THE

PHYSIOLOGY OF PLANTS

A TREATISE UPON THE
METABOLISM AND SOURCES OF ENERGY
IN PLANTS

BY

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SECOND FULLY REVISED EDITION

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PREFACE TO VOLUME III

As in the previous volume a certain condensation has been effected in the present one, in spite of a slight increase in the subject-matter. All additions or interpolations are, however, enclosed in square brackets, except in the sections dealing with tendril-climbers, with protoplasmic streaming, and with the mechanics of water-transport, to which a few explanatory figures have also been added. The appendix gives a summary of the more important literature which has appeared since the issue of the final part of the German edition, and notices of other recent works are interpolated in the foot-notes.

In regard to terminology, it has been the aim throughout to avoid the introduction of any new terms into the text of the English edition unless the weightiest reasons existed for their adoption. The present tendency to a redundant and overlapping phraseology in Plant Physiology, if unchecked, will ultimately lead to confusion similar to that existing in Taxonomy before the compilation of the Kew Index. The fact that a worker of the eminence, profundity, and breadth of Charles Darwin added only two or three terms to botanical terminology which could not be understood by reference to a standard English dictionary should make modern workers hesitate to encumber a developing science with more or less temporary pseudo-classical terms of doubtful utility or of none at all. Physieclexis and epitedeioperileipsis would have been poor substitutes for 'Natural Selection' and the 'Survival of the Fittest,' and the use of such terms would probably have considerably retarded popular acceptance of the Darwinian theory.

With the issue of the third and last volume of Professor Pfeffer's monumental work, a new point of departure has been gained by botanical physiology. Only those engaged in research can realize how much labour the preparation of these volumes, with their encyclopaedic compendium of modern literature, must have involved, and the completion of the work at so early a date in spite of a serious and almost fatal illness affords sufficient evidence of the devotion with which the author has pursued the stupendous task set before him to its conclusion. If the results of his labours have lost nothing in assuming their English dress, the task of the translator has been amply fulfilled.

ALFRED J. EWART.

Birmingham University,
December, 1905.

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PHYSIOLOGY OF PLANTS

VOLUME III

CHAPTER I

MOVEMENT

SECTION 1. **The Different Forms of Movement.**

NO plant is entirely without the power of movement, for even in rooted plants the growing parts move in space, and, since this continues until death, rhizomes and runners may traverse a considerable distance during their existence.

The tip of a growing organ usually does not follow a straight line, but describes a complicated curve in space. In many cases, indeed, the rates of growth on opposite sides are such that a pronounced curvature may be produced, or the tip may move to and fro, or trace a spiral curve in space as it elongates (circumnutation). These growth or nutation[1] movements naturally cease with the cessation of growth, although active movement may still be possible in some cases. For instance, the pulvini of many *Leguminosae*, and of other plants also, are organs specially adapted for pronounced movement by elastic shortening and lengthening[2]. The fact that in plastic shoots no movements occur after the cessation of growth simply shows that in these parts the activity of the plant is unable to produce any perceptible effect. If, however, growth is reawakened, as in the nodes of Gramineae by geotropic stimulation, we again encounter curvatures due to nutation.

In adult but still living parts which are externally rigid, an internal power of movement is never entirely absent, and is indeed permanently connected in every cell with metabolism and exchange, for in the protoplast itself movements and changes of shape continually occur.

In the absence of a cell-wall amoeboid movements and changes of shape are possible, as is especially well shown by Myxomycetes. Swarm

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[1] This term was first used by Duhamel (Naturg. d. Bäume, 1765, Bd. II, p. 115) and de Candolle (Pflanzenphysiol., 1825, Bd. II, p. 666), and subsequently restricted by Sachs to movements produced by growth (Sachs, Lehrbuch, 1873, 3. Aufl., p. 757), whether autonomic or aitionomic. Frank (Beiträge zur Pflanzenphysiol., 1868, p. 51) uses the term 'nutation' for growth-movements due to external stimuli, and distinguishes autonomic movements as 'inclination.'

[2] Pfeffer, Die Reizbarkeit d. Pflanzen, 1898, p. 9. (Reprint from the Verh. d. Ges. deutscher Naturforscher u. Aerzte, 1893.)

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cells, owing to the presence of special locomotory organs, cilia, or flagellae, are able to swim about actively in water.

Among plants it is only in the case of small organisms that active locomotion is possible, and frequently only during a particular stage of the life history. Since the response due to a stimulus is always dependent upon the character of the resulting movements, a freely motile plant may travel towards a source of illumination, whereas a rooted plant responds in a less degree by growing and curving towards the illuminated side. In spite of this difference, the actual perception and stimulation may be identical in the two cases.

The movements of free-swimming plants appear to have a more purposeful nature, simply because they resemble the movements of animals. As a matter of fact the power of perceiving and responding to stimuli is equally developed in plants rooted to the soil. Free-swimming plants, it is true, lend themselves more readily to experimental studies, because they usually react more rapidly than plants which can respond only by a change in the rate or character of growth. Since most plants fall in the latter class, and since curvatures are usually produced by growth, we shall confine ourselves at first mainly to movements of this character.

The fact that in large plants the power of growth and movement are not strikingly evident has caused plants to be popularly regarded as 'still life.' Hence the rapid movements of *Mimosa pudica* were regarded as extraordinary for a plant, and the same applies to the spontaneous movements performed by the lateral leaflets of *Hedysarum gyrans*[1]. If mankind from youth upwards were accustomed to view nature under a magnification of 100 to 1,000 times, or to perceive the activities of weeks or months performed in a minute, as is possible by the aid of a kinematograph, this erroneous idea would be entirely dispelled[2].

Movements serve a variety of aims and purposes, and need to be considered not only as regards the causes which produce them and the way in which they are carried out, but also as regards their importance to the plant. We are, however, less concerned with oecological explanations than with the determination of causes and mechanism.

In every case a response to a stimulus indicates a specific irritability, although the nature of the response will vary in different plants according to their nature and properties. We can, however, distinguish between autonomic, autogenic, or spontaneous stimuli on the one hand, and aitiogenic, induced or paratonic stimuli on the other, and the same applies to the movements resulting from internal or external stimula-

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[1] Pfeffer, Die Reizbarkeit d. Pflanzen, 1893, p. 9. (Reprint from Verh. d. Ges. deutscher Naturforscher u. Aerzte, 1893.)

[2] Pfeffer, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 738.

tion[1]. To invent names for each variety of movement such as gamotropic, carpotropic, and the like, as Hansgirg has done[2], aids nothing in elucidating the phenomena in question[3].

Curvatures produced by diffused stimuli are aitionastic, those produced by unilateral stimuli are orienting or tropic. The latter to which geotropism, heliotropism, and the other tropic movements belong, are the result of a sense of discrimination and have this in common, that the responding organ assumes a definite position in regard to the direction of the stimulus[4].

Both radial and dorsiventral organs respond in this way, whereas a curvature can be produced by a diffuse stimulus in dorsiventral (and anisotropic) organs in which the opposite halves respond by unequal growth and elongation.

The movements of *Mimosa pudica* produced by a blow, as well as the contraction of stamens of Cynareae, also take place in a definite direction predetermined by the structure of the organ. The curvatures produced by diffuse stimuli are termed 'nastic,' while by epinasty, hyponasty, and paranasty, the sides are indicated which elongate on stimulation.

These distinctions only apply to special types of movement between which transitions occur, not only because the two forms of movement may take place at the same time, but also because the same movement may be regarded as 'nastic' or as tropic, according to the point of view adopted. Thus a curvature which we term 'nastic' is primarily the result of tropic stimulation, which is awakened in spite of the homogeneous external conditions, owing to the dissimilar physiological properties of the sides of the curving organ. This would be the case if the formation of pigment or of a more opaque cuticle hindered the penetration of light on one side, as well as when one side was smeared with Indian ink. In the same way, a local increase in the permeability of the cuticle might cause stronger transpiration on that side, and thus produce hydrotropic stimulation and curvature. Further, equal contact on all sides of a physiologically radial tendril will produce a curvature if a protective layer is interposed on one side so that the stimulation on that side is less pronounced.

Autogenic curvatures which are produced under constant and homogeneous external conditions may be termed autonastic, and the single or

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[1] Cf. A. P. de Candolle, Physiologie des plantes, a German translation by Röper, 1883, Bd. II, p. 552; Dutrochet, Mém. anat. et physiol. d. végétaux et d'animaux, Bruxelles, 1837, p. 225.

[2] Physiol. Unters., 1893, p. 966.

[3] Pfeffer, Die period. Bewegungen d. Blattorgane, 1875, p. 2.

[4] Oltmanns (Flora, 1892, p. 206) suggests the term 'Photometry' to indicate the power of the plant to respond to light. [The term is inadvisable, since in correspondence with its physical usage it would suggest that plants detect and respond to the intensity of the light alone and not to its direction.]

periodic movements resulting from internal non-homogeneous stimuli or changes may be called autotropic. An autonomic movement resulting from a change of the geotropic irritability affords, however, an undoubted instance of tropic stimulation and would not be shown on a klinostat.

Further, the induction of a labile dorsiventrality by unilateral illumination produces the conditions for a photonastic reaction, and it is by no means easy to resolve the combination into its component factors. Indeed, all geotropic or phototropic curvatures may be regarded as the result of epinastic or hyponastic properties induced temporarily by the unilateral action of gravity or light.

There is, however, no necessity for rigid restriction in discussing these phenomena. Thus, the tropic movements of tendrils may be treated together with other adaptations for climbing, while various 'nastic' reactions will be first mentioned in connexion with the tropic orienting movements. Furthermore, the mechanisms for dehiscence and active dispersal are of economic importance, but of special character, and often not vital phenomena.

SECTION 2. **The Causes of Movement.**

All these movements are produced in response to stimuli of either internal or external origin. The first indication of a motile irritability is afforded by the realized movement, which forms at the same time an evidence of a power of perception. No movement is possible, however, if a block or gap occurs in the chain of processes intervening between perception and response.

In plants whose sensory and motor parts are some distance apart, the destruction of the sensory organ, or a break in the path of the stimulus, prevents response. Similarly no movement is possible if the responding organ has lost its power of movement, so that parts which have ceased to grow lose their motility, if they are only capable of growth-curvatures. A power of perceiving stimuli might, however, still be present, although the power of reacting to them appears to be absent.

In many such cases the processes of perception and induction appear to take place as before, as is evidenced by the fact that the rapidity and amount of response decrease when growth is enfeebled, but stop usually only when growth ceases and may again become perceptible if it is reawakened.

The power of movement in adult organs depends largely upon their structure and upon the properties of their cell-walls. Thus a fall of turgor which produces a pronounced shortening in the stamens of *Centaurea* or a curvature in the pulvinus of *Mimosa* does not cause any perceptible change of shape or curvature in the filament of a *Spirogyra*, or in the branch of a tree.

