual production of spores.

The result of the sexual process is, as we have seen, in all cases the production of one or more spores, but the effect of the sexual process is not necessarily confined to the cells or organs which directly take part in it. In very many cases it stimulates adjoining organs to active growth, leading to the formation of the structure which is termed the *Fruit*. For instance, in various Mucorini an outgrowth of filaments, forming a complete (*Mortierella*) or incomplete investment to the zygospore, takes place after conjugation: in *Coleochæte* the oogonium becomes surrounded, after the fertilisation of the oosphere, by a cellular investment formed by outgrowths from adjacent vegetative cells; and, as we have already learned, a cellular investment is formed in a similar manner round the fertilised procarpium of most Florideæ, and round the fertilised ascogonium of most of the sexual Ascomycetes, resulting in the formation of the cystocarp in the former case, and in that of the apothecium or perithecium in the latter. The most familiar instance of fruit-formation is that occurring in the Phanerogams. Here, in most cases the carpels, in some the perianth-leaves, and in some the floral receptacle (*torus*) grow actively after the fertilisation of the oospheres has taken place, giving rise not infrequently to a mass of succulent parenchymatous tissue. Something of the same kind, though less marked, is to be observed in the archegoniate plants. In these, the archegonium grows considerably, after the fertilisation of the contained oosphere, especially in the Muscineæ in

which group the enlarged archegonium is termed the *calyptra*. In connexion with this it may be mentioned that in various of the Heterosporous Vascular Cryptogams (Marsilia, Salvinia, Isoëtes), in which the female prothallium produces in the first instance only one or a few archegonia, the further growth of the prothallium depends upon whether or not fertilisation takes place : thus, if the first formed archegonium be fertilised, the prothallium grows no more ; but if it fail to be fertilised, the prothallium grows and produces one or more new archegonia. In the Phanerogams even pollination, which is only a preliminary process, affects the condition of the organs of the flower ; it is well known that pollination causes flowers to fade, and in some plants, notably in the Orchids, the development of the ovules in the ovary does not take place until the flower has been pollinated, so that it is clearly dependent upon the stimulus of pollination.

The spores of plants, whether sexually or asexually produced, may begin at once to develop into a new individual, that is, to germinate, or they may pass through a longer or shorter period of quiescence. Those which germinate immediately on their formation have, as described above, a thin wall, whereas those which are capable of passing through a period of quiescence have a thickened cell-wall. In some cases spores are incapable of immediate germination, notably sexually produced spores. For instance, immediate germination is only known to take place, among the Algæ, in the zygospores of *Botrydium* and of *Ectocarpus*, and in the oospores of *Fucus*. Among the Fungi, the oospores of the *Peronosporæ* and of the *Saprolegniæ* pass through a period of quiescence.

The mode of germination of the spore is, as might be expected, widely different in different cases. In most cases a spore gives rise to a single individual, either by protruding filamentous outgrowths which develop into the plant-body, or by division to form a compact mass of tissue. In some cases the spore behaves like a reproductive organ ; from its protoplasm are formed a larger or smaller number of cells, either motile or non-motile, which are set free and are either sexual

or asexual reproductive cells. Thus in *Acetabularia*, and under certain circumstances in *Botrydium*, the asexually produced resting-spore constitutes a gametangium, in that it gives rise to a number of planogametes; similarly the asexually produced spore of *Protomyces* produces a number of conjugating sporidia. In some *Peronosporæ* (always in *Cystopus*, occasionally, according to circumstances, in *Pythium*, *Phytophthora*, and *Peronospora*), the asexually produced spore behaves as a sporangium, and gives rise to a number of zoospores from each of which a new individual is developed.

The same thing happens occasionally also in the case of sexually produced spores. Among the Fungi, the formation of zoospores in the oospore occurs in various species of *Peronosporæ* and *Saprolegniæ*. Among the Algæ, zoospores are formed in the zygospores of *Pandorina* and *Ulothrix*, and in the oospores of *Oedogonium* and *Sphæroplea*. Cases of a similar kind are known in *Phanerogams*. Thus, in some *Coniferæ*, and notably in the Gnetaceous *Ephedra altissima*, a process of cell-formation goes on in the oospore, leading to the formation of a larger or smaller number of cells from each of which an embryo-plant is developed. All these cases in which the spore, whether sexually or asexually produced, gives rise to a number of cells, each of which is capable, by itself, of developing into a new individual, are instances of what is known as *polyembryony*.

In some cases free cells are formed in the reproductive cell which are not reproductive but somatic; this obtains in the *Hydrodictyæ*. In *Hydrodictyon utriculatum*, the protoplasm of the zygospore gives rise to two or four large zoospores which eventually come to rest and remain quiescent for several months; these resting-spores are termed, on account of their form, polyhedra. On germination the protoplasm of the polyhedron breaks up into a number of small ciliated motile cells, the endospore protruding as a delicate vesicle within which the motile cells are in active movement. The motile cells eventually come to rest, without escaping from the endospore, and arrange themselves so as to form the meshes of a small sac-like net which is a young *Hydrodictyon*. The endospore is then disorganised, and the young net is set free as an independent cœnobium.

Occasionally it happens that a portion only of the spore gives rise to the embryo. This is the case in the oospores of the Characeæ and of the Coniferæ. In Selaginella and in the Angiosperms one half of the oospore gives rise to a filamentous structure, *the suspensor*, the other half to the main body of the embryo.

In many plants the same individual does not produce both sexual and asexual reproductive organs, but they are borne by more or less completely distinct individuals. When this is the case the life-history of the plant includes at least two generations, one of which is sexual and the other asexual; that is, it exhibits what is known as *alternation of generations*. Such a life-history cannot, of course, be traced in those plants, already enumerated, in which the reproduction is effected solely by either sexually produced or asexually produced spores, nor in those, to be now enumerated, in which the same individual bears both sexual and asexual reproductive organs.

The following are plants in which both sexual and asexual reproductive organs are borne by the same individual :

Algæ: Vaucheria; Hydrodictyon; Ulothrix; Oedogonium; some Floridææ (e.g. *Polysiphonia variegata*).

Fungi: Many Mucorini; most Peronosporæ and Saprolegniæ; Monoblepharis; among the Ascomycetes, the Erysipheæ, Eurotium, Penicillium, Nectria: some Uredinææ (*Uromyces appendiculatus*, *Behenias*, *Scrophulariæ*, *Cestri*, *Puccinia Berberidis*).

The simplest case of alternation of generations is that in which there are but two generations, the one sexual, the other asexual; the sexually produced spore giving rise exclusively to the asexual or spore-bearing generation (*sporophore*), the asexually produced spore giving rise exclusively to the sexual generation (*oophore*). A typical instance of this is afforded by the life-history of Mosses. The sexual generation of the Moss is the moss-plant; its body is differentiated into stem and leaves and it bears the sexual reproductive organs, the antheridia and archegonia. The oospore, which is formed in the archegonium in consequence of fertilisation does not give rise to a moss-plant, but to the structure which is known as

the *sporogonium*, which is the asexual generation in the life-history. The body of this organism is not differentiated into stem and leaves, but consists usually of a longer or shorter stalk (*seta*) bearing a capsule (*theca*) in which the spores are developed. When one of these asexually produced spores germinates, it does not give rise to another sporogonium, but to an inconspicuous, usually filamentous, structure, the *protone-ma*, upon which are developed, as lateral buds, moss-plants which bear sexual reproductive organs. In other words, the sexually produced spore (oospore) always gives rise to the sporophore (sporogonium), the asexually produced spore to the oophore (moss-plant).

This kind of life-history is not peculiar to the Muscineæ, but it can be more or less clearly traced in all the vascular plants. In the Isosporous Vascular Cryptogams (Filices, Equisetaceæ, Lycopodiaceæ), the asexually produced spore gives rise, on germination, to a small inconspicuous organism, destitute of vascular tissue, termed the *prothallium*, on which the sexual reproductive organs are borne. The oospore, produced by fertilisation in the archegonium, gives rise to the plant, consisting of stem, root, and leaves, which produces the sporangia and spores. The prothallium, is clearly the oophore, and corresponds to the moss-plant: the fully developed plant is clearly the sporophore, and corresponds to the moss-sporogonium.

In the heterosporous vascular plants (Rhizocarpæ, Ligulataæ, Phanerogams) the asexually produced spores likewise give rise to prothallia, though they are rudimentary. The microspore gives rise to a prothallium which is reduced to a single antheridium, and which, with the exception of *Salvinia*, among the Rhizocarps, and of the Phanerogams, does not project from the spore. In *Salvinia* and in the Phanerogams it projects in the form of a closed tube which is known in the Phanerogams as the pollen-tube. Similarly, the macrospore of these plants gives rise to a small prothallium bearing one or more archegonia, which, in the Rhizocarps extends beyond the limits of the spore but does not become free from it; in the Ligulataæ (*Selaginella* and

Isoëtes) it is only partially exposed by the rupture of the coats of the spore, and in the Phanerogams, where it is termed the *endosperm*, it remains permanently and completely enclosed by the spore (embryo-sac). Thus the oophore-generation is represented, in the life-history of these heterosporous plants, by two sexual individuals, the male and the female prothallia, which are respectively developed from a microspore and a macrospore. The oospore develops into the sporophore which is the highly differentiated plant bearing the sporangia and spores.

We will now digress for a moment to consider the formation of the seed of Phanerogams. It has been already mentioned in the course of this lecture (p. 603), that the macrospore (embryo-sac) of these plants is peculiar in that it is not liberated from the sporangium (ovule) in which it is produced, and we have just learned that it not only remains within the sporangium but that it also germinates there. Further, the sporangium itself remains attached to the parent-plant. Hence we have this peculiar state of things, that the asexual generation (the plant) bears macrosporangia in which, at a certain time, the sexual generation (the female prothallium or endosperm) is enclosed. But this is not all. When the oosphere, which belongs to the endosperm, is fertilised, it develops into the embryo, the whole being still enclosed by the sporangial (ovular) tissue. The development of the embryo proceeds up to a certain point, and is then arrested. When this point is reached the conversion of the ovule into the seed is complete.

According to the structure of the seed, we find that two or more successive generations are represented by its various parts. Thus, in an "albuminous" seed we trace the presence of tissues belonging to three generations;

Integuments, and perisperm, if present	} = tissue of the parent-sporophore
Endosperm	
Embryo	= the new sporophore.

In an "exalbuminous" seed, only two generations can be traced;

Integuments	= tissue of parent-sporophore
Embryo	= the new sporophore.

There is also this further peculiarity of Phanerogams to be noted, that, whereas in all other cases the development of the embryo from the sexually produced spore goes on continuously until the adult form is reached, in the Phanerogams the development of the embryo is discontinuous. It takes place, namely, in two stages. The first of these, as mentioned above, terminates with the ripening of the seed; the second begins with what is known as the *germination* of the seed, and includes the escape of the embryo from the seed and the gradual attainment of the adult form; between these two periods there intervenes a longer or shorter period of quiescence. The degree of development which may be reached by the embryo within the seed is different in different cases; in an albuminous seed the embryo is small, occupying but a portion of the embryo-sac; in an exalbuminous seed the embryo-sac, to begin with, occupies the whole of the interior of the seed, and the embryo entirely fills the embryo-sac (see p. 179).

Returning now from this digression, we find that in the life-history of the Mosses and of the plants above them in the scale of organisation, there is a regular alternation of generations of such a kind, that twice in the life-history the plant is represented by a single cell, a spore, which in the one case has been produced asexually, in the other sexually; the asexually produced spore gives rise to the sexual generation; the sexual generation produces the sexually produced spore; the sexually produced spore gives rise to the asexual generation, which again produces spores asexually.

We have now to consider how far the life-histories of plants lower than the Mosses conform to this type. Beginning with the Algæ, and confining our attention to those plants which have distinct sexual and asexual forms, we find that in some, the Volvocineæ for example, no alternation

of generations can be traced since there is no certainty as to the nature of the form to which any given spore may give rise: the individual developed from the asexually produced spore is not, as in a life-history of the Moss-type, necessarily sexual, nor is the individual developed from the sexually produced spore necessarily asexual. In others a more or less regular alternation of generations is traceable. Thus in *Acetabularia* (*Siphonææ*), the plant produces resting-spores asexually, which, as already mentioned, behave as gametangia; the gametes conjugate to form a zygospore, and from the zygospore the *Acetabularia* springs. Here the alternation of generations is quite regular. The *Acetabularia*-plant is the asexual generation or sporophore; the resting-spore alone represents the sexual generation, or oophore, inasmuch as it directly gives rise to sexual reproductive cells. The life-history of *Botrydium* is essentially the same as that of *Acetabularia*, but it is frequently less regular; thus the *Botrydium*-plant may produce, instead of resting-spores, uniciliate zoospores by which it is directly reproduced, and in this way several asexual generations may succeed each other. The fact that the oophore may be actually asexual, as when the resting-spore develops directly into a *Botrydium*-plant, or when, as mentioned already, it produces zoospores instead of gametes, does not affect the alternation of generations; the oophore is present and from it the sporophore is derived; the asexual oophore may be conveniently distinguished as a *potential oophore*. In *Coleochæte* we have a case in which the normal alternation of generations is interfered with by the asexuality of several successive generations of what ought to be sexual forms. The sexual individual produces the oospore, and the oospore gives rise to a small individual which is asexual, and which produces zoospores; from these zoospores are developed individuals which resemble the sexual form in all respects save that they do not produce sexual organs, but produce only zoospores. At length, after a series of generations, a sexual plant is developed. The appearance of the sexual plant seems to be determined by the season of the year. The oospores germinate in the

spring, and the asexual reproduction goes on through the summer, the sexual plant making its appearance towards autumn. In Coleochæte it is only in the case of the sexually produced spore that the nature of the resulting individual can be predicted; it always gives rise to an asexual individual; whereas the asexually produced spores gives rise to an individual which may be either sexual or asexual, that is, to a potential oophore. The life-history of Coleochæte is, then, briefly this: the oospore gives rise to the sporophore; from the zoospore of the sporophore a potential oophore is developed; a succession of potential oophores then follows, until finally, when the external conditions are appropriate, an actual oophore is developed. In the Characeæ the oospore gives rise to a rudimentary individual, the *proembryo*, which represents the sporophore. However, it does not produce spores, but gives rise to the oophore (Chara-plant) vegetatively by budding.

The study of the life-history of the Fungi is attended with considerable difficulty, partly on account of the fact that in many cases the development of the sexual organs is dependent upon a combination of external conditions which may but rarely present itself, and partly on account of the great difference in habit which frequently exists between the sexual and asexual forms of the same plant, a difference which is sometimes accentuated, in parasitic Fungi, by the occurrence of the two forms on different plants as hosts (*Heteræcism*). But in some cases the life-history has, nevertheless, been traced, and it frequently exhibits more or less regular alternation of generations. Before entering upon the consideration of these cases, it must be clearly understood that the expression "sexually produced spore" will be applied not only to those the formation of which is known to be preceded by a sexual process, but also to those which though formed probably or actually without an antecedent sexual process, may be considered, as already explained, to be homologous with those which are actually sexually produced; and the individual producing such spores will be regarded as the oophore.

Beginning with the Mucorini, we find that, in *Mucor Mucedo* and *Phycomyces nitens* for instance, the zygospore gives rise on germination to a rudimentary individual (*promycelium*) which is entirely asexual; from one of the spores of this form a normal plant is developed, which produces spores asexually but may also bear sexual reproductive organs. Essentially the same life-history may be traced in certain Peronosporæ (*Phytophthora omnivora*, *Pythium proliferum*); in these the individual developed from the sexually produced spore is always asexual, whereas that developed from the asexually produced spore may be sexual, but it always produces spores asexually. In these cases there is not a strict alternation of generations, in consequence of the succession of potential oophores, as in Coleochaete.

In other cases the alternation is completely regular. In the Ustilagineæ, to begin with, the asexually produced spore gives rise to a rudimentary individual (*promycelium*) which is the sexual generation; this produces sporidia which conjugate in pairs, and from the product of conjugation springs the individual which produces spores asexually. Essentially the same life-history has been traced in some Ascomycetes and Uredineæ. In Claviceps, the sexually produced spore (ascospore) gives rise to an asexual form, long regarded as a distinct genus under the name of Sphacelia, from the spores of which the Claviceps is reproduced. In *Sclerotinia* (*Peziza Fockeliana*), a similar regular alternation occasionally takes place: the ascospore may give rise to an asexual form, long known as *Botrytis cinerea*, from the spores of which the *Sclerotinia* is in turn developed: but not infrequently the ascospore gives rise to a *Sclerotinia* at once, in which case there is of course no alternation. In *Polystigma* the ascospore gives rise to a promycelium which bears sporidia, and these sporidia give rise to the *Polystigma*. In *Endophyllum* (Uredineæ) the life-history is precisely the same as in *Polystigma*; the promycelium is the sporophore, the sporidia the asexually produced spores, and the plant itself is the oophore. In other Uredineæ the life-history is somewhat modified in that asexually produced spores of at least two kinds make

their appearance. The sexually produced spore (æcidiospore) gives rise to an individual which, in Gymnosporangium and Hemipuccinia, bears asexually produced spores, teleutospores (p. 603); in *Puccinia Graminis* the formation of teleutospores is preceded by that of somewhat different spores, the uredospores; in either case the teleutospore gives rise to a second asexual generation, the promycelium, which bears sporidia, from which the æcidium-bearing oophore is developed.

We may, in conclusion, briefly consider the relation of vegetative reproduction to the life-history of plants. It has been stated that in the life-history of a plant which exhibits regular alternation of generations, the alternate generations are developed from spores produced either sexually or asexually as the case may be. But to this there are exceptions, for, as we have already learned (p. 601), reproduction by means of spores may be replaced by vegetative reproduction, in the form either of apogamy or of apospory. Thus in the vegetatively apogamous Ferns already mentioned, the sporophore (fern-plant) is developed as a bud upon the oophore (prothallium). Similarly in the aposporous Ferns, Mosses, and Characeæ, the oophore is developed as a bud from the sporophore.

In some cases, namely when one generation gives rise to its like by vegetative budding, sporophore to sporophore, oophore to oophore, there is a combination of vegetative apogamy and apospory. For instance, when as in the Phanerogams mentioned above (p. 601), embryos are produced vegetatively from the tissue of the nucellus, sporophore springs from sporophore, the normally intervening formation of spores, first, by the asexual method, and secondly, by the sexual method, is suppressed. A striking instance of the same thing has been observed by Goebel in some species of *Isoëtes* in which a plant was developed on a leaf in place of a sporangium. Other instances are afforded by the various cases of multiplication by buds referred to at the beginning of this lecture (p. 601). Similarly, when a moss-plant gives rise by budding or by means of gemmæ to another moss-plant, or when a fern-prothallium gives rise to another by means of gemmæ,

oophore springs from oophore without the intervention of, first, a sexually produced spore, and secondly, of an asexually produced spore.

We are now in a position to fully understand what is meant by "apospory" and "vegetative apogamy" respectively. By apospory is meant the development of the oophore from the sporophore without the intervention of an asexually produced spore, in other words, by the substitution of budding for asexual spore-formation. By vegetative apogamy is meant the development of the sporophore from the oophore without the intervention of a sexually produced spore, in other words, the substitution of budding for sexual spore-formation. The difference between vegetative apogamy and that other form of apogamy which we have already distinguished as parthenogenesis now becomes apparent. In parthenogenesis spore-formation takes place, but the spore, instead of being the product of a sexual process, is developed without that process, that is, apogamously; hence the sporophore is developed from a spore which is the homologue of those which are sexually produced, but which, as a matter of fact, has not been sexually produced: sexual spore-formation is replaced by asexual.

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LECTURE XXIII.

REPRODUCTION (*continued*).

IN the present lecture we have to complete our account of the facts of reproduction, and then to endeavour to arrive at a comprehension of their physiological significance.

The next series of facts to which we have to turn our attention are those connected with development of the reproductive cells. Beginning with the asexual reproductive cells or spores, we have learned that they are produced by an organ which we have spoken of generally as the sporangium. In many cases there is no perceptible peculiarity in the sporangium itself, or in the mode of development of the spores from its protoplasm. In unicellular plants, like Yeast and Hæmatococcus, the cell which constitutes the body of the plant, constitutes the sporangium also; and in a number of multicellular plants, such as Ulothrix, Ulva, and Coleochæte, each cell of the body may act as a sporangium and give rise to spores.

In some cases the spores are apparently formed from the whole of the protoplasmic contents of the sporangium, so that probably in the protoplasm of each spore all the various parts of the protoplasm of the sporangium are represented. In many cases, however, it has been ascertained that not all the protoplasmic contents of the sporangium are used in the formation of the spores. For instance, in many Fungi a considerable portion of the protoplasm of the sporangium (or ascus) remains over, as the *epiplasm*, after the formation of the spores; and in the development of the zoospores of the Algæ (*e.g.*

macrozoospores of *Ulothrix*) a portion of the protoplasm is extruded in the form of a vesicle from the sporangium at the same time as the zoospores. In other cases of spore-formation a peculiar process has been observed by Strasburger. He finds, namely, that just previously to the division of the spore-mother-cell, a mass of substance, termed the *paranucleolus* is extruded from the nucleus.

Passing on to the development of the sexual reproductive cells, we find that in some cases these cells, like the spores, may be directly developed from a somatic cell, as in the case of the gametes of the *Spirogyra* and of the planogametes of *Ulothrix*. In *Acetabularia* the planogametes are developed from a single cell, the resting-spore, which we cannot but regard as being somatic, inasmuch as it represents (p. 632) the entire sexual generation (oophore) of the plant. In not a few cases the sexual reproductive cells appear to be developed from the whole of the protoplasm of the sexual reproductive organ, be it differentiated or undifferentiated; for example, the gametes of *Spirogyra*, the oospheres of *Fucus*. But in very many cases a portion of the protoplasmic contents of the reproductive organ remains unused. Thus, in the development of the planogametes of *Ulothrix* and of *Acetabularia*, a considerable portion of the protoplasm is extruded with the planogametes from the gametangium in the form of one or more vesicles.

Something similar has been observed in connexion with the development of the antherozoids in the *Muscineæ* and *Pteridophyta*. When the antherozoid is set free there is attached to its posterior end an appendage which is usually described as a protoplasmic vesicle. Now as to the nature of this vesicle. It has been ascertained that the antherozoid is developed mainly from the nucleus of the mother-cell, the cilia alone being derived from the protoplasm. The vesicle therefore probably consists to a large extent of the unused protoplasm of the mother-cell. But it has been suggested by Dodel-Port, and his suggestion is fully confirmed by the researches of Belajeff on the development of the antherozoids of *Isoëtes* and *Selaginella*, that the so-called protoplasmic

vesicle contains a portion of the nucleus of the mother-cell which is excluded from taking part in the formation of the antherozoid. Probably in all cases a portion of the nuclear substance of the mother-cell is thus excluded. The excluded portion of the mother-cell is termed a *polar body*.