We must, as far as possible, endeavour to distinguish the processes of sensation, induction, and movement from one another, and to resolve these further into their component factors. At present, this is possible to a very limited extent and only in a few cases, for the best knowledge of the conditions for stimulation and reaction, as well as of the position, shape, and structure of the percipient organs and of the conducting paths, affords no insight into the processes which underlie perception and induction. Since perception and induction are usually so closely connected that they cannot be separately considered, we shall discuss both at the same time.

If we restrict the term 'perception' to the first physiological interaction involved in stimulation, we must not apply the same term to the whole series of sensory processes, when these cannot be resolved in detail. Preparatory processes may take place which render possible or initiate perception and response. This is the case, for instance, when cutting the stem of *Mimosa* produces a movement of water which calls forth a response in the pulvini, or when the sinking of dense particles in the cell acts as the cause of a geotropic response. Further, the same would be the case when light or some endosmosing substance produced a chemical change in which one of the products acted as a stimulus.

Just as one speaks generally of the processes of induction, so also may we group all these preparatory processes together as instances of indirect stimulation—although they may be varied and complicated in character. In any case the introduction of special terms for phenomena which are not yet understood, and for facts which are largely unknown or uncertain, is hardly to be recommended[1].

The movement of zoospores towards light or away from it when intense can be regarded as the result of tropic stimulation. Further, the conversion of a positive into a negative heliotropic curvature involves a change in the sensory processes alone when the change from weak to strong light which produces this alteration acts on the sensitive tip of a seedling leaf of *Avena*, but not on the responding basal portion. But when light or any other agency directly stimulates the responding region, a change in the response may result either from an alteration of irritability or from some influence upon the course of the reaction. The sensory processes themselves may be of greater or less complexity, and hence may be influenced in a variety of ways so as to lead to changed responses. In such cases a change in the final result affords no indication as to whether it is due to a modification of the primary act of perception or of some one of the resulting stages leading from perception to response.

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[1] Cf. Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, pp. 214, 302; Centralbl. f. Physiol., 1900, Bd. XIII, p. 209.

It follows, therefore, that when two different organisms respond similarly to the same stimulus the processes of perception and response may be alike in both, but need not necessarily be so. We do not know, for instance, whether the mode of perception of light and of other tropic stimuli is in all cases the same. Even if this were the case the power of response may vary indefinitely, and can never be the same in a rooted plant as it is in a free swimming one. The former may respond by movements due to growth or to changes of turgidity, whereas the latter is dependent entirely upon the special mode of locomotion it possesses. The same stimulus may produce different responses according to the properties of the responding organism, and widely dissimilar stimuli produce the same type of movement in a particular plant. It is only natural, for instance, that swarm-cells should always use the locomotory organs they already possess in moving from one place to another as the result of stimulation, and should not seek out and utilize currents of water or other external mechanical agencies for this purpose. Similarly, we may assume that the curvatures resulting from heliotropic, geotropic, and chemotropic stimuli are in many cases, at least, carried out in a similar manner in all rooted plants.

Every organ which has the power of responding to one or more tropic stimuli, singly or conjointly, must possess a special power of perceiving each such stimulus, and the power of perception as regards one stimulus may be lost or destroyed without the general perception being affected. This remains true, in spite of the fact that plants possess no special sense-organs, and that we are unable to say how it is that of two apparently similar protoplasts one may temporarily or permanently possess a different irritability and power of response to the other. The response is always dependent upon the existent condition of tone, which again depends upon the stage of development and upon the existing and previous external conditions[1]. Furthermore, the resultant action of two conjoint stimuli is not necessarily the arithmetical sum of their individual actions. Supposing that the power of movement remains unaltered, either two separate impulses may be exercised upon it, or the two stimuli may fuse during perception and act as a single excitation.

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[1] The terms 'tone' and 'tonic condition' may be used in the same sense as in animal physiology, so that by 'tonic stimuli' we may denote the conditions which render possible an irritable response. Cf. Massart, Biol. Centralbl., 1902, Bd. XXXII, p. 41; Miehe, Jahrb. f. wiss. Bot., 1902, Bd. XXXVII, p. 571. Miehe distinguishes between 'anatonic,' 'katatonic,' and 'metatonic' stimuli, according to whether the reaction is increased, decreased, or reversed by them. Engelmann's 'photokinesis' is merely an instance of light acting as a tonic stimulus, as when illumination excites the movement of certain motile forms. (Engelmann, Pflügers Archiv f. Physiol., 1882, Bd. XXX, p. 169.) On the equally unnecessary term 'chemokinesis,' cf. Rothert, Flora, 1901, p. 374, and also Nagel, Bot. Ztg., 1901, Ref., p. 298. Garrey (The Effects of Ions upon the aggregation of flagellate Infusoria, 1900, p. 291) has used the term 'photokinesis' in another sense, to indicate the changes of movement produced by sudden alterations of illumination.

The resulting movement affords no indication as to the mode of perception, and no movement at all may occur when two opposed stimuli neutralize each other, or when the resulting attempts at movement are similar and of opposite kinds. If, however, one stimulus preponderates, and a movement results, the same amount of energy will be expended as when a similar movement is produced by a single stimulus.

The resultant reaction due to conjoint stimuli is neither quantitatively nor qualitatively the sum of their separate actions. This is still the case when the stimuli are of like kind, for since the power of reaction is always limited, the superposition of a supra-maximal stimulus upon a sub-maximal one may produce little or no additional response. Hence also with stimuli progressively increasing in intensity, the later responses do not increase in proportion to the increases of excitation.

A satisfactory solution of problems of this kind is not at present possible, although sufficient is known to show that the mechanism of irritable perception and response is not always the same. It is clear that a changed response to a particular stimulus must be due to some change in the mode of perception if the responding mechanism is unaltered. Even when the percipient organ is distinct from the responding region, however, any agency which affects the former may cause modifying influences to radiate from it to the responding mechanism. Hence a tonic stimulus which primarily acts on the percipient organ alone may indirectly modify the character of the curving zone, so that the capacities of both perception and response are altered.

Without doubt a change of irritability is in many cases largely or entirely the result of alterations in the sensory and related processes. Modifications of irritability very commonly take place during the life of an organ, so that a particular tropic stimulus does not always produce the same result. It is not however certain whether, for instance, the lack of response to shaking in an etherized plant of *Mimosa* is the result of an inhibition of the power of perception, of induction, or of motion.

Similarly it is difficult or impossible to say whether in a particular case two simultaneous stimuli fuse in the act of perception, or whether they act singly upon the motor mechanism. The former appears to be usually the case when two dissimilar tropic stimuli act conjointly, whereas a fusion of this kind does not appear to occur between tropic and photonastic or contact stimuli. In all cases, however, it must be remembered that the independence of the processes of sensation and response is only relative, and that a modification of the one is certain to react upon the other.

A perceptible response is in all cases only produced when the stimulus reaches a certain minimal intensity, while between stimulation and response a latent period of variable duration always intervenes. The resulting movement is nearly always gradually accelerated to a maximum, beyond which the effect of the stimulus gradually diminishes and disappears.

The duration of the latent period lies between a few seconds and a few hours in the case of the slow movements usual in plants. A stimulus impressed upon a plant continues to act for a time after it has been removed, and the greater the difficulty of producing an irritable response the longer will be the persistent after-effect. Hence a stimulus may produce a response some time after it has ceased to act. Similar relationships hold good for the rapid movements of the leaves of *Mimosa pudica* and of the staminal filaments of Cynareae or of *Berberis*, although they become more immediately perceptible when the duration of the reaction is lengthened by low temperatures. The irritability of the plant, as well as its power of response, are dependent upon the external conditions, although naturally the most favourable external conditions cannot increase the response beyond a certain limit.

When the reaction is rapid, all the phases of stimulation must be passed through in a very short time, but when it is slow the delay may occur either in the perception of the stimulus or in the responding mechanism, or in both. It is presumably owing to the lessened power of movement that the nutation of the older parts of stems and roots is a little later in time, and also less pronounced than in the younger parts. In many cases a stimulus is only gradually perceived, and frequently a long time elapses before the motor-mechanism begins to be called into action. This is especially well shown when a conducting zone intervenes between the percipient and responding organs. A prolongation of the latent period in an organ capable of rapid response is probably in most cases the result of slow perception.

Except in the case of motile organisms, the movements of plants have almost always the purpose of gradually bringing the organs into a definite functional position, and it is only rarely that for special purposes a power of rapid movement is developed. In such cases we are usually dealing with transitory reactions produced by sudden changes, as, for example, when a blow or a sudden change of transpiration causes the leaves of *Mimosa* to close. Reactions of this kind may be termed temporary, transitory, or shock effects, whereas the slower movements involve a condition of permanent or stationary stimulation. Here a condition of equilibrium is maintained so long as the external conditions and the properties of the organism remain unaltered, and a response of this kind is possible not only to orienting stimuli such as gravity or light, but also to diffuse ones such as temperature. No sharp distinction can however be drawn, for often both forms of stimulation act together, and it is in fact in this way that the peculiar sequence observed in thermonastic and photonastic movements is produced. The leaflets of *Mimosa pudica* return to their original position in spite of repeated stimulation by blows, whereas tendrils and the leaflets of *Oxalis*, for instance, on a repetition of the stimulation, take up a new position of equilibrium. Similarly, if stimuli are repeated on a muscle before relaxation has taken place, the muscle responds to each and remains contracted in a condition of tetanus.

Furthermore, *Mimosa* is exceptional in that any shock-stimulus to which the leaflets respond produces the maximal possible movement. Usually, however, as for example in the leaflets of *Oxalis*, a single blow may act as a sub-maximal stimulus, and the full sinking of the leaflets be produced only by repeated shocks. The existence of a labile condition is not essential for the realization of an irritable movement, and in fact in many cases the latter may not involve an increase in the general activity of growth, but merely its guidance and regulation. Naturally, however, the accumulation of potential energy in the form of high tissue-strains and the like is necessary for the performance of rapid movements.

Except in those cases where any operative stimulus produces the maximal effect, increasing intensity of excitation produces increasing and more rapid response. This applies to transitory as well as to intermittent and continuous stimulation. Weak heliotropic, geotropic, or photonastic stimulation, for instance, produces a less pronounced curvature than strong stimulation. There is, however, no exact relation between the intensity of the stimulus and the amount of response, or of the sensory excitation. These physiological processes usually increase less rapidly than the stimulus does, so that a greater increase in the intensity of the stimulus is required in a strongly excited organ than in one under weak stimulation to produce the same increase of excitation or response. This rule is well known in animal physiology, and in addition, beyond a certain intensity of stimulus, the response may alter, as when organisms swim towards diffuse light but away from strong sunlight, and hence collect at a definite distance from a local source of illumination. Rooted plants also curve towards a strong source of illumination when far away from it, take on a diaheliotropic position when nearer, and curve away from it when still nearer.