In order to complete our study of the peculiarities attending the development of male reproductive cells, we must enquire whether any indication of the formation of a polar body can be detected in connexion with the processes already mentioned (p. 615) as going on in the germinating pollen-grains of Phanerogams. In all cases the nucleus and the protoplasm of the pollen-grain, in the first instance, undergo division, so that two cells are formed which Strasburger distinguishes respectively as the *vegetative* and the *generative*. Of these, the former is much the smaller in the Gymnosperms, whereas the converse is the case in the Angiosperms. In the Gymnosperms the two cells are permanently separated by a cell-wall, but in the Angiosperms the cell-wall sooner or later undergoes absorption, so that the only permanent evidence of the cell-division is the presence of the two nuclei. In some Gymnosperms two or three more vegetative cells may be successively cut off from the generative cell. The vegetative cell is usually considered to represent the rudiment of the vegetative portion of the male prothallium, but Strasburger attaches to it the physiological significance of a polar body. In view of the fact that in the majority of observed cases the whole of the generative nucleus takes part in the sexual process, no portion of it being excluded, it seems probable that Strasburger is right in regarding the vegetative cell as being physiologically a polar body.

Strasburger extends his view to the vegetative cell which is formed in the germinating microspore of the Heterosporous Vascular Cryptogams. In this we are unable to follow him, since, as mentioned above, a polar body is formed in each mother-cell of an antherozoid in these plants. The vegetative cell in this case is simply of morphological, and not of physiological, significance.

Turning now to the development of well-differentiated female gametes, we find many more or less well-marked cases

of the formation of a polar body. A comparatively simple case is afforded by the Peronosporæ. It was mentioned in the last lecture (p. 619) that the oosphere of these plants is developed from a portion only of the protoplasmic contents of the oogonium, and there is reason to believe that a certain portion of the nuclear substance of the oogonium is excluded from the process. It appears, namely, from Schmitz's researches, that the protoplasm of the oogonium is multinucleate, and that during its development nuclear division frequently takes place. The periplasm of the oogonium is certainly nucleated, and it may therefore be regarded as a polar body. In certain of the Algæ (*Vaucheria*, *Oedogonium*) an extrusion of a portion of the protoplasmic contents of the oogonium has long been known to occur, and something of the same kind has recently been observed by Dodel-Port in *Cystoseira barbata*. It has not been definitely ascertained whether or not the extruded protoplasmic masses are nucleated, but they probably are, and may therefore be considered to be polar bodies. There is no such doubt as to the corresponding cells formed in the female organ of the Muscinæ, the Pteridophyta, and of most Gymnosperms. In these plants the central-cell of the archegonium divides into two, a large and a small cell: the former becomes the oosphere, the latter is termed the *ventral canal-cell*, and subsequently undergoes degeneration. There can be no doubt that the latter is a polar body.

We have yet the case of the Angiosperms to consider. A number of nuclear divisions take place in connexion with the development of the oosphere, but it is not clear which of these is to be taken as indicating the formation of a polar body. The facts are briefly as follows. The nucleus of the young embryo-sac divides into two, one of which travels to each end of the sac: each nucleus then divides, and each of the new nuclei divides again, so that there is a group of four nuclei at each end of the embryo-sac. Of those at the micropylar end, one becomes the nucleus of the oosphere, two the nuclei of the synergidæ (see fig. 70, p. 616), and the fourth (polar nucleus), which is the sister-nucleus of that of the

oosphere, travels towards the middle of the sac where it fuses with one of the chalazal nuclei, which has likewise travelled towards the middle of the sac, to form the definitive nucleus of the embryo-sac. It may be suggested that the division which leads to the formation of the nucleus of the oosphere and of the so-called polar nucleus, is the one which we are seeking; in that case the so-called polar nucleus would be the polar body.

There remain yet a few cases to be considered in this connexion, cases which are of somewhat doubtful nature, but which nevertheless seem to have the same physiological significance as those which we have just been discussing. In these, the sexual organ undergoes complete cell-division as a preliminary to the sexual process. Thus, in the *Mucorini*, the apical portion of each of the conjugating hyphæ is cut off by a cell-wall from the remainder, and it is these two portions which coalesce. Again, in *Sirogonium sticticum*, one of the *Zygnemæ*, as described by de Bary, each of the two conjugating cells undergoes division so as to form two or more sterile portions and a fertile portion. These cell-divisions may be fairly compared with those already described as taking place in the pollen-grains of Phanerogams, and, inasmuch as they lead to the distinction of vegetative and generative portions in the sexual reproductive organ, they may be regarded as being of the same physiological significance. It may be that the cell-divisions which take place in the oogonium of the *Characeæ* and lead to the formation of the sterile "Wendungszellen" (Braun) ought to be included here.

We have now ascertained that the development both of spores and of gametes is marked, in very many cases, by certain peculiarities having essentially this result, that the original nuclear substance of the reproductive organ, whether it be a sporangium or a gametangium, does not all go to form the nuclear substance of the one or more reproductive cells produced by the organ, but that a portion of the original nuclear substance is excluded, at some stage or other, from forming part of the reproductive cell or cells.

In connexion with the development of the gametes, it will be convenient to discuss the nature of the sexual process. We already know that it consists in the fusion of the protoplasm of two sexual reproductive organs, and that the fusion may take place either within or outside them. But it appears that the essential part of the process is the fusion of the two nuclei. It has been observed in the case of lowly-organised plants, such as *Spirogyra* and *Pythium*, that not only does the protoplasm of the two gametes fuse into one mass, but that the two nuclei do so likewise. This fact does not, of course, prove that the fusion of the two nuclei is the essential part of the process; but the observation of the process in plants which have well-differentiated gametes proves that it is. The antherozoid of such plants consists, with the exception of the cilia, almost entirely of nuclear substance: for instance, as Strasburger points out, the antherozoid of *Fucus* consists of a mass of nuclear substance enveloped by a delicate layer of protoplasm which includes the "eye-spot," and is prolonged into the cilia. Since it cannot be doubted that the antherozoid fertilises the oosphere, it is clear that a quantity of cell-protoplasm (cytoplasm) is not essential to the process. This is even more strikingly brought out in the process of fertilisation in Phanerogams, in which no protoplasm accompanies the nucleus (*male pronucleus*) derived from the pollen-tube, as it enters the oosphere to fuse with the nucleus of the oosphere (*female pronucleus*).

The details of the sexual process in Phanerogams are, according to Strasburger, as follows. In the Gymnosperms a generative nucleus or male pronucleus escapes through the mucilaginous end of the pollen-tube, enters the oosphere, travels to the female pronucleus, and fuses with it (see Fig. 71, p. 617, Fig. 76). In the Angiosperms, when the pollen-tube comes into contact with the synergidæ, a portion of its protoplasm enclosing a generative nucleus passes out through the mucilaginous apex of the pollen-tube, and travels between the disorganised synergidæ to the oosphere. The generative nucleus or male pronucleus then enters the oosphere, leaving behind it the protoplasm which had served as a vehicle, and fuses with the female pronucleus (Fig. 75).

Before we enter upon the discussion of the physiological significance of these facts of reproduction, we will turn our

attention to certain other points. In the first place, we may enquire why it is that plants reproduce themselves by means of spores; for, as we have seen, their somatic cells so generally possess the reproductive capacity that the necessity for the production of specialised reproductive cells may well be questioned. There can be no doubt, however, that the formation of spores is of great biological importance in maintaining the existence of the various kinds of plants. Spores

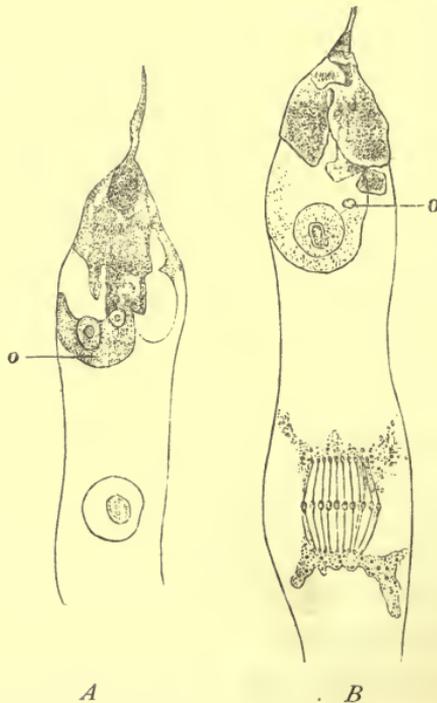


Fig. 75 (after Strasburger). Fertilisation in an Angiosperm (*Monotropa Hypopitys*). In A, the male and female pronuclei are present in the oosphere *o*. In B, the male and female pronuclei have nearly completed their fusion; the nucleoli have not, however, quite coalesced.

are capable, namely, of retaining their vitality under external conditions, such as long drought, lack of food, extremes of heat or cold, etc., which would prove fatal to the individual plant. But this property is also possessed in a high degree by the variously modified buds (bulbs, bulbils, gemmæ, corms) which subserve vegetative reproduction. But spores afford

this further advantage that they facilitate the distribution of individuals of the same species. They are light, readily transportable by wind or water, and in some cases they are actively motile. Hence that close aggregation of individuals which would result from continued vegetative reproduction, and which would be disadvantageous to the species, is obviated by their formation.

Admitting, then, the advantage accruing from the production of spores, the further question arises why the asexual production of spores should not suffice, why there should be

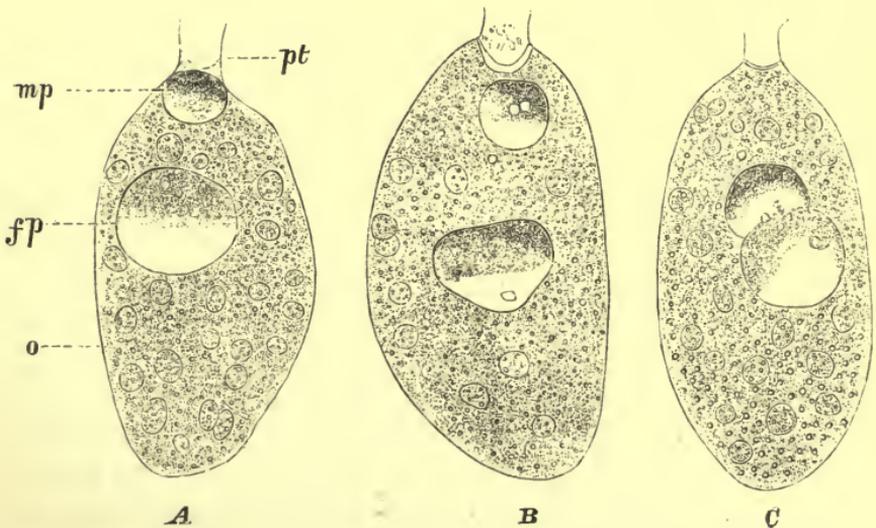


Fig. 76 (after Strasburger). Fertilisation in a Gymnosperm (*Picea vulgaris*): *pt*, pollen-tube; *o*, oosphere; *mp*, male pronucleus; *fp*, female pronucleus. *A* shows the first appearance of the male pronucleus in the oosphere; *B*, its movement towards the female pronucleus; *C*, the fusion of the two pronuclei.

any sexual production. In view of the often elaborate arrangements by which the performance of the sexual process is ensured, it may be inferred that it is an advantage to the species that spores should be produced sexually; that is, that spores should be produced containing nuclear substance derived from two more or less distinct sources. In illustration of this, reference may be made to those plants in the life history of which alternation of generations occurs: it is clear that, normally, the sexual production of a spore is

absolutely necessary in such a case. In some plants it suffices that the nuclear substance should be derived from two organs borne by the same individual, in which case the sexual process is one of *self-fertilisation*. In some plants, such as the Fungi which have pollinodial antheridia (Peronosporæ and some Ascomycetes), self-fertilisation alone is possible. But in most cases the conditions under which the sexual process is effected, for instance, the formation of free-swimming planogametes and antherozoids, and of spermatia and pollen-grains which are readily transportable, are such as to render possible the fusion of sexual cells derived from two distinct individuals, that is, *cross-fertilisation*. In some cases there are special arrangements for ensuring cross-fertilisation, the most general of which is *diœcism*; that is, the production of the male and female organs by distinct individuals. Thus in certain Fucaceæ (*Fucus vesiculosus*, *nodosus*, *serratus*, *Himantalia lorea*) some individuals have only antheridia and others only oogonia; in Spirogyra and other Zygnemæ the cells of one filament act as male organs, those of the other as female organs; among the Muscineæ the plants frequently bear only either antheridia or archeogonia; in the Isosporous Vascular Cryptogams the prothallia are usually hermaphrodite, but exclusively male or female prothallia occur not infrequently in the Filices, and as a rule in the Equisetaceæ. In heterosporous plants diœcism is brought about in a somewhat different manner. These plants, as mentioned in the previous lecture (p. 603), have two kinds of spores, macrospores and microspores; the former always give rise on germination to a female (archegoniate) prothallium, the latter to a male (antheridial) prothallium; hence the male and female organs are necessarily borne by distinct individuals.

It is usual to speak of these Phanerogams only as being diœcious in which the microspores (pollen-grains) and macrospores (embryo-sacs) are borne by distinct individuals; but this usage requires explanation. All Phanerogams, being heterosporous, are essentially diœcious, for the sexual process takes place between the two distinct individuals represented by the pollen-tube on the one hand, and by the more or less

complete prothallium developed in the embryo-sac, on the other. Hence, even in a *cleistogamous* flower, one, namely, which does not open, so that the only pollen-grains which can reach its stigma are those developed in its own anthers, self-fertilisation, morphologically speaking, does not take place, though, physiologically speaking, it does, as we shall subsequently see.

Even in monœcious Phanerogams diœcism is practically attained in various ways. In some cases the structure of the flower is such that, in view of the visits of insects which are attracted by the colour of the perianth-leaves, or by the scent, or by secreted nectar, the probability that foreign pollen, derived at least from a different flower of the same plant, will reach the stigma is very much greater than that its own pollen will do so. A striking case of this is afforded by *heterostyled* flowers, such as those of various species of *Primula* and *Oxalis*, *Lythrum Salicaria*, etc. In other cases the same end is attained by *Dichogamy*, that is, that the two kinds of spores come to maturity at different times: in some plants, termed *proterandrous*, the pollen-grains mature first, in others (*proterogynous*) the embryo-sacs. In either case it is impossible that the pollen of any one flower should fertilise the oospheres of the ovules of that flower.

Proterandry is very common; in fact, as Sir John Lubbock observes, the greater number of flowers which contain both stamens and pistil, are more or less proterandrous. The following are proterogynous; *Scrophularia nodosa*, species of *Plantago*, *Aristolochia*, *Arum*, *Euonymus*, many *Rosaceæ*.

Again, apart from any structural arrangements for ensuring cross-fertilisation, there are in some cases imperceptible physiological conditions which lead to the same result. It is in some cases impossible for sexual reproductive cells of nearly allied origin to fuse together. An indication of this is afforded in *Acetabularia* and *Ectocarpus* by the fact that conjugation can only take place between planogametes derived from distinct gametangia, and it attains complete expression in *Dasycladus*, among the lower plants, in which conjugation only takes place between planogametes derived

from distinct individuals. Amongst Phanerogams, Darwin has ascertained that in many cases the pollen of one flower is incapable of fertilising the oospheres of its own ovules, and that the pollen from another flower of the same plant is only slightly, if at all, more potent. The pollen from a flower of another individual of the same species is potent, and this the more so the wider the difference between the individuals: the pollen from an individual of a different variety is more potent than that from an individual of the same variety. This physiological relation is well illustrated by Darwin's observations on heterostyled plants. Not only is the structure of these flowers such as almost certainly to ensure the conveyance of the pollen from anthers of a particular height to the stigmas of styles of corresponding length, but the pollen from other, shorter or longer, stamens is either altogether impotent, or its fertilising action is much feebler, so that the number of seeds produced by an illegitimate union is only a fraction of that produced by a legitimate union.

Though, as we have seen, cross-fertilisation is most effectual when the individuals differ widely from each other, there is a limit to the possibility of cross-fertilisation. Still cases of cross-fertilisation between different species of the same genus, and even between species assigned to different genera, are on record, the products of such cross-fertilisation being termed *hybrids*. But hybridisation is accompanied by a diminished production of seeds, and in many cases the hybrids produced have been found to be altogether sterile.

Hybridisation is commonly *reciprocal*; that is that the pollen of a species A will fertilise the oospheres of a species B, and that the pollen of B will likewise fertilise the oospheres of A. But in many cases this has not been found to be the case.

We see, then, that it is important that a certain relation, a certain degree of *sexual affinity*, should exist between the sexual reproductive cells. When the limit is overstepped in the direction of either a too close or a too remote relation, the union will either not take place at all, or the offspring will be few and feeble. From this point of view we are able to explain the apparent anomaly, to which attention has already been

drawn, that though monœcious Phanerogams are strictly speaking diœcious, yet they are not so physiologically. The explanation is this; that in the life-history of the Phanerogams the female oophore-generation has come to be merged in the sporophore-generation, so that oosphere and pollen-grain in the monœcious forms stand in the same physiological relation to each other as two gametes produced by the same plant, a relation which is too close to admit, in many cases, of a fertile sexual process taking place between them.

By his extended observations on the relative efficiency of cross- and self-fertilisation, Darwin proves that the offspring of the union of sexual reproductive cells derived from two distinct individuals have an immense advantage in height, weight, constitutional vigour, and fertility, over the self-fertilised offspring of one of the same plants. This fact affords the clue which we are seeking as to the importance of the sexual process. By means of the sexual process the production of more numerous and more vigorous individuals by cross-fertilisation is rendered possible, and the maintenance of the species ensured.

We will now briefly refer to the fact of sexual degeneration. It is remarkable that this is characteristic of plants which are either parasitic or saprophytic in habit, such as the Fungi and certain Phanerogams (Balanophoræ, Loranthaceæ, Santalaceæ), but we are unable at present to give any satisfactory explanation of this interesting correlation.

We go on now to consider the relation of the offspring to the parent or parents, to consider in other words, the facts of *Heredity*. We can readily understand that an individual produced by vegetative reproduction resembles its parent. This is also the case with regard to an individual developed from an asexually produced spore, at least in those plants which have no alternation of generations. In plants which have an alternation of generations, it is, as we have seen, the alternate generations which resemble each other; sporophore resembles sporophore, and oophore resembles oophore. The hereditary characters of the sporophore are transmitted through the oophore to the succeeding sporophore; and

similarly, the hereditary characters of the oophore are transmitted through the sporophore to the succeeding oophore. We will in our further discussion of Heredity, as far as concerns plants with alternation of generations, regard two successive sporophores or oophores as standing to each other in the relation of parent and offspring.

With regard, next, to individuals developed from sexually produced spores, we would naturally expect that they should present a combination of the characteristics of the two parents; and this they actually do in various degrees. Darwin has pointed out that when two individuals, belonging to the same family, but distinct enough to be recognised, or two well-marked varieties, or two species, are crossed, the usual result is that the immediate offspring are intermediate between their parents, or resemble one parent in one part and the other in another part. But this is by no means an invariable rule; for in many cases the characters of the one parent are much more marked in the offspring than those of the other; that one parent is prepotent over the other. In illustration of such a result from the crossing of varieties, Darwin mentions the following examples. Plants with striped flowers when crossed with others of the same species having uniformly coloured flowers give rise to seedlings which have uniformly coloured flowers. Again, when a plant of Snapdragon (*Antirrhinum majus*) with peloric flowers was crossed with pollen from a flower of the common form, and the latter, reciprocally, with pollen from the peloric form, none of the seedlings had peloric flowers, a result which was also obtained by Naudin with a peloric *Linaria*.

The relation between the parents is still more strikingly shewn in the case of hybrids. In many cases when species are crossed, the hybrid produced is the same whether A has been fertilised by pollen from B, or B by A; in other words, the hybrid BA is precisely similar to the reciprocal hybrid AB. In such cases the influence of the reproductive cells is clearly equal. In some cases, however, the hybrid resembles the one parent more than the other; so that the hybrid BA is not quite similar to the hybrid AB. There is a ready method

for determining the relation of the hybrid to its two parents. If hybrids, namely, are fertilised through several generations by pollen from one or other of the parent forms, the progeny, the *derivative hybrids* as they are called, gradually reassume the parent form. If then a hybrid be precisely intermediate in character between its two parents, it will require just the same number of successive fertilisations by the pollen of each parent form to produce derivative hybrids which exactly resemble each parent form. If, on the other hand, the hybrid partakes more of the nature of one parent than of the other, the number of fertilisations necessary to reproduce the one parent form will be less than that necessary to reproduce the other. For instance, Gärtner observed that when the hybrid of *Dianthus chinensis* and of *D. Caryophyllus* was fertilised in successive generations by the pollen of *D. Caryophyllus*, the derivative hybrid of the third or fourth generation was a *D. Caryophyllus*; whereas when fertilised by the pollen of *D. chinensis*, it was not until the fifth or sixth generation that the *D. chinensis* was reproduced. In this case *D. Caryophyllus* was clearly prepotent over *D. chinensis* in the production of the hybrid.

There is a fact of great interest, which may be conveniently mentioned here, that hybrids may be produced not only by means of sexual, but also vegetative reproduction. Hybrids produced in this way are termed *graft-hybrids*. As a rule, in the process of grafting neither the graft (or *scion*) or the stock is affected; each, as it grows, manifests in all its organs its own characteristics. But instances are on record of their mutually affecting each other. A well-known case of this kind is that of the *Cytisus Adami*. The origin of this form is stated as follows: a shoot of *Cytisus purpureus* was grafted on a stock of *Cytisus Laburnum*: from this were produced many shoots, one of which grew vigorously, and developed larger leaves than those of *C. purpureus*, and from this shoot plants were propagated constituting the *Cytisus Adami*. On flowering, it was found that the flowers were of a dingy red. Various other cases of the same kind, notably of the effect produced on the stock by grafting scions with variegated leaves, are given by Darwin.

But it does not always happen that an individual produced sexually presents the characters of its parents ; it is sometimes the case that it possesses new characters. This is true, though it is much less common, even of individuals produced vegetatively. This development of new characters constitutes what is known as *Variation* ; when it occurs in an individual developed from a seed, it is termed *seed-variation*, when in one produced vegetatively *bud-variation*. Bud-variation is most commonly manifested in this way, that a branch of the plant produces leaves which differ in form or colour—variegated leaves, for example,—from those of the other branches ; or a flower which is abnormal in form or colour ; or a peculiar fruit, as when a branch of a Peach-tree bears a nectarine. By these means new forms, termed *varieties*, are produced. The varietal characters are not, however, reproducible with certainty by means of sexual reproduction, for there is in the offspring of varieties a tendency to assume the specific form, a tendency which is known as *Reversion*. The hereditary characters are, namely, of different values. There are, first of all, those which are characteristic of the class to which the plant belongs : then those which are characteristic of the Natural Order, of the genus, of the species, and finally those of the variety. Of these, those which are characteristic of the wider groups are the most constantly transmitted ; and even the specific characters are transmitted almost equally well by sexual as by asexual reproduction. But this is not the case with regard to the varietal characters. As Darwin says, when a new peculiarity appears, we can never predict with certainty that it will be transmitted by sexual reproduction ; but if both parents present the same peculiarity, the probability is great that it will be transmitted to at least some of their progeny. The varietal peculiarities can only be reproduced with any certainty by vegetative reproduction, and it is on this account that propagation by means of cuttings, grafts, etc., is so much resorted to in horticulture.