These effects are the result of a change of tone, which may often be due to the fact that some of the factors involved in sensation are affected more than others by increasing stimulation. This is shown especially well when with increasing concentration a negative osmotropism overcomes a positive chemotropism.

Every disturbance of equilibrium inducing curvature excites reactions directed towards the restoration of equilibrium. Hence on the removal of a tropic stimulus, the organ affected returns to the original position assumed in virtue of its autotropism, so long as the power of movement is retained. Even in adult organs which have ceased to grow, curvatures may be removed if a power of potential growth resides at the nodes.

The rapidity of the return movement depends on the prevailing conditions, but it is usually much slower than that induced by the original stimulation, as is strikingly shown by comparing the sudden closure of the leaflets of *Mimosa* or of the leaf-lobes of *Dionaea*, induced by a blow or by contact, with their subsequent gradual re-expansion.

Since autogenic factors are always in play, even the movement resulting from a single external stimulus is as much the result of conjoint stimuli as when two external stimuli act simultaneously. As the result of the co-operation of these autogenic and aitiogenic factors and of the reactions due to the movement itself, the final curvature assumed is usually preceded by a series of oscillations. The movement of the mercury in the gas-regulator of a hot chamber when the temperature is raised to a new level forms a suitable analogy, for here also the excessive movement excites factors tending to its reduction, and to a rapid diminution in the amplitude of the vibrations. Oscillations of this kind occur during tropic and nastic movements, as well as during the return of stimulated leaves of *Mimosa* to their original position. The persistent after-effects of the daily movements are also the result of oscillations of this kind, although oscillations having a purely internal origin may exist.

These general remarks apply not only to the higher and lower plants but also to each individual protoplast, for in each case the functionally dissimilar parts and organs are variously affected by stimuli and are unequally responsive and active. We do not, however, know either the organs of perception or by what changes the latter may be modified. Just as particular powers and properties may appear and disappear under particular conditions, so also may the power of perception not always be present. Furthermore it is possible that in many cases the perception of a stimulus may involve the simultaneous awakening of different processes, and that the incapacity for any one of these may make the organism irresponsive.

Since the organs of the protoplast are capable of a variety of functions, it is hardly to be expected that any of them should be capable of response to a single stimulus only, or that special sense-organs capable only of limited excitation should be developed. It is, however, possible that in particular cases the nucleus may perceive the stimulus or act as a reflex centre, whereas in others it may take no part. Thus in non-nucleated masses of cytoplasm functions such as streaming and ciliary movement may continue and be affected by external stimuli, as is especially well shown when non-nucleated fragments of Infusoria exhibit galvanotaxis. Even when interaction with the nucleus is necessary for the performance of a response by the cytoplasm, it does not follow that the nucleus perceives the stimulus. For instance, the unicellular rhizoid of *Marchantia* or of a fern prothallium responds by a negatively heliotropic curvature when the tip is exposed to light, although the nucleus is at its base and is not directly exposed to the stimulus of light.

The different parts of the cytoplasm have without doubt different and changeable powers, but even when a particular stimulus is perceived by the isolated cilia of a motile organism, the ectoplasmic membrane and other parts may also be sensitive to this stimulus. The ectoplasmic membrane may in fact be specially sensitive to orienting stimuli, but it is uncertain whether stimuli inducing movement in the chloroplastids are perceived in the chloroplast itself, and it is very doubtful whether the eye-spot of zoospores is an organ specially adapted for the perception of light.

The process of sensation is not revealed by the movements or changes in the protoplast which result from or accompany stimulation. Thus the movement of a swarm-spore towards light, or the local accumulation of the cytoplasm or chloroplastids produced by tropic stimuli, afford no insight into the processes of perception and induction. In many cases local accumulations of the protoplasm form the purely mechanical result of a realized curvature, but in others preparatory processes of this nature may precede or accompany the actual perception of a stimulus.

Historical. From the beginning of the nineteenth century attempts have been made to explain the causes and mechanism not only of the rapid movements of *Mimosa pudica*, but also of heliotropic and other growth curvatures. It was naturally only at a somewhat later date that the smaller and less known motile organisms were also drawn into consideration. At first it was attempted to explain the movement as being the direct mechanical result of the exciting stimulus. Thus the partial etiolation of the shaded side of a stem, or the modification of the elasticity of the cell-walls by the direct action of light, were considered to be the causes of heliotropic curvature, while geotropism was supposed to result from the plastic curvature of the root or of the growing apex under its own weight, or to the unequal distribution of food-materials of different densities brought about by the action of gravity.

The true nature of these complicated manifestations of irritability was therefore not recognized, although Dutrochet[1] in 1824 expressed the opinion that light and gravity were only the inducing causes of heliotropic and geotropic curvatures, and not the direct mechanical agencies in producing them. This author, however, can hardly have thoroughly comprehended the phenomena in question, since at a later date he arrives at direct contradictions to his original principles[2]. Even in the brilliant Experimental Physiology of Sachs[3] the mechanical explanation of the slower growth movements retains the upper hand. Pfeffer in 1877[4] pointed out that the movements were in all cases the responses of irritable structures to stimuli, and brought the subject up to our present standpoint. The researches of Darwin were of the utmost value in this connexion since they showed that the processes of perception, induction, and movement might take place some distance apart[5].

Darwin[6] considered all curvatures to be modified forms of circumnutation, but

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[1] Dutrochet, Rech. s. la structure intime d. animaux et d. végétaux, 1824, pp. 107, 117, 130, &c.

[2] Dutrochet, Mém. anat. et physiol. d. végétaux etc., 1837.

[3] Sachs, Experimentalphysiologie, 1865.

[4] Pfeffer, Osmot. Unters., 1877, p. 202; Pfeffer, Pflanzenphysiologie, 1881, Bd. I, p. 3; Bd. II, pp. 117, 178, 286, 327 u. s. w. Sachs, Vorlesung über Pflanzenphysiologie, 1882, p. 717, then pointed out the general character of irritability, but was wrong in supposing that for every irritable response a labile condition is essential. Cf. also Pfeffer, Die Reizbarkeit d. Pflanzen, 1893, p. 10 (Reprint from the Verh. d. Ges. deutscher Naturf. u. Aerzte zu Nürnberg).

[5] Darwin, Insectivorous Plants, 1875; The Power of Movement in Plants, 1880.

[6] Darwin, The Power of Movement in Plants. Darwin himself doubted whether the movements

this view leaves out of consideration the special forms of irritability which the plant has developed for particular purposes. In the case of either a growing plant or a motile zoospore, a curvature or change of direction is due to an external or internal stimulus modifying the previous activity, but in the nodes of grasses when laid horizontal the external stimulus of gravity first awakens growth and then determines its direction. Aitiogenic and autogenic curvatures, although they may co-operate, do not always occur together. Hence a plant showing active circumnutation may only respond to external stimuli by a feeble curvature, while an active power of response may be accompanied by very slight circumnutation. There are, indeed, plants in which aitiogenic movements are carried out in a different manner to autogenic ones.

SECTION 3. **The Mechanism of Movement.**

Amoeboid movement and the locomotion of zoospores are effected in a different way to the growth curvatures resulting from modifications of nutation, and these again are of different origin to the temporary movements resulting from changes of turgidity coupled with the elastic contraction and expansion of the cell-walls.

All active nutation curvature is the result of unequal growth on the two sides of the cell or curving organ. If the more active growth occurs first on one side and then on the other, the apex will move to and fro more or less regularly, but if the zone of more active growth travels round the growing region, the apex will describe an ascending spiral in space. The latter is especially well shown in the case of climbing plants and these may twine around a support with or without torsion of the stem[1].

Most plants only carry out movements of nutation, and in such cases the power of curvature is lost with the cessation of growth, but is regained with the resumption of growth, as in the geotropically stimulated nodes of grasses. The absence of curvature may also be due to the fact that the energy of growth is unable to overcome the mechanical rigidity of the organ affected. The woody stems of Conifers, for instance, may be able to curve as the result of cambial activity up to their second or even third year, but not beyond this[2]. Similarly the curvatures shown when a herbaceous stem is split longitudinally give evidence of tissue-strains,

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of the leaflets of *Mimosa* and of the tentacles of *Drosera* could be regarded as modified circumnutation. Cf. also Wiesner, Bewegungsvermögen der Pflanzen, 1881, p. 202.

[1] Nägeli und Schwendener, Mikroskop, 2. Aufl., 1877, p. 416; Schwendener und Krabbe, Abhandlg. d. Berl. Akad., 1892, p. 56; Kolkwitz, Ber. d. bot. Ges., 1895, p. 495; and the literature quoted in these works.

[2] [Errera (Proc. British Ass., 1904) states that the trunks of tall adult trees may curve geotropically at their bases. The curvatures observed were, however, undoubtedly produced when young, for to bend an old stem upwards at its base, the developing wood-elements would have to overcome a mechanical moment representing in them pressures of many hundred or thousand atmospheres.]

which if they existed on one side only would suffice to produce a curvature of the entire stem, if its mechanical rigidity were not too great.

In organs adapted for temporary or variation movements the structure is such as to give a considerable freedom of movement. Thus in the pulvini of Leguminosae and other plants the relatively rigid and inelastic vascular bundle is curved and surrounded by active tissue in which, owing to the elasticity of the walls and the changes of shape in the cells, considerable shortening and lengthening is possible[1]. The vascular bundle at the middle of the pulvinus (Fig. 1) lies in the neutral zone, and is but little affected by the curvature produced by a rise of turgidity on the lengthening side of the pulvinus or by a fall on the shortening one. In the first case the shortening of the concave side is due to the cells being compressed by the expansion of those on the upper convex side[2], just as happens when a pulvinus is moderately bent by applying an external force.

In the case of a nutation movement, however, the median axis undergoes permanent elongation, and it depends upon the mean activity of growth, upon the degree of curvature, and upon the thickness of the organ whether the concave side becomes longer, shorter, or retains the same length as before[3]. The amount of curvature is naturally dependent not only upon the relative growth of the antagonistic connected tissues, but also upon the resistance offered by the vascular bundles and other inactive elements. The importance of this resistance is shown by the fact that when a young pulvinus still capable of growth is caused to curve the vascular cylinder undergoes a slight permanent elongation.