The discussion of the causes of variation will be deferred for the present, but it may be pointed out that variability is promoted by cultivation and by crossing. In fact there is

scarcely a plant which has long been cultivated and propagated by seed, which is not highly variable.

Now that we have become acquainted with the main facts of reproduction in plants, we will endeavour to elucidate their physiological significance, to form some general theory of reproduction. Many such theories have been propounded at different times, but we will confine our attention to some of the more recent. Beginning with Darwin's theory of Pangenesis, we find its main assumption to be this, that each separate part or unit of the body throws off minute gemmules, not only in the adult state, but during all stages of development of the organism. These gemmules are capable of multiplying by division, and they may either develop immediately on their formation, or they may remain dormant for a longer or shorter period, and so be transmitted from generation to generation. When the gemmules are especially aggregated in certain parts of the organism, these parts constitute the reproductive organs. In organisms of high organisation the gemmules are confined to the specialised reproductive organs; but in organisms of lower organisation they are not thus confined, but are dispersed throughout the body, so that almost any member which may be isolated can develop into a new individual.

The theory of Pangenesis certainly facilitates a reasonable apprehension of the main facts of reproduction. We can account for the great capacity of plants for vegetative reproduction, by attributing it to a dispersion of the gemmules throughout the body. For instance, a cutting, when planted, produces roots and thus constitutes a new individual; and it is able to produce roots because at the time of separation from the parent-plant it contained root-gemmules. Similarly, it eventually produces reproductive organs, because it contained reproductive gemmules. Again, on this theory, spores are reproductive cells which are so rich in gemmules, that they can develop into a complete individual; whereas gametes are reproductive cells which do not individually contain a sufficient number of gemmules for independent development. Hence the significance of the sexual process

is, that by the fusion of two incomplete sexual reproductive cells, a complete reproductive cell, a spore, is formed. The throwing off of the polar bodies indicates the impoverishment, as it were, of the sexual reproductive cells, which presents parthenogenesis, and renders cross-fertilisation, with all its attendant advantages, a possibility. Further, it affords an explanation of heredity, crossing, and hybridisation. A new individual, whether produced by vegetative reproduction or by spores, will more or less closely resemble its parent or parents, because it contains gemmules derived from all parts of the parent or parents. When a cross or hybrid is intermediate in character between its parents, it is so, as we have seen, because the sexual cells agree in power; we restate this, according to the theory of Pangenesis, by saying that each parent contributes an equal number of equivalent gemmules to the offspring. When, on the other hand, a cross or a hybrid resembles one parent more than the other, when the one parent is prepotent over the other, it is because the gemmules derived from the prepotent parent have some advantage in number, affinity, or vigour, over those derived from the other parent. Reversion is explained by the assumption that the gemmules remain dormant through several generations, and when they proceed to develop in any individual it manifests the characters of the individual from which the gemmules were originally derived. This property of the gemmules to lie dormant may also be used to explain alternation of generations. In plants exhibiting this it is, as we have seen, the alternate generations which resemble each other; sporophore resembles sporophore, and oophore resembles oophore. The gemmules derived from a sporophore lie dormant in the oophore, and develop in the succeeding sporophore; similarly, the gemmules derived from an oophore are dormant in the sporophore and develop in the succeeding oophore. Finally, the increased variability which is induced by changed conditions, cultivation for instance, is ascribed to an influence on the reproductive organs which leads to an irregular aggregation of the gemmules in them, some being in excess and others deficient. As to the variation which results from the

direct action of changed conditions, the gemmules derived from the modified parts will be themselves modified, and when sufficiently multiplied, will supplant the old gemmules and be developed into structures possessing the new characters.

Although the facts of reproduction can be so readily explained on the theory of Pangenesis, still there are objections to its being literally accepted. In the first place, there is no experimental evidence that the gemmules actually exist; and in the second, it requires a great stretch of imagination to conceive that a spore could possibly contain all the gemmules necessary for the development of an individual; for amongst these gemmules there must be representatives of every cell of the parent in every stage of its development; and not only these, but dormant gemmules also, transmitted from countless ancestors.

The theory of Pangenesis has been restated by Brooks in a form so modified as to meet the objection raised to the Darwinian statement of it on the score of the countless number of the gemmules which must be assumed to be present in a reproductive cell. According to Brooks each cell of the body has the power of throwing off gemmules; but it only exerts this power when, through a change in its environment, its function is disturbed and the conditions of life become unfavourable. The gemmules may be carried to all parts of the body. They may penetrate to the female cell, or to a bud, and the male cell has acquired, as its distinctive function, a peculiar power to gather and store up the gemmules. In the process of fertilisation, each gemmule from the male cell conjugates with or impregnates that particle of the female cell which corresponds to the one which produced the gemmule; or else it unites with a closely related particle, destined to give rise to a closely related cell. When this cell becomes developed in the body of the offspring it will be a hybrid, and will therefore tend to vary. A cell which has thus varied will continue to throw off gemmules, and thus to transmit variability to the corresponding part in the bodies of successive generations of

descendants until a favourable variation is seized upon by natural selection. As the female cell which produced the organism thus selected will transmit the same variation by direct inheritance to the female cells which it itself produces, the characteristic will be established as an hereditary characteristic, and will be perpetuated and transmitted, by the selected individuals and their descendants, without gemmules.

This restatement certainly gets over the difficulty which it was framed to meet, but it raises new difficulties. Without contesting the possibility of cells throwing off gemmules, it may be enquired why it is that gemmules should only be thrown off under the stimulus of unfavourable conditions, and how it is that the reproduction of those parts which do not throw off gemmules is effected. Darwin's theory is at least consistent in that it applies to the reproduction of all parts whatsoever, whereas Brooks' theory is not. The restatement is certainly not less open to objection than the original theory.

In connexion with his restatement of the theory of Pangenesis, Brooks proposes a theory of the sexual process which may be mentioned here, but which will not be discussed until later. It is generally assumed that both the male and the female cells transmit to the offspring of their union the characters of the two individuals which have produced them respectively. Brooks, however, considers that the function of the two cells in relation to the progeny is different. According to his view the male cell is the originating, and the female the perpetuating, factor; the ovum is conservative, the male cell progressive. Heredity, or adherence to type, is brought about by the female cell; variation and adaptation through the male cell; the female cell is the essential, the male cell the secondary, factor in heredity.

The next theory of reproduction which we will consider is that put forward by Naegeli. Before entering upon the discussion of it, a short account must, for the sake of clearness, be given of his views as to the constitution of protoplasm. He distinguishes in protoplasm two parts, the fluid (*Hygroplasma*) and the solid (*Stereoplasma*). The active

organising part of the protoplasm he considers to be a part of the Stereoplasm, which he terms *Idioplasm*; the rest of the protoplasm he regards as being simply nutritive. He conceives of the idioplasm as forming a continuous network throughout the organism, but its properties are not the same in all parts, the differences being, not of a material, but of a dynamical nature. The idioplasmic network of the adult organism has been gradually formed by growth from the idioplasm of the spore: the idioplasm of the spore is the microcosmic image of the macrocosmic organism. Reproductive cells are formed by the return of portions of the somatic idioplasm to the condition of the idioplasm of the spore from which the organism sprang, in a word to the embryonic condition, the return consisting in a dynamical change. A complete reproductive cell, that is, a spore, contains just so much idioplasm, and that in the same condition, as did the spore of the previous generation; incomplete reproductive cells, that is, gametes, contain a smaller amount of embryonic idioplasm than this, and hence comes the necessity for a sexual process. The sexual process takes place in virtue of a specific attraction between the gametes of the two sexes, and consists in the fusion of the idioplasm of the two cells. Naegeli leaves it an open question whether this fusion is material, or, as it were, dynamical, but he distinctly inclines to the latter alternative. Heredity depends upon a transmission of the properties of the idioplasm. The law of heredity is the analogue of the physical law of inertia. Just as a body in motion continues to move in the same direction and with the same velocity unless acted upon by some external force, so the dynamical condition of the idioplasm of the parents is continued in the children. But the return of the somatic idioplasm of the parent, in the formation of reproductive cells, to the embryonic condition of the spore from which the parent sprang is not exact; so that the offspring never quite resemble their parent or parents. Hence comes variation. The difference between offspring and parents which is due, on Naegeli's assumption, to inherent variability, is the expression of the

advance made in one generation,—the nature of the advance being determined largely by the external conditions. With regard to reversion, he assumes that newly acquired properties of the idioplasm may remain latent, and thus the older properties of the idioplasm will be able to assert themselves.

It is impossible, within our present limits, to enter into the detail of Naegeli's theory of the constitution of the idioplasm, and it is therefore also impossible to minutely criticise it. The distinction of an active protoplasm, the idioplasm, in the organism is certainly an assistance to our apprehension of physiological facts; it leads us to regard the protoplasm of the plant-body as constituting a whole. And, like the theory of pangenesis, it enables us to obtain an insight into the facts of reproduction, with this advantage, that it is not so inherently improbable.

We come now to Strasburger's theory of reproduction. He agrees with Naegeli in the opinion that the active properties of protoplasm reside in a particular portion of it. He distinguishes, alike in the nucleoplasm and in the cytoplasm, a nutritive hyaloplasm and a formative hyaloplasm, the latter corresponding to Naegeli's idioplasm; the nucleohyaloplasm constitutes a single coiled filament (see p. 27); whereas the cyto-hyaloplasm has no constant arrangement. But Strasburger differs from Naegeli in that he attributes a functional predominance to the nucleo-idioplasm. So long as a cell is capable of growth, it is the nucleus which determines the growth and the mode of growth. The metabolism of the nutritive cytoplasm is directed by the nucleus so that the products are of a particular kind and nourish the idioplasm in a particular manner. Thus, in a germinating spore, the formative activity of the cyto-idioplasm is controlled so that the characteristic form of the developing organism is gradually evolved. Strasburger agrees with Naegeli that the reproductive capacity of a cell depends upon its being in the embryonic condition, and points out that the characteristic feature of this condition is the enormous size of the nucleus in relation to the cytoplasm. From this point of view the great capacity of plants for vegetative reproduction

is to be accounted for thus, that almost all parts of plants contain embryonic cells, or that their cells are capable of readily returning to the embryonic condition: in other words, the nuclei of certain cells in these parts are either already rich in nucleo-idioplasm, or are capable of becoming so.

In harmony with this conception, Strasburger regards the extrusion of the paranucleolus in the development of spores, and of the polar body in the development of gametes, as being the expression of the return of the corresponding nuclei to the embryonic condition: but he does not consider that the extrusion of a polar body is an essential condition of the development of a gamete. He says, namely, that the differentiation of the nucleus of the male or the female gamete does not depend upon the extrusion of definite constituents, but upon a rearrangement of its substance, this rearrangement being, however, accompanied in many cases by an extrusion of a portion of the nuclear substance. In his opinion the extrusion of a portion of the nuclear substance does not take place in the majority of cases, but only an excretion or a delimitation of a portion of the cytoplasm, which has the effect of ensuring the appropriate nutrition of the nucleus by the remaining cytoplasm. On another page of his work, however, Strasburger seems to take a somewhat different view, for he insists there that the differentiation of generative nuclei depends upon their idioplasm being reduced to one half the mass of that in a fertilised female cell. This reduction is affected by indirect nuclear division. Hence, the two nuclei are assumed to be exactly alike, so that the extrusion of a polar body does not mean the extrusion of particular constituents of the nucleus but simply its reduction by one half. When, as in the pollen-tube, the two nuclei thus formed clearly differ in function, Strasburger accounts for it by assuming that the nuclei, though quite similar at first, have come to differ in consequence of having been somewhat differently nourished.

Strasburger is not disposed to admit that there is any essential difference between the sexual reproductive cells. He considers that two gametes, for instance an oosphere

and an antherozoid, do not differ in nature, and the various external sexual differences he regards as being simply means to ensure the coalescence of the appropriate gametes.

With regard to heredity, Strasburger is of opinion that the nucleus of the reproductive cell is the means by which the hereditary characters are transmitted, and he adduces evidence to prove that the idioplasmic filament of the nucleus consists of a number of segments derived from previous generations. Such a view clearly puts a limit to the time within which reversion may manifest itself, for, in the course of a few generations the amount of nucleoidioplasm in the spore which can be traced back to any particular ancestor must be very small. Strasburger himself points out that in the twentieth generation it would be scarcely one millionth part. The fact that all the ancestral characters may not manifest themselves in any given individual is explained by Strasburger, in agreement with Naegeli, on this wise, that inherited characters may remain latent; that is, the inherited properties of the nucleoidioplasm of the spore may not all influence the cytoplasm simultaneously. Strasburger also agrees with Naegeli in assuming inherent variability, and in denying the inheritance of acquired characters.

Finally, there is Weismann's Theory of a special reproductive substance (*Keimplasma*). He assumes that each generation passes on to its offspring a certain amount of this reproductive substance; in the individual the amount of the reproductive substance is increased, the individual in fact produces from it its own reproductive cells, but the increase in quantity is not accompanied by any change in kind. There is then a "continuity of the reproductive substance" from one generation to another. As to the exact seat and nature of the reproductive substance, Weismann considers, in view of the importance of the two nuclei in the sexual process, that it is contained in the nuclei of the reproductive cells; his reproductive substance appears in fact to be nucleoidioplasm.

The account which he gives of the extrusion of the polar

body in the development of gametes is the following. He considers that the nucleus of the developing gamete contains two kinds of nucleoplasm, namely, reproductive substance and histogenic (or somatic) substance, and that in the extrusion of the polar body the histogenic substance is eliminated. Agreeing with Strasburger as to the physiological equivalence of male and female gametes, he believes the significance of the sexual process to be this, that the sudden increase in the bulk of the nucleus determines the division of the cell. Vegetative reproduction takes place in plants because the reproductive substance is widely disseminated throughout the somatic cells.

Weismann's theory is framed specially with the object of explaining the phenomena of heredity. He denies that acquired characters can be transmitted by sexual reproduction. Hence he cannot accept either the theory of Pangenesis, which assumes the presence in the reproductive cells of gemmules from all parts of the organism, or the view of Naegeli and Strasburger, that a somatic cell may return to the embryonic condition, in other words, that a conversion of somatic substance into reproductive substance may take place. Under these circumstances the assumption of the continuity of the reproductive substance becomes a logical necessity. His theory of variation is also based upon the negation of the inheritance of acquired characters by sexual reproduction. Acquired characters, he asserts, can only be transmitted by asexual reproduction. He therefore refers the origin of acquired characters to the ancestral unicellular plants which multiplied only asexually. These unicellular plants, after multiplying asexually through countless generations, acquired a great variety of characters in response to changes in the external conditions, and then, when sexual reproduction was evolved, the ancestral characters of the two parents were combined in the sexually produced individual. The whole process of evolution since the first appearance of sexual reproduction is then simply the expression of the repeated recombination in various ways of the characters acquired by the asexual unicellular progenitors of the race.

We will now, in briefly criticising these various theories of reproduction, endeavour to ascertain which of them most naturally explains the facts before us.

There can be no doubt the idea which underlies Naegeli's theory of reproduction, the idea, namely, that the protoplasm of each organism constitutes one complete whole, is the only reasonable foundation on which to frame a theory of reproduction. The protoplasm of every plant presents a certain definite form, or a certain external segmentation, and if a portion of that protoplasm be isolated it will, if it can grow at all, grow in such a way as to reproduce the form and segmentation of the mass of protoplasm of which it once formed part. This may be illustrated by an analogy borrowed from Pflüger. If a small imperfect crystal of any salt be placed in a saturated solution of that salt, it will first repair its crystalline form, and then increase in size. An exact parallel is afforded by a cutting. The cutting, let us say, formed part of a plant the protoplasm of which was segmented into stem, leaf, and root. The segmentation of the cutting is incomplete; it has no roots; it is comparable to the imperfect crystal. On being planted, however, the cutting completes its segmentation by producing roots, just as the imperfect crystal in the saturated solution completed its crystalline form.

It may be objected that this analogy does not hold good in all cases. There is the fact, for instance, that when a stem is cut across, a new stem is not developed at the cut surface. On examination, however, it will be found that this objection has no real weight. In the case of most plants, though it is true that the original stem will not be replaced, and that the surface of the wound will become covered by a layer of callus, yet a new shoot is developed from one of the lateral buds; so that after all the protoplasm of the plant is still segmented into root and shoot. In the case of plants which have no lateral buds, there is no possibility of repair, and so the injury proves fatal.

We may regard the development of an individual from a spore in like manner. The protoplasm of a spore may be compared to a minute complete crystal; and just as such a

crystal will, under appropriate conditions, grow into a large one, so the protoplasm of the spore, possessing the power of growth and of cell-division, will, under favourable conditions, grow into an individual resembling that from which it was derived.

Without expressing any opinion as to the propriety of Naegeli's assumption of the idioplasm, we simply regard the reproductive capacity as being one of the fundamental properties of protoplasm (see p. 6). From this point of view we cannot but regard the assumption of reproductive gemmules in the theory of Pangenesis, and of a special "reproductive substance" as in Weismann's theory, as altogether unnecessary. Just as it is superfluous to suppose that the repair of a broken crystal, to return to our illustration, is due to the presence of gemmules or of a special reproductive substance, so also is the supposition superfluous to explain the development of roots by a cutting.

But, as we have seen, it is not all the cells of a complex individual that are capable of reproduction. Only those are capable which are in a particular condition, a condition which we may term, with Strasburger, the embryonic condition. This condition of the cell doubtless depends mainly on the nucleus, and the appropriate state of the nucleus may be determined, as Strasburger suggests, by the presence of an adequate proportion of nucleo-idioplasm.

From this point of view, the facts of vegetative reproduction are susceptible of ready explanation. Vegetative reproduction is effected by means of what we may term embryonic somatic cells. In a growing plant such cells are always present, and give rise to new organs and tissues. When a portion of a plant containing such cells is isolated and placed under favourable conditions, these cells give rise to the members necessary to complete the segmentation of the imperfect individual.

It may, however, happen that a part of a plant which contains no embryonic cells, may subserve vegetative reproduction; for instance, the propagation of *Begonias* from pieces of leaf: probably all cases of leaf-proliferation are

instances of this. In such a case we can only assume that some of the adult somatic cells of the leaf have returned to the embryonic condition.

We will now discuss the significance of the processes which accompany the development of reproductive cells, and which lead to this result, that the original nuclear substance of the mother-cell does not all go to form the nuclear substance of the one or more reproductive cells to which it gives rise, but that a portion of the original nuclear substance is, at some stage or other, excluded from taking part in the formative process. We have seen that, in the case of spores, the process is a comparatively simple one, consisting merely in the extrusion of a portion of the nuclear substance of the mother-cell, whereas, in the case of gametes, it is more complicated, involving at least nuclear division, and not uncommonly cell-division.

With regard to the extrusion of the paranucleolus from the spore-mother cell, we have no direct evidence to prove that it is essential to the differentiation of the spores as reproductive cells, but the peculiarity of the process is eminently suggestive. Strasburger suggests that the extrusion of the paranucleolus is the expression of the return of the cell to the embryonic condition; but, if we consider that spores are specialised reproductive cells, differing from the somatic embryonic cells of the plant in that they add neither to the tissues nor the organs of the parent, but develop into distinct organisms, we are led to conclude that the extrusion of the paranucleolus, if it means anything, means more than this. The significance of the process is probably this, that it marks the differentiation of a reproductive from a somatic cell. We may put the case in this way, that if the extrusion of the paranucleolus did not take place, the division of the spore on germination would lead to the production, not of the body of a new organism, but of mere repetitions of itself. It may be that the extrusion of the paranucleolus is the expression of the elimination of what Weismann terms the histogenic nucleoplasm.

Passing now to the consideration of the significance of the

extrusion of the polar body in the development of gametes, we find that there is reason to regard it as of profound physiological significance. There is, in the first place, the fact that a gamete, in the development of which the extrusion of a polar body has taken place in any form, is, as a rule, incapable by itself of developing into a new individual. In the second place, there are, in families of plants in which the differentiation of the gametes is usually accompanied by the extrusion of a polar body, instances in which this process does not take place; and in these instances the cells produced are not gametes, but parthenogenetic spores.

Of these two points, the first is sufficiently clear not to require elucidation, but it will be advantageous to illustrate the second. The case which we will take is that of the Saprolegniæ (see p. 619). Pringsheim observed, and his observations have been confirmed by de Bary, that under certain circumstances plants of *Saprolegnia ferax* and of *Achlya polyandra* bear no antheridia, and yet their oogonia produce oospores; and, as we know, de Bary has come to the conclusion that even when antheridia are present, no sexual process takes place. The oospores of the Saprolegniæ are then parthenogenetically produced, and this is probably to be correlated with a peculiarity in their development. In the allied Peronosporæ the development of the oosphere, as already stated (p. 619), depends upon the differentiation of the protoplasmic contents of the oogonium into ooplasm and periplasm. This differentiation does not take place in the oogonium of the Saprolegniæ; still there is not an indication of it. During the development of the reproductive cells, the protoplasm of the oogonium is in active movement, and portions of it are from time to time thrown off. These portions doubtless correspond to the periplasm in the oogonium of the Peronosporæ; but in the Saprolegniæ the separation of the periplasm is only temporary, for the extruded portions subsequently coalesce with that from which the reproductive cells are formed. The explanation of the fact that the reproductive cells formed in the oogonia of the Saprolegniæ are oospores and not oospheres, appears to be

this: that in their development the necessary exclusion of a portion of the protoplasmic contents of the oogonium does not take place.

We may digress for a moment to consider a form of parthenogenesis, occurring among plants in which sexual differentiation is comparatively rudimentary, namely, in *Botrydium*, *Ectocarpus*, and *Ulothrix*, which differs from that of the *Saprolegniæ* and therefore merits special consideration. With regard to *Botrydium* there can be no doubt that the motile reproductive cells produced from the resting-spore are morphologically gametes, but they are only physiologically gametes provided that the resting-spore is young; when the resting-spore is old, the cells to which it gives rise are simply zoospores (see p. 607). In the absence of any evidence to shew that the process of development of the motile reproductive cells is different in a young and in an old resting-spore, we can only explain the facts by assuming that during the prolonged quiescence of the resting-spore, changes take place within it the result of which is that it is converted from a sexual into an asexual reproductive organ; the changes being probably of this nature, that the amount of the nucleo-idioplasm increases, so that the cells eventually produced contain sufficient nucleo-idioplasm to enable them to germinate independently. The case of *Ectocarpus* and of *Ulothrix* is somewhat different. Here the reproductive cells are gametes when they are first formed, but if they fail to conjugate they are capable of independent germination. In this case, possibly, an increase of the nucleo-idioplasm to the degree necessary to permit of independent germination takes place in the reproductive cells themselves.