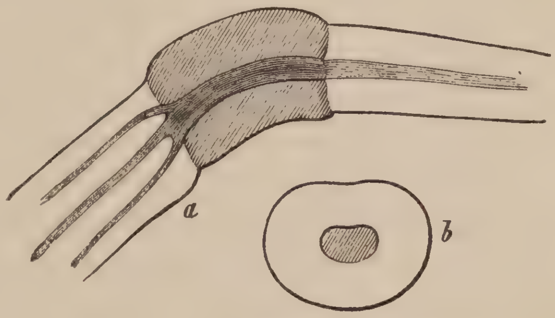

FIG. 1. Pulvinus of *Phaseolus vulgaris* (magnified), (*a*) longitudinal, and (*b*) transverse sections.

The realized curvature affords no evidence as to whether one or both zones are active, or in the latter case whether the response is of similar character but unequal amount on the two sides, or of dissimilar character. As a matter of fact various combinations occur. Thus the variation movement of *Mimosa pudica* is produced by a fall of turgidity on the concave side, the expansive energy of the unstimulated convex side then

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[1] Pfeffer, Die period. Bewegungen d. Blattorgane, 1875, pp. 3, 157. On the anatomy of pulvini see also A. Rodrigue, Bull. de la Soc. bot. de France, 1894, T. 41, p. 128; Schwendener, Sitzungsb. d. Berl. Akad., 1896, p. 535; 1897, p. 228; 1898, p. 176; M. Möbius, Festschrift für Schwendener, 1899, p. 37.—E. Pantanelli, Studii d'anatomia e fisiologia sui pulvini motori di *Robinia* et *Porliera*, 1901; Haberlandt, Physiol. Anat., 2. Aufl., 1896, p. 475.

[2] Pfeffer, Physiol. Unters., 1873, p. 73.

[3] Pfeffer, Die period. Bewegungen d. Blattorgane, 1875, p. 17.

producing the curvature. On the other hand, during photonastic curvatures the energy of expansion increases or decreases in both halves of the pulvinus, but more rapidly in one half than in the other, so that the original curvature is in time partially or entirely eliminated. The movements produced as the after-effect of the daily movements, and the spontaneous movements of variation are produced by a rise of pressure on the one side and a fall on the other. The same takes place when a heliotropic or geotropic curvature is produced in a pulvinus.

All possible combinations may be involved in the different kinds of nutation movements. Thus most geotropic and heliotropic curvatures are produced by an acceleration of the growth upon the convex side, and a retardation on the concave one, the mean growth of the median axis being unaltered only slightly so. On the other hand, the curvatures produced in tendrils by contact as well as the aitionastic nutation movements of stems, involve a general acceleration of growth, but this is more rapidly produced on one side than the other. It is possible but not certain that some curvatures may be produced by an acceleration or retardation of growth on one side only, or even by an active growth contraction on one side. Active growth contractions do actually occur in roots, and Kohl erroneously assumed that the tropic nutation movements were the result of the shortening of the concave side. The curvatures produced in split stems owing to the release of the tissue-strains may undergo a secondary increase owing to the resumption of growth in the two halves, and a tissue like the pith, which when isolated grows straight, experiences a curvature in the split stem. Hence the curvature realized in an organ depends upon the powers and activities of its inter-related cells and tissues. Frequently inactive tissues are curved by the active ones, and it may happen that the concave side is shortened and its cells compressed, owing to the more rapid growth on the convex side, although both sides strive to grow more rapidly than before but not equally so. Many curvatures are produced as the direct result of the fact that certain tissues grow and elongate more rapidly than others.

Observations made upon Thallophyta and unicellular trichomes show that individual cells may curve owing to one side of the cell-wall elongating more rapidly than the other. In multicellular organisms the curvature may either be directly produced in the curving cells or tissue, or may result from the antagonism between connected but unequally elongating parts. In the former case we can speak of the photonasty or heliotropism of the responding cell or tissue[1], whereas in the latter case the organ responds more as a whole. A sharp distinction is impossible in many cases, for often both types may act together, and the mechanical action of the realized

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[1] Pfeffer, Druck- u. Arbeitsleistungen, 1893, p. 414.

curvature may originate stimuli tending to the modification and correlation of growth in the different zones. Some such regulation is necessary even when the curvature is produced by the activity of the different cells, for unless they all act at the same time and in the same direction no curvature could be produced in an organ having a moderate mechanical rigidity. During tropic curvatures each lamella from the concave to the convex side seems to grow more actively than the one before it, so that all the lamellas tend to curve actively. On the other hand, many aitionastic and autonastic curvatures seem to be produced by the antagonism of unequally elongating tissues.

Even when a curvature can be ascribed to the distribution of the active and passive zones and to their relative rates of growth, we have still to determine the causes which induce the latter. Growth curvatures may be produced in various ways, either by plastic growth, growth by intussusception, or by changes of shape of the cells affected. Hence similar curvatures need not necessarily be produced in the same way in all plants.

The intermittent elongation and the related nutation movement of *Oedogonium* are due to its plastic mode of growth, and the same peculiarity may be responsible for many nutation movements. The rate of growth is usually not regulated by changes of turgidity, but in other ways, and in fact the turgidity usually sinks slightly in the cells on the convex side which are growing most rapidly. It is quite possible for the increased growth which produces curvature to be the result of a rise of turgidity on one side, but hitherto not a single instance has been established. The positive conclusions of various authors are based upon uncertain facts, and are in part derived from incorrect views as to the mode of growth in surface extent of the cell-wall[1]. A change of turgidity can hardly be responsible for a curvature due to the unequal growth of the cell-wall on the opposite sides, although a rise of turgor will aid in stretching a wall which has become more extensible. There can, however, be little doubt that, as in the case of the tissue-strains, turgidity forms an important factor in the growth of the cell-wall, and in enabling the growing cells to react mechanically upon other parts.

The expansions and contractions involved in variation movements are usually the result of changes of turgidity which bring about elastic expansion or contraction of the cell-wall. If the cell-wall is highly elastic and but little stretched, a slight contraction will be sufficient to restore turgor after a fall in the internal osmotic pressure, but if the cell-wall is considerably

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[1] Thus de Vries (Sur les mouvements auxotoniques des organes végétaux, 1880, Repr. from Archives Néerlandaises, T. 15) considers nutation to be the result of changes of turgidity, and proposes the term 'auxotonic' for movements produced by a rise, and 'allassotonic' for movements due to a fall of turgor. It is, however, difficult to see the need for these terms.

stretched it may undergo a pronounced decrease in size before turgidity is restored. In most cases the cell-wall is so little stretched that the shortening of the cell on plasmolysis is slight or hardly measurable. In cells of the staminal filaments of Cynareae, however, the walls are stretched to such an extent that a slight fall of turgor produces a pronounced contraction[1].

A curvature may be produced in a tissue by a fall of turgor even when the individual cells do not undergo any active contraction. For instance, if the turgidity and hence also the rigidity of the cells in the stimulated half of a pulvinus of *Mimosa pudica* diminishes, these cells will be compressed by the tendency to expansion of the cells in the upper half until equilibrium is reached. In other cases, as in the variation movements due to light and gravity, the turgidity decreases on one side of the pulvinus and increases on the other.

Changes of turgor produced as physiological reactions act in exactly the same way as changes due to plasmolytic action or to excessive transpiration. The drooping movement of herbaceous parts is the direct result of the diminished turgor with its correlated decrease of rigidity in the stretched thin-walled cells. An artificial removal of turgor produces no perceptible movement when the cells possess sufficiently thick and rigid walls, and in such cases no fall of turgor resulting from stimuli can produce any movement.

If the turgidity remains constant, an active variation movement can only be produced by a change in the properties of the cell-wall, a decreased elasticity resulting in increased stretching, while an increase of elasticity diminishes the stretching due to the osmotic pressure. In addition an alteration in the power of imbibition may produce an active change of shape in the cell. It must be admitted that the protoplast is able to produce temporary or permanent changes of this kind in the cell-wall, but hitherto no pronounced reversible movement has been traced to this cause.

Owing to the usual semi-fluid consistency of the protoplasm, the pressure exercised upon the cell-wall is almost solely the result of the osmotic concentration of the sap. Whenever the protoplasm attains a high cohesion it may by its own changes of shape bring localized pressure to bear against a resistance. This is evidenced by the movement of cilia, and it is possible, especially in the case of minute organisms, that the protoplast may be able to exert considerable pressure against the cell-wall, or to antagonize a portion of the osmotic pressure exerted within the cell. If the expansion or contraction were localized, curvature would readily be produced in cells with equally distensible walls, whereas a

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[1] Cf. Pfeffer, Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, p. 325; Studien zur Energetik, 1892, pp. 216, 221, &c.

general rise or fall of the internal hydrostatic pressure can only produce curvature when the opposed sides are unequally extensible, or are made so by the action of the protoplast.

Even when a variation movement is found to be due to changes in the osmotic pressure, the elasticity of the cell-walls remaining constant, it still remains to be determined in which of a variety of ways the alterations in the osmotic pressure are produced. For instance, a fall of turgor may be produced by a precipitation of the dissolved osmotic materials, by their conversion into larger molecules of less osmotic activity, by the physiological combustion of the osmotic materials or by their removal in other ways, as when they are allowed to diosmose out of the cell. If in the latter case they remained dissolved in the imbibed fluid saturating the cell-wall, the osmotic pressure against the cell-wall would be diminished in exactly the same way as when a plasmolysing solution is applied. By the reabsorption of the excreted materials, or by the production of new ones, the original condition of turgor may be restored. Here, as in other cases, the disturbance due to a reaction excites activities tending towards the restoration of equilibrium.

A fall of turgor causes the cell to contract with an escape of water, until the concentration of the sap again balances the decreased tension in the cell-wall. If the fall of turgor is sudden, the cell readily permeable to water, and if the latter is able to escape into the intercellular spaces, then rapid movements may occur, as in the leaves of *Mimosa* and the staminal filaments of Cynareae. That the cells are capable of rapid filtration under pressure is shown by the rapidity with which they contract or become plasmolysed when placed suddenly in strong solutions of salt.

In the case of nutation movements, we have primarily to determine whether the curvature does or does not involve any change in the average rate of growth, and whether the latter is accelerated on the concave side as well as on the convex one. Even in the case of small objects this can be ascertained by the use of suitable micrometers. In measuring short distances the chord of an arc may be taken as the length of the curved surface of the arc [1].

A change of osmotic concentration can only be detected by plasmolytic methods when it persists for some time, and is not as rapidly readjusted as it is in the pulvinus of *Mimosa*. Furthermore, the contraction or compression of the cell will always cause a rise of the internal osmotic pressure if only water escapes from it. In fact, it does not follow that a rapid movement must always be produced by a change of turgor affecting the elastic stretching of the cell-wall.