But to return. Weismann strongly opposes the view that in the extrusion of the polar body any portion of the reproductive substance, or nucleo-idioplasm, is thrown off: he considers that, as already mentioned, the extrusion of the polar body is simply the elimination of the histogenic nucleo-plasm. If this be admitted, then it follows that the process of development of a gamete does not differ essentially from that of a spore. This is just the position which Weismann

takes up : he states, namely, with regard to the ova of animals, that the process of development of a normal ovum is precisely the same as that of a parthenogenetic ovum. If this be so, why is the parthenogenetic ovum capable, and the normal ovum incapable, of independent germination? The answer to this question is by no means definite. Weismann admits that a reproductive cell is only capable of independent germination when it contains a certain proportion of reproductive substance. Clearly then, a parthenogenetic ovum must contain more reproductive substance than a normal ovum. But how is this difference to be accounted for? If the process of development has been the same, there is no ground for assuming that the parthenogenetic ovum contains *ab initio* more reproductive substance than the normal ovum, and we are therefore led to suggest that the reproductive substance in the parthenogenetic ovum may have been increased by growth. But Weismann brings forward arguments to prove that a sufficient increase cannot be attained in this way. There is therefore no means whatever of accounting for the difference between a parthenogenetic and a normal ovum.

Weismann appears to have been conscious of this difficulty, for he goes on to say that the capacity of the ovum for subsequent development does not solely depend upon the mass of nucleus, that is, upon the amount of "reproductive substance" in it, but upon certain internal conditions which he does not define. And yet he asserts that the determining cause of the development of the fertilised ovum is the sudden doubling of the mass of nucleus.

There is a matter of fact bearing upon this subject to which we will briefly refer. If, as Weismann insists, the extrusion of the polar body simply means the extrusion of the histogenic nucleoplasm, it is a fair inference that the nucleus of a gamete and that of the corresponding polar body will have different reactions. It has been already pointed out that the generative and vegetative nuclei in a pollen-tube stand to each other in the relation of sexual and polar nucleus. Now Strasburger has observed that there is

a difference in reaction between the generative and the vegetative nucleus; that the former, namely, stains more deeply than the latter, a reaction which indicates the presence of a larger proportion of nutritive hyaloplasm in the former. If this be so, then, conversely, the proportion of nucleo-idioplasm in the vegetative nucleus is greater than in the generative nucleus. It is not possible to press this fact closely, for it is not clear that Weismann's "reproductive substance" corresponds exactly to Strasburger's nucleo-idioplasm, and Weismann says nothing about the staining properties of the "reproductive substance"; but as far as it goes it seems to shew that the vegetative nucleus not only contains some nucleo-idioplasm or "reproductive substance," but that it actually contains more than the generative nucleus.

The conclusions, as to the physiological significance of the extrusion of the polar body, to be drawn from the foregoing discussion are the following. It appears, in the first place, in view of the parthenogenesis of the *Saprolegnieæ*, the only case of parthenogenesis, be it said, which has been thoroughly investigated, that the extrusion, in some form, of a polar body is an essential part of the development of a gamete. We cannot, therefore, agree with Strasburger's views on the subject (see p. 659). It is true that the extrusion of a polar body has not been observed in the case of all plants, but the observations on the subject are not so numerous or extended as to warrant the inference that the process does not take place in all. In the second place, in view of the fact that the essential feature of the sexual process is the coalescence of the nuclei of the two gametes, we cannot but conclude that the extrusion of the polar body involves in all cases the extrusion of a portion of nuclear substance. Here again we are at issue with Strasburger. Thirdly, we conclude that Weismann's view as to the nature of the substance of the polar body is not established: what facts there are go to prove that the nucleus of the polar body consists not of histogenic nucleoplasm, but of nucleo-idioplasm. Finally, we conclude that it is this reduction of its nucleo-idioplasm which determines the sexuality of the

reproductive cell; when the reduction does not take place the product is not a gamete, but a parthenogenetic spore. We accept Balfour's view, that the extrusion of the polar body is the means by which parthenogenesis is prevented, and, we may add, the means by which cross-fertilisation, with its attendant advantages, is rendered possible. A gamete is, as a rule, converted into a spore by means of the sexual process; two reproductive cells, neither of which contains sufficient nucleo-idioplasm for independent germination, form by their coalescence one which does. But it appears that in some of the lower forms, the necessary increase of the nucleo-idioplasm may be effected by nutrition, so that a gamete may become converted into a spore without the sexual process.

Having arrived at these conclusions respecting the sexuality of gametes, we go on to enquire into the nature of sex.

We have learned that Strasburger and Weismann are of opinion that male and female gametes, oospheres and antherozoids for example, or at least their nuclei, are essentially similar. From this point of view it is then merely the external adaptive peculiarities of the gametes which constitute their sex. But we shall endeavour to shew that this opinion is not in harmony with the known facts of reproduction.

In the first place it appears that, as a matter of fact, there is a material difference between male and female gametes, at least when they are highly differentiated. Zacharias has found, as the result of extended observations on the antherozoids and oospheres of Characeæ, Muscineæ, and Ferns, and on the oospheres and pollen-tubes of Phanerogams, that the nucleus of the male cell has either no nucleolus or but a small one, whereas that of the female cell has one or more large nucleoli; and further, that the male nucleus is rich in nucleïn, whereas the female nucleus is poor in nucleïn, but rich in albuminous substance. Much stress will not, however, be laid upon these facts, for, after all, the material difference between a male and a female gamete upon which the physiological difference between them essentially depends, may be

such as to elude any methods of investigation. Still these facts have their significance.

The main objection to the view of Strasburger and Weismann is that it fails to afford any explanation of the phenomena of sexual reproduction. If male and female gametes are essentially alike, why is it that two oospheres or two antherozoids never coalesce, but only antherozoid with oosphere, and how are the manifestations of sexual affinity, as we find them in the case of *Acetabularia*, *Ectocarpus*, *Dasycladus* (p. 647), and in the Phanerogams (p. 648) to be accounted for?

Strasburger and Weismann attempt to meet this objection by reference to Pfeffer's observation (see Lect. XX. p. 529) that, in cases in which the sexual cells are well differentiated, the female organ excretes a substance which has an attracting influence, and that it is only the corresponding male cells which are susceptible to this influence. The reason why two antherozoids or two oospheres do not coalesce is then this, that they do not attract each other; and it is for the same reason that a coalescence of gametes of opposite sexes, but not of the right degree of sexual affinity, does not take place. But the facts observed by Pfeffer do not really touch the point at issue. The attractive substances in question serve, it is true, to bring the motile male gametes, which may be produced at a distance, into proximity with the female gamete, but there is no evidence that they determine the actual coalescence of the two gametes. Pfeffer's observations do not account for the sexual process.

We cannot but conclude that the facts of sexual reproduction cannot be satisfactorily accounted for, otherwise than on the assumption that male and female gametes are essentially diverse. It is in fact because they are diverse that they are male and female: it is just this essential diversity that constitutes sex. External differences do not constitute sex; they are adaptive differences of only secondary importance. We assume that even in those plants which have externally similar gametes, there is yet a sexual difference between them. It is easy to conceive that objection may be taken to this view; but it appears to be quite necessary to

explain the facts of conjugation. It is impossible to explain why it is that, in *Ulothrix*, only those planogametes coalesce which have been derived from different cells, that in *Acetabularia* only those planogametes coalesce which have been developed in different resting-spores, that in *Dasycladus* only those planogametes coalesce which have been produced by different individuals, and many other similar cases might be mentioned, otherwise than on the assumption of a difference of sex.

From the facts of the development of the gametes it is probable that the sexual diversity depends upon a difference in the constitution of the nuclei. The coalescence of two appropriate gametes may be regarded as taking place in consequence of an attraction existing between them, an attraction which may be attributed to the difference between their nuclei. From this point of view, sexual affinity becomes intelligible. The fertility of the union between two gametes will depend upon the relation between their nuclei: when the nuclei are exactly complementary, the union will be fully fertile: when the relation is less perfect the union will be less fertile: when there is no relation, no union will take place. In illustration of this, reference may be made to the facts already mentioned, concerning the prepotence of some pollen over others, the relative fertility of fertilisation by pollen from various sources, etc.

Strasburger denies that any such attraction exists between the nuclei of coalescing gametes, but some of his own facts tend to prove its existence. In describing the fusion of the male and female pronuclei in the oosphere of *Phanerogams*, he speaks of the male pronucleus as being passively conveyed by the cytoplasm to the female pronucleus. But the question at once arises, why does the cytoplasm convey the male pronucleus in just such a direction that it meets the female pronucleus? Even assuming that Strasburger's statement of the case is correct, it must be admitted that it is under the influence of the female pronucleus that the cytoplasm conveys the male pronucleus to it. But it is probably nearer the truth to say that the male pronucleus is attracted by the

female pronucleus—or that the attraction is mutual,—and that it travels towards and fuses with the female pronucleus because it is so attracted.

In support of his view that no attraction exists between the male and the female pronucleus, Strasburger adduces the well-known fact that nuclear fusion may take place between somatic cells, as, for instance, in the embryo-sac of Angiosperms; between nuclei, that is, which might *a priori* be regarded as quite similar. But this is by no means conclusive evidence on his side. It is quite clear, in this case as in the preceding, that there must be some force which determines the fusion of the nuclei, and it may be that in this case also that force is an attraction existing between the nuclei, an attraction which may be the expression of a qualitative difference between them. There is another fact which is suggested by these considerations, namely, the production of graft-hybrids, and which may be appropriately considered here. Strasburger has rightly pointed out that the production of a graft-hybrid, as for instance the *Cytisus Adami*, probably depends upon a process of nuclear fusion taking place between the cells of the scion and of the stock, a process which does not usually take place in grafting. If this be so, it is difficult to explain the facts otherwise than by assuming that the nuclear fusion between the scion and the stock only takes place when there exists such a qualitative difference between the nuclei as to determine their coalescence. We adhere, then, to the view that there is a qualitative difference between the nuclei of the corresponding male and female gametes, and that it is upon this difference that their coalescence depends.

It seems probable that the difference between a male and a female gamete is brought about in the course of their development, and it is probably closely connected with the extrusion of the polar body. It may be that the loss of substance is not qualitatively the same in the development of a male and of a female gamete respectively. This view has been stated by Minot and van Beneden in this way, that in the extrusion of the polar body from the developing female

cell, the male constituent is removed; and, similarly, that in the extrusion of the polar body from the developing male cell, the female constituent is removed.

The next point to be considered is the functional relation between two coalescing gametes. When they are externally similar, there is no reason to suppose that the two gametes are functionally different. For example, when two planogametes of *Ulothrix* or *Acetabularia* coalesce, there is no ground for the supposition that one of the planogametes is fertilised by, or fertilises, the other. They are, as we believe, qualitatively different, but, in the sexual process, they are functionally alike; each is complementary to the other, and each transmits to the offspring the characteristics of the parent individual.

In the case of two corresponding gametes which are externally different, for instance an oosphere and an antherozoid, it is customary to regard the passive gamete as being the female, and the active as being the male. And not only so, but the sexual process is termed fertilisation, that is to say, it consists in the fertilisation of the female by the male gamete. This view involves the assumption of a considerable functional difference between the gametes; namely, that it is from the female gamete that the embryo is actually developed, whilst the male gamete simply stimulates the female gamete to development. This is the assumption which underlies Brooks' theory of the sexual process to which allusion has been already made (p. 656).

Careful consideration of the facts of the sexual process shews, however, that this assumption cannot be admitted. The fact which seems to give it most support, the fact of the difference in mass between an antherozoid and an oosphere, is really of no weight. It may be urged, on account of the difference of mass, that the oosphere contributes more to the embryo than does the antherozoid. But it must be remembered that the difference in mass between an oosphere and an antherozoid depends mainly upon the cytoplasm; hence, although it is true that the antherozoid contributes but little cytoplasm in the sexual process, it contributes probably

quite as much nucleo-idioplasm as does the oosphere, and this is without doubt by far the more important matter.