Especially in the case of movements of variation, measurements of rigidity afford

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[1] Pfeffer, Druck- und Arbeitsleistungen, 1893, p. 293; Periodische Bewegungen, 1875, p. 15; Physiol. Unters., 1873, p. 27. [If the object is strongly curved, the length of its curved surfaces can be satisfactorily found by reconstructing the figure on paper from a series of measured chords, or by measuring the curved surface by means of an opisometer.]

some evidence as to the expansion or contraction in the antagonistic tissues. Thus the rigidity will increase if the force of expansion becomes greater either in one or in both halves of the pulvinus, but will be lessened if it falls in one or both halves, while if the rigidity remains constant we have evidence to show that one side expands and the other contracts in equal degree. Brücke[1] measured the rigidity by noting the bending when the organ was held horizontally, firstly with the curvature upwards, then with it facing downwards. The angular divergence was read off on an arc having its centre at the median point of the pulvinus. In the same way an increased rigidity is shown when a load produces less bending in an organ kept in the same horizontal position[2].

During its geotropic curvature a root may lift a considerable weight, and by finding the weight required to prevent curvature a measure may be obtained of the energy of curvature[3]. Slender plastic roots which are easily bent can naturally exert no great pressure unless lateral displacement is prevented. Nutation movements may also take place against considerable external resistance since they result from irregular growth. In such cases the external resistance antagonizes a portion of the osmotic pressure acting against the stretched cell-wall. Similarly in variation movements, either a rise of turgor takes place or a fall enables the previous stretching of the cell-wall to come into play.

If the antagonistic tissues are symmetrically displaced, as in a radial organ, no curvature is shown until the organ is split in half. The energy of curvature is greater when the active tissues are some distance from the neutral axis, since the leverage or bending moment they exert is increased. The bending moment therefore depends upon the energy of expansion and upon the distribution of the active tissues[4]. The problem is the same whether the curving zone is short or long, and the curving zone may in fact be made extremely short by preventing the attempted movement by means of bandages over the greater part of the length[5].

Thin organs can naturally bend more sharply and rapidly than thick ones, since in the latter a considerable difference in length has to be produced between the convex and concave sides[6]. The most pronounced curvature does not always occur in the most actively growing zone, since the conditions for curvature are often later in development. Curvature is influenced by external conditions in exactly the same way as is growth in general. In certain cases, as in tendrils, it is favoured by abundant supplies of water, whereas the movement of the pulvini of *Mimosa* is for obvious reasons decreased or prevented when the intercellular spaces are injected with water.

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[1] Brücke, Müller's Archiv f. Physiol., 1848, p. 452. Cf. Pfeffer, Period. Bewegungen, 1875, p. 89.

[2] Schwendener (1897), Gesammelte Abhandlg., Bd. II, p. 237.

[3] The best form of apparatus is a very stiff spring which can be adjusted by a screw. Cf. Pfeffer, Period. Bewegungen, 1875, pp. 9, 97; Druck- und Arbeitsleistungen, 1893, p. 389; Meischke, Jahrb. f. wiss. Bot., 1899, Bd. XXXIII, p. 345.

[4] Cf. Pfeffer, 1875, l. c., p. 99; 1893, l. c., p. 392.

[5] Meischke, l. c., p. 348.

[6] Cf. Rothert, Cohn's Beiträge z. Biologie, 1896, Bd. VII, p. 173.

CHAPTER II

MOVEMENTS OF CURVATURE

PART I

AUTONOMIC MOVEMENTS

SECTION 4. **Occurrence and Distribution.**

SPONTANEOUS, autogenic, or autonomic movements would arise in the normal course of development even if the external conditions could be kept rigidly constant. Locomotory and streaming movements will, however, be discussed in a subsequent chapter. Movements may either be periodical, as when a shoot nutates or a leaf folds at night, or may be incapable of repetition (ephemeral or climacteric), as when a bud unfolds or a capsule dehisces[1]. Periodic or nutation movements are shown by the growing apices of both vascular and non-vascular plants, and in the latter by the growing tips of single cells such as the branching mycelium of *Mucor*, and by filaments formed by chains of cells such as those of *Penicillium* or *Spirogyra*[2]. This was first shown by Darwin[3], and Fritsch has repeated some of the observations under conditions kept as constant as possible, and has found that the autonomic movements still continue.

When the movements are pronounced, their independence of the external conditions is easily seen. Thus the growing ends of the stems of climbers sweep round in wide circles, as also do many tendrils; while the lateral movements of the peduncle of *Tulipa* and *Allium* may cause the flower to be bent downwards during development[4]. Individual cells or

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[1] A. P. de Candolle (Mémoires d. savants étrangers de l'Institut de France, 1806, T. I, p. 338) termed flowers opening once ephemeral, and those opening repeatedly equinoctial.

[2] F. Darwin, Bot. Ztg., 1881, p. 474; Fritzsche, Ueber die Beeinflussung d. Circumnutation durch verschiedene Factoren, Leipziger Dissertation, 1899, p. 9 (*Phycomyces*); Wortmann, Bot. Ztg., 1881, p. 384 (*Mucor stolonifer*).

[3] Darwin, The Power of Movement in Plants, 1880. Darwin and, later, Fritzsche have shown that a slight change in the external conditions may influence the movements. On Fungi cf. Reinhardt, Jahrb. f. wiss. Bot., 1892, Bd. XXIII, p. 479; Sokolowa, Das Wachsthum d. Wurzelhaare und Rhizoiden, 1897. In most of Darwin's experiments the attached indicator exercised a certain disturbing action.

[4] Cf. Darwin, l. c., and the works already quoted; also Hofmeister, Pflanzenzelle, 1867, p. 323; Lecoq, Bull. de la Soc. bot. de France, 1867, p. 153 (Leaf of *Colocasia*); F. Müller, Jenaische Zeitschr. f. Med. u. Naturw., 1870, Bd. V, p. 134 (Peduncle of *Alisma*); Sachs, Lehrbuch, 3. Aufl., 1873, p. 827; Rodier, Compt. rend., 1877, T. LXXXIV, p. 961 (*Ceratophyllum*); Wiesner, Bewegungsvermögen, 1881; Vöchting, Bewegungen d. Blüthen u. Früchte, 1882, p. 186, &c.; Hansgirg, Phytodynamische Unters., 1889; Beihefte z. Bot. Centralbl., 1902, Bd. XII, p. 248; Phycol. und phytophysiol. Unters., 1893; Askenasy, Ber. d. bot. Ges., 1890, p. 77 (Root of Maize); A. Schulz,

chains of cells are also capable of spontaneous movement, as is shown by the stolons of *Mucor stolonifer*, as well as by *Spirogyra* and other Conjugatae. The threads of *Spirogyra* may often curve into rings or spirals, and subsequently straighten themselves. As in the case of growth in length, periods of rest and of activity alternate, and during the latter, curvature may appear in a few minutes, and a complete circle be formed in ten minutes to half an hour [1]. In connexion with its peculiar mode of growth, lateral bending may be produced in the filaments of *Oedogonium*, presumably because the cell-wall splits and the ring of plastic cellulose stretches sooner on one side than on the other.

All stages are shown between trifling and pronounced nutation, according to the plant, to the stage of development, and to the external conditions. The curves are not always regular and similar, even when there is a pronounced tendency to linear, elliptical, or circular nodding, as the case may be. Even when the last named is most pronounced it may temporarily alter into to-and-fro pendulum movements. Slight circumnutation may change to a single large circular or lateral movement, although a very irregular curve is produced when the movement of the

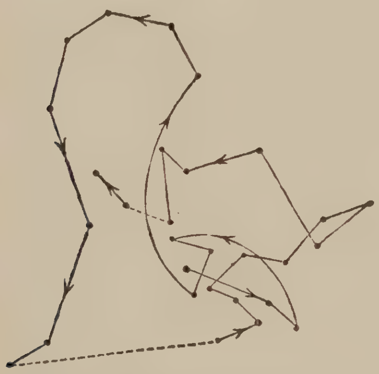

FIG. 2. Nutation of the sheathing leaf of the seedling of *Zea Mays*, from 8.30 a.m. on Feb. 4 to 8 a.m. on Feb. 6. The movement is magnified 25 times. (After Darwin.)

FIG. 3. Circumnutation of a cotyledon of *Lagenaria vulgaris* 1½ inches long, from 7.35 a.m. July 11 to 9.5 a.m. July 14. Magnified 8 times. (After Darwin.)

Ber. d. bot. Ges., 1902, pp. 526, 580; Neubert, Jahrb. f. wiss. Bot., 1902, Bd. XXXVIII, p. 149 (*Allium*); Richter, Ber. d. bot. Ges., 1903, p. 175 (Seedlings).

[1] The movements of Zygnemaceae were known to Link, Grundlehren d. Anatom. und Physiol., 1807, p. 263; Meyen, Pflanzenphysiol., 1839, Bd. III, p. 567; and were studied in detail by Hofmeister, Jahreshefte d. Vereins f. vaterländ. Naturkunde in Württemberg, 1874, Bd. XXX, p. 211, and Oltmanns, Flora, 1892, p. 199. That they occur under constant conditions has been shown by Winkler, Krümmungsbewegungen von *Spirogyra*, 1902, who also found that when suddenly killed the curvatures were retained. To show the movement single threads may be observed in white porcelain dishes.

growing tip is projected from above on to a plane surface[1]. In flattened organs, for mechanical reasons, the movement takes place mainly in a definite plane, and for physiological reasons the same applies to dorsiventral organs, and also to variation movements which in general are more regular than nutation movements. During linear nutation the rapidity of the return movement increases to a maximum and then gradually diminishes up to the point of reversal. Secondary oscillations always occur, however, and these are sometimes very pronounced.

Pronounced circumnutation[2], such as is shown by twining plants and by many tendrils, usually maintains a constant direction. Nevertheless, in the case of certain tendrils, the shoots of some leaf-climbers, and even of a few twining plants, a periodic reversal of the circumnutation has been observed[3]. In all cases the circumnutation results from the progression of the more rapidly growing (epinastic) zone around the apical region. Hence both the convex side and the front flank are continually changing, a transverse section of the stem moving around the axis of revolution in the same way that the earth would move around the sun if it had no daily rotation. Under such circumstances no torsion is produced, but this is at once shown if the same side always keeps in front. A hanging shoot subjected to torsion will naturally show a revolving movement.

In both young erect twining plants, and in the stems of older ones projecting beyond the support, the entire growing zone is capable of nutation. The growing and nutating zone of the Hop is 20 to 30 cm. and of *Hoya carnosa* up to 80 cm. long[4]. In the case of tendrils the period of circumnutation is limited, and it stops when growth ceases. Further the nutation only begins when the tendril has expanded and attained a fair length[5]. Even in twining plants circumnutation does not begin until the seedling has attained a certain size, the first one or more internodes showing no circumnutation[6].

Under favourable conditions a revolution is performed in one or two hours in the case of *Akebia quinata*, *Convolvulus sepium* and *Phaseolus vulgaris*, whereas *Lonicera brachypoda* requires five to six hours, and *Adhatoda cydoniaefolia* 24 to 48 hours[7]. The non-twining stems of *Passiflora gracilis* and the tendrils of *Cobaea*

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[1] Cf. Darwin, Climbing Plants, 1875, p. 113; Dutrochet, Ann. d. sci. nat., 1843, 2e sér., T. XX, p. 314; Fritzsche, l. c.

[2] Darwin (The Power of Movement in Plants, 1880, p. 1) employed the term 'Circumnutation,' Dutrochet (Ann. d. sci. nat., 1844, 3e sér., T. II, p. 157) that of 'Revolutive (rotary) Nutation.'

[3] Darwin, The Movements and Habits of Climbing Plants, 1875, p. 34 seq.; O. Müller, Cohn's Beiträge z. Biologie, 1887, Bd. IV, p. 103; Wortmann, Bot. Ztg., 1887, p. 65; Baranetzsky, Die kreisförmige Nutation u. das Winden d. Stengel, 1883, p. 11.

[4] Darwin, The Movements and Habits of Climbing Plants, 1875, p. 3.

[5] Darwin, l. c., p. 5; Wortmann, l. c., p. 51; Fitting, Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 547.

[6] Mohl, Ranken- und Schlingpflanzen, 1827, p. 104; Darwin, l. c., pp. 4, 26, 33; Schenck, Beiträge z. Biologie u. Anatomie d. Lianen, 1892, I, p. 128.

[7] Darwin, l. c., p. 26; Simons, Contrib. from the Bot. Lab. of Pennsylvania, 1898, Vol. II, p. 66.

scandens circumnutate as rapidly as the best twining plants[1]. In all cases, however, the rapidity of movement is subject to pronounced variations even under constant external conditions.

Variation movements. Spontaneous variation movements appear to be shown by all motile pulvini. These are very slight in the leaflets of *Acacia lophantha*, more perceptible in those of *Mimosa pudica* and *Phaseolus vulgaris*, and very pronounced in those of *Oxalis acetosella* and *Trifolium pratense*. The leaflets of *Oxalis* swing to and fro through an angle of 20° to 70° in from 45 minutes to 2 hours, those of *Trifolium* through an angle of 45 to 150 degrees in $1\frac{1}{2}$ to 4 hours[2]. The basal leaflets of *Desmodium gyrans* describe an elliptic curve and require only 85 to 90 seconds for a single revolution at 35° C.[3]

FIG. 4. Leaf of *Desmodium gyrans*. Nat. size. *s* = paired basal leaflets.

The movements of *Desmodium* are very dependent upon temperature, for Kabsch found that at 28° to 30° C. a revolution takes four minutes, and at 22° C. the movement is reduced to a minimum. Apparently also the excentricity of the elliptic path alters with the speed. The fact that the ascent takes longer than the descent is the natural result of the extra amount of work done in raising the leaf[4].

The column in the flower of *Stylidium adnatum* shows a distinct to-and-fro movement. When it presses against the labellum a trigger arrangement on the latter holds it until the attempted return movement has produced considerable strain, when release is followed by sudden movement. Kabsch, observing that contact was able to produce this movement, considered it to be a physiological response to stimulation, whereas Gad has shown that the rapid movement does not take place if the labellum is removed, or if a piece of paper is laid upon it. The latter prevents the catch arrangement from acting, so that the column leaves the labellum as soon as the return movement begins. A similar rapid movement can be produced by retarding

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[1] Darwin, The Power of Movement in Plants, 1880, pp. 106, 153.

[2] Pfeffer, Periodische Bewegungen, 1875, p. 133; Darwin, l. c., p. 352.

[3] Kabsch, Bot. Ztg., 1861, p. 355; Hofmeister, Pflanzenzelle, 1867, p. 332; Meyen, Pflanzenphysiol., 1839, Bd. III, p. 553; Treviranus, Physiologie, 1838, Bd. II, p. 766. The older literature on these long-known movements is given by these authors. Cf. also Stahl, Bot. Ztg., 1897, p. 98.

[4] Cels, Sylvestre and Hallé, Annal. d. Botanik von Usteri, 1796, Stück 19, p. 63; Kabsch, l. c., p. 355.

[5] Gad, Bot. Ztg., 1880, p. 216; Schilling, Der Einfluss der Bewegungshemmung auf d. Arbeitsleist. d. Blattgelenke v. *Mimosa pudica*, Habilitationsschrift, 1895, p. 18. According to Burns (Flora, 1900, p. 344) we are dealing with a growth-movement. Haberlandt, Sinnesorgane im Pflanzenreich, 1901, p. 73. Whether the movements of the labellum of *Megaclinium falcatum* and of *Pterostylis* observed by Lindley and Morren (Ann. d. sci. nat., 1843, 2^{e} sér., T. XIX, p. 91) are growth or variation movements is not yet certain, or even whether these movements are really spontaneous. Cf. the literature given by Hansgirg, Phycol. u. phytophysiol. Unters., 1893, p. 149.

the movement of the leaflets of *Desmodium*, *Trifolium*, or *Oxalis* until a sufficient pressure has been produced in the pulvinus, and then releasing the leaflet. Similar strains are produced by the growth of the flower-buds of *Genista* and other Papilionaceae, which finally lead to the sudden opening of the flower [1].

Ephemeral movements. Under constant external conditions the whole progress of development, including the formation of organs, consists of a series of ephemeral movements. Such are all the movements involved in the opening of foliage and flower buds, in the straightening of the arched stems of embryoes, or of the flower stalk of the Poppy, and the fruit stalk of *Campanula.* In fact, all movements due to autonomic changes in the rate of growth of opposed sides of an organ are of this character.

In many cases the organ oscillates a few times before assuming a constant position, so that no precise boundary can be laid down between ephemeral and periodic movements. Each stamen of *Ruta graveolens* (Fig. 5), for instance, after the flower has opened, bends away from the ovary, then applies itself to it, and then again bends outwards towards the perianth. Similarly some flowers open and close more than once, so that in both cases we may term the movements periodic [2].

In many cases the older and younger zones of a growing region exhibit dissimilar curvatures. Thus a developing fern frond has a somewhat S shape, owing to the fact that the circinately coiled apex unrolls by epinastic growth and is carried beyond the position assumed by the adult basal portions. Similarly the stems of etiolated seedlings of *Pisum sativum* and *Vicia sativa* show wavy curvatures extending over a few internodes, and lying in the same or in different planes. Wiesner terms this 'undulating nutation,' and the lateral displacement of the internodes often produced by the formation and development of lateral buds he calls 'interrupted nutation [3].' The latter may lead to the formation of sympodial stems, but the curvatures themselves are the result of special ephemeral movements.

FIG. 5. *Ruta graveolens.* The anterior stamens and perianth leaves have been removed. The stamen (*a*) is pressed against the ovary, (*b*) will do the same later on, while (*c*), whose anther has dehisced, was pressed against the ovary a short time ago.

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[1] Cf. Ludwig, Biologie der Pflanzen, 1895, p. 472.

[2] On ephemeral flowers see A. P. de Candolle, Mémoires d. savants étrangers de l'Institut de France, 1806, T. I, p. 338; Dutrochet, Mémoires, &c., Bruxelles, 1837, p. 238; Royer, Ann. d. sci. nat., 1868, 5e sér., T. IX, p. 350; Hansgirg, Physiolog. u. phycophytolog. Unters., 1893, p. 163, Beiheft z. Bot. Centralbl., 1902, Bd. XII, p. 268; Oltmanns, Bot. Ztg., 1895, p. 31; Schulz, ibid., 1902.

[3] Wiesner, Die undulirende Nutation d. Internodien, 1876 (Sep. a. Sitzungsb. d. Wiener Akad., Bd. LXXVII, Abth. i); Bewegungsvermögen, 1881, p. 22; Sitzungsb. d. Wiener Akad., 1883, Bd. LXXXVIII, Abth. I, p. 454. On similar peculiarities in Algae, cf. Nägeli, Pflanzenphysiol. Unters., 1855, Heft 1, Taf. 5; Berthold, Jahrb. f. wiss. Bot., 1882, Bd. XIII, p. 638. See also Goebel, Organography, 1905.

The torsions of the stems of climbers and many forms of loose winding are autonomic in origin. The same applies to the contortion of the flower-bud of *Convolvulus*, the bending of the apex of the peduncle of *Cyclamen*, and of the labellum of *Himantoglossum*, the twisting of the internodes of *Chara* and of the peristome of *Barbula*[1], the coiling of the stalk of the female flower of *Vallisneria*, of the pods of *Medicago*, and of tendrils which have failed to reach a support.

Although many of the movements taking place during development are the result of external stimuli, an equally large number are autogenic in origin. Among these are most of the movements of the sexual organs, which ensure proper pollination. In addition to *Ruta*, similar movements of the stamens are shown by *Dictamnus*, *Parnassia*, and *Saxifraga*, of the style by *Saxifraga* and *Nigella*, and of the stigmas by *Mimulus*, *Martynia*, *Epilobium*, and Compositae[2].

Historical. The remarkable movements of the basal leaflets of *Desmodium gyrans* attracted attention two centuries ago, and Hales also mentioned a few ephemeral nutation curvatures[3]. At a later date the circumnutation of twiners was investigated by Palm and by Mohl, that of tendrils by Dutrochet[4]. After a number of pronounced periodic and ephemeral movements had been recognized, Darwin showed that all growing organs perform spontaneous periodic movements, which in many cases are only perceptible when magnified[5], but in others have been increased in amplitude by adaptive modification. This applies to the circumnutation of twiners and tendrils, while Darwin considers that the pronounced curving nutation of subterranean stolons makes it easier for them to pass between obstacles in the soil. The same result may, however, be produced by the mechanical displacement of the growing tip, so that roots grow equally well through soil, although they usually perform only very slight autonomic oscillations[6]. The pronounced periodic curvatures of Zygnemaceae may aid in movement, or in escaping from deposited layers of mud. This may also apply to the movements of *Oscillaria*, but the exact importance of periodic variation

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[1] A few instances are given by Wichura, Flora, 1852, p. 39; Jahrb. f. wiss. Bot., 1860, Bd. II, p. 201. On forced torsion cf. de Vries, Jahrb. f. wiss. Bot., 1892, Bd. XXIII, p. 13; Dingler, Flora, 1897, Erg.-bd., p. 289.

[2] Beyer, Die spontane Bewegung d. Staubgefässe u. Stempel, 1888; Hansgirg, 1893, l.c., and the literature here quoted.—Cf. also A. P. de Candolle, Pflanzenphysiol., 1835, Bd. II, p. 71; Schulz, l. c., 1902.