If, then, the male cell contributes as much nucleo-idioplasm to the germ as does the female, we should expect to find, that, in cases of cross-fertilisation for instance, the characteristics of the male parent are transmitted as well as those of the female; and, as a matter of fact, we do. Brooks, however, argues that the facts of hybridisation do not prove the transmission of characters by means of the male reproductive cell, and he supports his contention by reference to the fact that the reproductive cells produced in female organs are frequently parthenogenetic, whereas no case of male parthenogenesis is known. If, he says, a perfect organism could be developed from a male cell, we should have the means of proving that each sexual cell transmits to the offspring the entire organisation of the individual producing it.

Cases of the male parthenogenesis for which Brooks enquires, as he believes, in vain, are to be found among plants. We have already stated the grounds for the belief that in plants with externally similar gametes, those gametes are really of two sexes. When, as sometimes happens, in *Ulothrix* for instance, these gametes, having failed to conjugate, germinate independently, it must be assumed that both male and female parthenogenesis takes place. If such cases be considered inconclusive, no such objection can be taken to the case of *Ectocarpus*, in which it is possible to distinguish the male planogametes and to ascertain that they are capable of independent germination, though it must be added that the individuals developed from them are less vigorous than those developed in the ordinary way. It is true that male parthenogenesis is not known among plants of higher organisation than *Ectocarpus*, but the explanation is quite simple. In these higher plants the adaptive differentiation of the male cell, especially the reduction of the cytoplasm, is clearly such as to render independent germination quite impossible; whereas, in the case of the female cell, the differentiation which it has undergone is favourable to independent germination.

Under these circumstances we see that Brooks' theory is untenable, and that the male cell is not to be regarded as simply stimulating the female cell to development, but as contributing materially to the development of the embryo. In continuing to use the terms "fertilisation" and "conjugation" with reference to the sexual process, we must bear in mind that they have only a morphological significance; by conjugation we mean the coalescence of externally similar gametes; by fertilisation we mean the coalescence of externally dissimilar gametes: the physiology of the process is the same whether the coalescing gametes are externally similar or dissimilar.

In conclusion, we have to discuss the theories of variation to which allusion was made above; but in doing so nothing more than a very general treatment of the subject will be attempted. We will begin by setting forth, somewhat more fully than we have done as yet, Darwin's views, and then we will briefly discuss those views which differ from his.

In all cases, says Darwin, there are two factors in variation; the nature of the organism, which is the more important, and the nature of the conditions of life. By the "nature of the organism" is meant especially the variability of the organism, for, clearly, if an organism is not variable it cannot vary. The first point which we have to deal with is then the origin of variability. Some authors regard variability as an ultimate fact, and as much an aboriginal law as inheritance. Darwin, however, does not accept this view, but comes to the conclusion that variability of every kind is directly or indirectly caused by changed conditions of life. "If," he goes on, "it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability." A change in the conditions of life has the effect, which Darwin terms the indefinite effect, of promoting the plasticity of the organism, thus leading to much fluctuating or indeterminate variation. In support of Darwin's view it may be again pointed out that cultivated plants are far more variable than wild ones, and this may be correlated with the fact that

cultivated plants rarely remain exposed to closely similar conditions during any considerable length of time. Again, sexual reproduction, especially in connexion with cross-fertilisation, increases variability. It appears that greater variability, like greater vigour and fertility, is one of the advantages gained by means of sexual reproduction.

It appears probable, from the foregoing considerations, that variability was first induced as the response of the organism to changes in the conditions of life, and that it has become intensified by sexual reproduction and by cultivation. We know, from such observations as those of Kölreuter and Gärtner, who found that when two species were crossed, if either one was variable, the offspring were variable, that variability is hereditary; and we may therefore conclude that variability has come to be a general property of protoplasm. We may, in fact regard variability as a form of irritability, which, like all other forms of irritability, originated in the action of external stimuli and has become permanent.

We will digress for a moment to consider Brooks' view that variability is especially transmitted by the male cell. In support of this view he adduces the fact, ascertained by Gärtner and Wichura, that the progeny of a pure species crossed with a hybrid as the father are more variable than the progeny of the hybrid fertilised by the pollen of the pure species. It must be borne in mind, however, that, as just mentioned, there are facts which indicate that variability may be transmitted by either sex. Further, this particular case will not establish Brooks' position unless it be proved that the variability of the hybrid is transmitted by its male cell in a higher degree than its other characters. We know, namely, that the characters of an individual are frequently more readily transmitted by the one cell than by the other. This may be especially so in the case of hybrids; it may be that in hybrids there is a peculiar difference in potency between the male and female cells, and that all the characters, and not only the variability, of the hybrid, are transmitted more perfectly by the male than by the female cell. The difficulty in determining this point lies in the high variability of the

offspring. The fact cannot therefore be accepted as affording conclusive evidence.

But to return. The second point to be considered is the nature of the variation manifested by the variable organism. Darwin points out that, besides the indefinite effect already mentioned, a change in the conditions of life has what he terms a definite effect upon the organism in determining the nature of the variation. The effect, he says, may be considered definite when all or nearly all the offspring of individuals exposed to certain conditions during several generations vary in the same manner. At the same time he points out that it is very difficult to decide how far changed conditions have acted in a definite manner; and the difficulty is increased with regard to variations which are advantageous, to *Adaptations* that is, inasmuch as in this case we cannot tell how much to attribute to the definite action of the changed conditions on the one hand, and to the accumulative action of natural selection on the other. Yet, he concludes, there is reason to believe that in the course of time the effect of the definite action of the changed conditions has been greater than can be proved by clear evidence. Darwin considers, then, that changes in external conditions are ever acting upon living organisms and that consequently new varieties are ever being produced.

An altogether different view of the origin of varieties is held by those who, like Weismann, deny that characters acquired by individuals under the influence of changed external conditions can be transmitted in sexual reproduction. It is true that in many cases the modifications thus produced, especially those due to a change in climate or nutrition, are individual and transitory. For instance, a wild plant which naturally grows in poor soil will, when transplanted into rich soil, assume a very different habit; and the seeds of the modified plant, if sown in poor soil, will produce, not the modified, but the wild form. But Darwin especially points out that it is not these sudden variations which become permanent, but those slowly produced by what he terms the accumulative action of changed conditions of life.

Further, it is not possible to frame a satisfactory explanation of the fact of Adaptation without assuming the direct influence of the conditions of life, for Weismann's explanation of this fact cannot be regarded as satisfactory (p. 661). He endeavours to account for adaptation by attributing it to recombination, in an infinite variety of ways, of the characters acquired under the influence of changes in the conditions of life by the unicellular asexual progenitors of the race. But it is hardly possible to conceive how that by any combination of ancestral characters an individual could be produced which should be adapted to prevailing conditions of life. How is it conceivable, for instance, that the adaptations in the forms of their flowers, or in the structure of their fruits and seeds, which are exhibited by Phanerogams, are due to combinations of characters acquired by their unicellular asexual ancestors?

A second objection to Darwin's view may be stated in his own words: "instances could be given of similar varieties being produced from the same species under conditions of life as different as can well be conceived; and, on the other hand, of dissimilar varieties being produced under apparently the same external conditions." With regard to this, it must be pointed out that it is by no means easy for the observer to assure himself of the nature and extent of the difference between any two sets of external conditions, and of the nature and extent of the modification which the organism under observation may have undergone. The conditions may be, to the observer, apparently very different in the two cases, and yet in the points which most affect the plant they may be identical; and the converse applies to conditions which are apparently similar. In illustration of the possible failure in observing the modifications in the organism, the following passage from Darwin may be quoted. "When man can perceive no change in plants or animals which have been exposed to a new climate or to different treatment, insects can sometimes perceive a marked change. A Cactus has been imported into India from Canton, Manilla, Mauritius, and from the hot-houses at Kew, and there is

likewise a so-called native kind which was formerly introduced from South America. All these plants belong to the same species and are alike in appearance, but the Cochineal insect flourishes only on the native kind."

Weismann and those who agree with him in denying the influence of changes in the conditions of life in causing variation, maintain that variation is wholly dependent upon crossing. We have already pointed out that this view fails to account for Adaptation, and we will now briefly suggest other objections to it. In the first place, as we have already learned, variation may occur quite independently of sexual reproduction, in the form of bud-variation. In the second place it appears that crossing does not, in the case of wild plants, lead to the appearance of new characters, that is, to variation; though this is apparently the case with species which have been already rendered in some degree variable by cultivation. Gärtner states, for instance, that when he crossed native plants which had not been cultivated, he never saw in the offspring any new character. Now if, as Weismann insists, variation is simply a new combination of old characters, why is it that cross-fertilisation leads to it in cultivated but not in wild plants? The more reasonable view seems to be, that the variation of cultivated plants is the expression, not of a recombination of old characters, but of the acquisition of new in virtue of their high variability; and that variation is less common in wild plants because they are less variable than cultivated plants.

We conclude then that the production of varieties is the result of the influence of the conditions of life. These conditions act upon the whole protoplasm of the individual, and affect therefore those portions of its protoplasm which the individual throws off as reproductive cells. The modification is less readily transmitted by sexual than by asexual reproduction, when only one of the parents has been modified in the particular manner, for the modifications transmitted by the modified parent are, as it were, toned down by the infusion of protoplasm from the unmodified parent. But, as already mentioned, when both parents are similarly modi-

fied, the modification is almost as certainly transmitted by sexual as by asexual reproduction.

Without attempting to enter upon the large question of the Origin of Species, we will briefly discuss one or two points bearing on the subject which have been raised in the course of this lecture. When varieties arise, it is assumed that those which are most perfectly adapted to the prevailing conditions persist by natural selection, whereas those which are less perfectly adapted die out. By the gradual extinction of these varieties, the intermediate forms between the persistent varieties disappear; hence the persistent varieties appear to be so distinct from each other that they rank as species. Similarly, by the extinction of intermediate species, species come to rank as genera.

There can be no doubt that the multiplication of plant-forms has taken place in this way, but the question has been raised whether or not this is an adequate account of the evolution of more and more highly organised forms; for more complete adaptation to the environment by no means involves a higher organisation. For instance, we may account for the various forms of the lower Algæ as being the outcome of variation and natural selection, but can we account in this way for the evolution of the higher Algæ, of the Mosses, or of the Vascular Plants? It may be urged that variations in the direction of higher organisation may take place, and may be gradually rendered permanent. But it is questionable if the evolution of plants could ever, by this means, have reached the point to which it has attained, especially when we consider that much of it must have taken place in forms reproducing themselves by the sexual method, in which, therefore, in order for the variations to have been made permanent and hereditary, the same variation must have occurred in many individuals simultaneously. There seems to be some ground for believing that the evolution of plants is the expression of something more than fortuitous variation. As already mentioned (p. 657) Naegeli suggests, and his suggestion is worthy of serious consideration, that there is an inherent tendency to a higher organ-

isation, so that each succeeding generation represents an advance, though it may be a slight one, on its predecessors. The advance may not be at all perceptible for many generations, but then a new and distinctly more highly organised form appears, as in cases of what is termed *saltatory* evolution. Naegeli conceives the matter in this way, that the idioplasm of every organism tends to become more and more complex; that is, to become more and more completely differentiated physiologically and therefore also morphologically. On this view we can readily understand how that, step by step, there have sprung from simply organised plants others of increasingly complex organisation. Evolution is no longer a matter of chance, but is the inevitable outcome of a fundamental property of living matter.

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