[3] Meyen, Pflanzenphysiol., 1839, Bd. III, p. 553.

[4] Palm, Ueber das Winden d. Pflanzen, 1827, p. 16; Mohl, Ueber den Bau u. d. Winden d. Ranken- u. Schlingpflanzen, 1827, pp. 105, 112; Dutrochet, Ann. d. sci. nat., 1844, 3e sér., T. XII, p. 156.

[5] Darwin, The Power of Movement in Plants, 1880.

[6] Pfeffer, Druck- und Arbeitsleistungen, 1893, p. 362. [This may under normal conditions be due to the geotropic irritability suppressing any pronounced oscillations. At any rate the radicles of Maize, Pea and Bean show more pronounced oscillations (two to six times greater) when rotated horizontally on a klinostat, than when at rest or rotated with the apex downwards. In each case the observations were made every few hours by comparing the position of the radicle by means of a horizontal microscope with a triangular framework of glass threads attached to the seed but not touching the root. The rotation was too rapid (twelve revolutions per hour) to permit of the result being due to the inductive action of gravity.]

movements in general is uncertain. Stahl's suggestion that they serve mainly to favour transpiration is in the highest degree improbable[1].

Dutrochet[2] was the first to distinguish between spontaneous (autogenic) and induced (aitiogenic) movements, and also held correct views as to the importance of the external conditions as regards growth and movement. It is, however, often forgotten that a movement can still be considered autogenic when, by the activity of the plant itself, an external agency is used for purposes of orientation[3].

Methods. A hemispherical glass vessel, or a plane sheet of glass, may be placed over the plant, and the position of the growing apex, as seen vertically above, marked on the glass with indian ink, or an oil pencil[4]. This gives a projection of the movement, but unless the growing apex and the glass are near together the error of parallax becomes considerable. Photographs may also be taken in one or two planes and afterwards compared[5]. Slight movements may be measured by means of a vertical microscope containing a micrometer ruled in squares[6]. The attachment of a glass thread is inadvisable, since this may readily produce disturbances of growth[7].

SECTION 5. **The Causes of Autonomic Movement.**

It is often the case that a change in the properties of the organism or in the irritability of certain portions may cause constant external conditions to act as stimuli producing response. Thus if the geotropic irritability of an organ alters from positive to negative, a corresponding curvature will be produced in the growing zone. Diffuse stimuli may also be utilized in the same way. Thus supposing that at a particular stage of development one of two opposed tissues is excited to more active growth by the existing temperature than the other, then we should have a curvature produced although the temperature remained constant. Curvatures produced in this way under constant external conditions are spontaneous or autogenic, those produced by variations in the external conditions are aitiogenic. In the former case we have to decide whether a constant external agency is made use of in the manner indicated for directive purposes, or whether the stimulus is of purely internal origin[8]. The importance of autogenic and aitiogenic changes of irritability for tropic movement will

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[1] Pfeffer, Druck- und Arbeitsleistungen, 1893, p. 362; also Stahl, Bot. Ztg., 1897, p. 98.

[2] Cf. Sachs, Flora, 1863, p. 449.

[3] [If this were strictly applied, all physiological movements would be autogenic, since without the activity of the plant, only the direct mechanical action of physical agencies could produce movement.]

[4] Darwin, Climbing Plants, 1876, p. 86.

[5] Dewèvre and Bordage, Revue gén. d. Bot., 1892, T. IV, p. 65.

[6] Fritzsche, Ueber die Beeinflussung d. Circumnutation durch verschiedene Factoren, 1899, p. 6.

[7] On the methods of magnifying the movement cf. Darwin, The Power of Movement in Plants, 1880, p. 5; Wiesner, Bewegungsvermögen, 1881, p. 158.

[8] Movements resulting from the accumulation of secreted products or from the growth of an organ into a dissimilar medium may be classed as aitiogenic.

be discussed later. At present we have merely to deal with the fact that certain spontaneous movements are produced by the autogenic utilization of external factors for directive purposes.

This applies to ephemeral as well as to periodic movements, which can be produced in plants as well as in animals, although hardly in so striking a form as the respiratory movements or the pulsation of the heart in mammals[1]. All organic life is a repetition in the individual of the course of development of the parents, and we have mechanical instances of rhythm in clocks, and in the movements of planets under the action of constant external conditions. Similarly the rhythmic beat of the interruptor of an induction machine is dependent upon an external agency (gravity) when the interruptor falls back by its own weight, but solely upon the inherent properties of the mechanism when the break is effected by an elastic spring.

Each motile organ possesses a considerable degree of independence as regards the inception and performance of movement. Thus similar and dissimilar organs of a plant may perform various movements simultaneously, and even the leaflets on the same leaf of *Oxalis*, *Trifolium*, or *Mimosa* may move in different directions at the same time. This can be very strikingly shown by shading the pulvini of some of the leaflets, while the remainder are exposed to bright sunlight so that they fold up. On now exposing to slightly weaker general illumination the expanded leaflets fold up, while the folded ones partially re-expand[2]. In addition, similar organs of a plant do not always respond alike to the same stimulus, owing to autogenic modification of the responding organs. The resulting movement is in fact always due to the conjoint action of external and internal factors, sometimes the latter and sometimes the former predominating[3].

It is often the case that an organ performs a spontaneous curvature and assumes a new direction of growth as the result of a change of its geotropic irritability, the external conditions remaining unaltered. The part played by gravity in such cases is readily ascertained by the aid of the klinostat, and in fact a large number but not all of the autogenic tropic movements performed by plants require the aid of gravity. When a factor such as light undergoes continual change as regards direction and intensity, observations in nature often suffice to determine the part it plays in a particular movement, but it is only under light of constant intensity and direction that a satisfactory decision can be made as to whether the stimulus of light is involved in a particular autogenic movement. That periodic movements may occur under such conditions is

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[1] On the production of rhythm by periodic changes in the external conditions cf. Darwin and Pertz, Annals of Botany, 1892, Vol. VI, p. 245.

[2] Ewart, The Effects of Tropical Insolation, Annals of Botany, Vol. XII, 1898, p. 448.

[3] Cf. Pfeffer, Periodische Bewegungen, 1875, pp. 35, 153.

shown by the movement of swarm-cells to and from a constant source of illumination, owing to the alteration of their phototactic irritability, according to the intensity of illumination. Similar movements have also been observed as the result of autogenic changes in both the phototactic and chemotactic irritability of micro-organisms.

The curvatures of the peduncles of *Papaver*, *Tussilago*, and of many other plants are due to changes of geotropic irritability, whereas the autogenic movements of the pedicels of *Asphodelus luteus* and the peduncles of *Allium controversum* appear to be produced without the aid of any external agency[1]. Similarly the movements of many stamens, styles, and stigmas appear to be purely autotropic in character, whereas in the flowers of *Dictamnus*, *Aesculus*, and *Epilobium* the movements of the sexual organs are due to changes of geotropic irritability[2]. The curvatures of the hypocotyl of *Helianthus* and of the epicotyl of *Faba* and *Pisum* are produced when the seedlings are revolved on a klinostat[3], whereas the bending of the apex of the stem of *Ampelopsis* and of other plants is due to a geotropic reaction[4], the straightening of the older growing zones being the result of a change in the geotropic irritability co-operating with the autogenic orthotropism of the stem.

Since the curvatures result from the joint action of gravity with internal factors, it is hardly surprising that in some cases they should not entirely disappear when gravity is eliminated. Plants grown on a revolving klinostat in fact perform a variety of movements, and the torsions in the internodes of *Chara* and in the peristome of *Barbula* are produced independently of gravity. Whether the same applies to the coiling and uncoiling of the peduncle of *Vallisneria* has yet to be determined.

The pronounced movements of the leaflets of *Desmodium gyrans* and of *Trifolium*, as well as those of the gynandrophore of *Stylidium* appear to be independent of the action of gravity, but direct proof is wanting. The movements of cilia continue, however, even when the rotation of a

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[1] Vöchting, Bewegungen d. Blüthen u. Früchte, 1882, p. 192; Scholtz, Cohn's Beiträge z. Biol., 1893, Bd. VI, p. 306; Hansgirg, Photodynam. Unters., 1889, p. 250 (Repr. from Sitzungsb. d. böhm. Ges. d. Wiss.); Physiolog. u. phycophytol. Unters., 1893, Neue Unters. über d. Gamo- u. Karpotropismus, 1896 (Repr. from Sitzungsb. d. böhm. Ges. d. Wiss.).—According to Vöchting (l. c., p. 137) the bending of the stem of *Viola* is due to geotropism, a statement which Schwendener u. Krabbe (Gesamm. Abhandl. von Schwendener, 1892, Bd. II, p. 336) contradict.

[2] Dufour, Arch. d. sci. phys. et nat., 1885, III, T. XIV, p. 418; Vöchting, Jahrb. f. wiss. Bot., 1886, Bd. XVII, p. 340; J. af Klercker, Die Bewegungserschein. der *Veronica*-Blüthen, 1892 (Repr. from Bihang till Svenska Vet.-Akad. Handlingar, Bd. XVIII).

[3] Vöchting, Bewegungen d. Blüthen u. Früchte, 1882, p. 186; Darwin, The Power of Movement in Plants, 1880, pp. 45, 553; Sachs, Arbeit. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 403; Lehrbuch, 3. Aufl., p. 75. That these and other curvatures are not the direct result of the weight supported, as supposed, has been shown by Vöchting, l. c., and Scholtz, Cohn's Beiträge z. Biologie, 1892, Bd. V, p. 400. Cf. also Rothert, Cohn's Beiträge z. Biologie, 1896, Bd. VII, p. 141.

[4] Scholtz, l. c., 1892, p. 401.

motile organism diffuses the action of gravity. Similarly the feeble nutation movements of most stems continue on a rotating klinostat[1], whereas the pronounced circumnutation of the shoots of twiners[2], of tendrils[3], and of the stolons of *Mucor stolonifer*[4] cease sooner or later when the action of gravity is eliminated, feeble and irregular nutation movements taking their place.

Baranetzsky showed that when the stem of a climber is slowly rotated horizontally, the curved growing zone straightens, and its circumnutation ceases. Gravity here is utilized by the plant as a directive stimulus, the power of reaction progressively and periodically altering on the different sides, so that the growing zone bends alternately to all quarters of the compass as it performs its circumnutation. This power of producing an autogenic change of irritability is a special adaptation, for the apices of non-climbers do not exhibit any such pronounced circumnutation when bent from the perpendicular[5], but usually show slight pendulum movements, owing to variations in the growth of opposite sides. If the plant is very slowly revolved horizontally on a klinostat, the growing apex circumnutates as the result of the curvatures produced by gravity, and light will act in exactly the same way. This, however, results from the orthotropism of the plant which causes the repeated elimination of the progressively changing geotropic or heliotropic curvature.

It is not certain whether autogenic changes of irritability take place when the plant is rotated on a klinostat, or whether the geotropic curvature of the apex is essential for their initiation. A fact worthy of note in this connexion is that a shoot of *Cuscuta* not only ceases to circumnutate when rotated horizontally on a klinostat, but also loses its irritability to contact[6]. In many cases also the direction of circumnutation may change periodically, while a large number of plants only show circumnutation under special conditions, as for instance when the stems of *Tropaeolum majus* or *Polygonum Fagopyrum* are etiolated[7]. It is, however, uncertain whether this is due to the greater power of response of the thin-walled cells of the etiolated tissues, or whether an inherent tendency to circumnutation has been excited or allowed to become manifest.

The apices of twining stems primarily curve out of the vertical as the result of their klinogeotropism, whereas when longer their own weight produces a certain

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[1] Fritzsche, Ueber d. Beeinflussung d. Circumnutation durch verschiedene Factoren, 1899, p. 16.

[2] Baranetzsky, Die kreisförmige Nutation u. d. Winden d. Stengel, 1883, p. 24; Ambronn, Mechanik d. Windens, 1884, Th. 1, p. 6; Wortmann, Bot. Ztg., 1886, p. 314. Cf. II, § 84.

[3] Wortmann, Bot. Ztg., 1887, pp. 86, 97.—Darwin (Climbing Plants, 1875, p. 131) observed that the circumnutation of a tendril of *Echinocystis lobata* almost ceased when it was bent downwards, but recommenced when it was placed in a horizontal position.

[4] Fritzsche, l. c., p. 21.

[5] Id., l. c., p. 20. Baranetzsky (l. c., p. 14) states that the previously erect stem of a twiner begins to circumnutate when bent out of the perpendicular.

[6] Peirce, Annals of Botany, 1894, Vol. VIII, pp. 86, 116. Ordinary tendrils remain irritable to contact after prolonged rotation on a klinostat.

[7] Noll, Bot. Ztg., 1885, p. 664. Cf. also M. Scholtz, Cohn's Beiträge z. Biologie, 1892, Bd. V, p. 393.

amount of drooping curvature[1]. The existence of such mechanical curvatures is easily shown by hanging the apex downwards or by laying it on a horizontal sheet of paper and noting the remaining curvature. The straightening of the apex on a klinostat shows that this curvature results from the antagonism of klinogeotropism and orthotropism. The somewhat irregular character of the curve described is due to the action of disturbing factors.

SECTION 6. **The Influence of the External Conditions.**

Autonomic movements like all vital phenomena are dependent upon the external conditions, and are accelerated or retarded according to the temperature and the supply of food, oxygen, or water. The stimulating action of light or gravity may also form an essential or favouring condition for movement. The effects of a change in the external conditions may persist for a long time, and since a local or general stimulus may modify or awaken various correlated activities, it is not always easy to distinguish between autogenic and aitiogenic movements. Nor can any general rules be laid down. For instance an increased rate of growth, or in general a greater demand, results in a diminution of the autogenic movements in some cases, whereas in others they increase[2]. It is, however, commonly observed that any serious general disturbances are reflected in the autonomic movements, with the result that when these are normally feeble they are excited to greater activity.

A certain temperature is necessary for all autogenic movements, the optimum in the case of the leaflets of *Desmodium gyrans* being as high as 35° C., and the movements becoming slower as the temperature falls. Dutrochet[3] observed that the tendrils of the Pea circumnutated once in 9 to 11 hours at 5 to 6° C., but in 1 hour 20 minutes at 24° C. Darwin[4] observed that the pronounced circumnutation of the internodes and tendrils of *Eccremocarpus scaber* ceased in a cool house, in which slow growth continued. Fritzsche[5] found that any rise of temperature below the optimum increased the rapidity and amplitude of the feeble nutation-movements of the stems of seedlings. It is, however, also possible that the rapidity of movement might increase while the amplitude decreased, and in fact Darwin[6] observed a result of this kind when the leaflets of *Averrhoa bilimbi* were subjected to rising temperatures.

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[1] Baranetzsky, l. c., pp. 19, 48. A drooping shoot curves geotropically upwards at the apex, where the static moment is least, and hence attains a ∽ shape.

[2] Askenasy (Ber. d. bot. Ges., 1890, p. 77) states that the nutation of roots decreases when growth is active, whereas Fritzsche (l. c.) obtained in some cases exactly opposite results.

[3] Dutrochet, Ann. d. sci. nat., 1843, 3e sér., T. XX, p. 312. Cf. also Simons and MacKenney, Bot. Jahrb., 1898, I, p. 594.

[4] Darwin, Climbing Plants, 1875, pp. 72, 103.

[5] Fritzsche, Die Beeinflussung der Circumnutation durch verschiedene Factoren, 1899, p. 23.

[6] Darwin, The Power of Movement in Plants, 1880, pp. 331-5. A rapid oscillation is also

LIGHT and DARKNESS exercise effects dependent largely upon the duration of the exposure. The autonomic[1] variation and nutation[2] movements of plants in a condition of phototonus continue at first unaltered in darkness. In the prolonged absence of light, however, the variation-movements gradually decrease, and cease with the onset of dark-rigor[3]. Nutation-movements, on the other hand, continue as long as growth does, becoming actually more pronounced in some plants, but decreasing in others. For instance etiolated plants of *Tropaeolum* and *Polygonum* show pronounced circumnutation, whereas circumnutation decreases so much in etiolated shoots of *Dioscorea Batatas* and *Mandevillea suaveolens*[4] that the plants are no longer able to twine. Etiolated shoots of *Phaseolus* and *Ipomoea purpurea*, however, circumnutate actively and twine readily in darkness[5]. Other special peculiarities have without doubt yet to be discovered, and it is highly probable that changes of photonasty involve alterations in the power of autonomic movement[6].

Autonomic movements are affected by the conditions of turgidity, by the supply of food and by various chemical stimuli[7]. Darwin found, for example, that the absorption of a little ammonium carbonate excited active oscillating movement in the two leaf-segments of *Dionaea muscipula* and in the leaf-tentacles of *Drosera*[8]. The action of shaking, in retarding growth and in equalizing the tissue-strains, enables us to understand why

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excited in the leaflets of the frond of *Asplenium trichomanes*, according to Asa Gray and Loomis, Bot. Gazette, 1880, pp. 27, 43 (quoted by Darwin, l. c., 1880, p. 257). Fritzsche (l. c., p. 15) considers this to be due to the changes of temperature influencing the transpiration and hence the position of the leaflets.

[1] Pfeffer, Periodische Bewegungen, 1875, p. 155.

[2] Darwin, Climbing Plants; The Power of Movement in Plants (Twiners); Fritzsche, l. c., p. 14 (Seedlings); Dewèvre et Bordage, Revue gén. de Bot., 1892, T. IV, p. 73 (Coloured Light). Rothert (Cohn's Beiträge z. Biologie, 1894, Bd. XXVI) states that the cotyledons of *Avena* and *Phalaris* nutate somewhat more actively in darkness.

[3] Pfeffer, l. c., p. 155. According to Maige (Ann. d. sci. nat., 1900, 8e sér., T. XI, p. 331) strong light diminishes the movements.

[4] Duchartre, Compt. rend., 1865, T. LXI, p. 1142. The torsion is also absent from these plants in darkness. Stems of *Dioscorea* developed in light are able to twine in darkness, according to de Vries, Arb. d. Bot. Inst. in Würzburg, 1873, Bd. I, p. 328.

[5] Mohl, Ranken- u. Schlingpflanzen, 1827, pp. 122, 150; Sachs, Bot. Ztg., 1865, p. 119; Fritzsche, l. c.

[6] Heckel (Du mouvement végétal, 1875, p. 551) finds the movements of the stamens of *Ruta* and *Saxifraga* to be slower in darkness. Carlet (Compt. rend., 1873, T. LXXVII, p. 538) states that the stamens of *Ruta* do not move at all in darkness. Organs pressed against one another or against a support may not be able to move (cf. Pfeffer, l. c., p. 48). Stahl (Bot. Ztg., 1898, p. 103) concludes that the autonomic movements decrease in darkness, in order not to disturb the night-position, but teleological conclusions are valueless in comparison with empirical facts.

[7] Cf. Fritzsche, Die Beeinflussung d. Circumnutation durch verschiedene Factoren, 1899. The statement that weak electrical currents increase the movements of the leaflets of *Desmodium gyrans* requires further proof. Cf. Kabsch, Bot. Ztg., 1861, p. 358; Meyen, Pflanzenphysiol., 1839, Bd. III, p. 557.

[8] Darwin, The Power of Movement in Plants, 1880, pp. 237–9.

the circumnutating apices of many climbers become partially erect after shaking[1]. Slight injuries do not affect the power of curvature, and this may even be retained when the root-tip is cut off in such fashion as not to induce any traumatic curvature[2]. Since severe injury to the root-system does not perceptibly affect the nutation of the shoot, the lessened circumnutation of the cut shoots of twiners is either due to the manipulative disturbance, or to a diminution of turgidity[3].

SECTION 7. **The Mechanics of Autonomic Movement.**

It is not definitely known in a single case whether the average rate of growth alters or not during spontaneous movement. Presumably, however, the nutation curvatures of *Oedogonium* and of Zygnemaceae are attended by an acceleration of growth, and it is not unlikely that the feebler nutation movements are connected with the continual variations in the activity of growth in length. It is, however, uncertain whether the circumnutation of twiners involves an increase in the average rapidity of growth. In any case it does not follow that the maximum curvature should take place at the period of most active growth, so that during elliptical nutation growth would be most active during the passage of the extremities of the major axis of the ellipse of curvature[4].

Autonomic growth curvatures are certainly not always produced in the same way. Plastic growth takes place in *Oedogonium*, but it is not known in a single case whether rises of turgor come into play, de Vries' researches being inconclusive in this respect. The curvatures of shoots, and of filaments of *Spirogyra* persist when the plant is suddenly killed by immersion in hot water, so that the growth responsible for the curvature takes place without any perceptible preparatory elastic stretching[5].

The movements of the leaflets of *Trifolium pratense* and of *Oxalis acetosella* are produced by the expansion of one half of the pulvinus coupled with a corresponding contraction in the other half[6]. This is shown by the fact that the rigidity of the leaflet remains constant even during active movement. If the tendency to expansion increased in both halves of the pulvinus, but in one more than the other, the rigidity of the leaflet would

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[1] Baranetzsky, Die kreisförmige Nutation und das Winden der Stengel, 1883, p. 20.

[2] Darwin, l. c., 1880, p. 540; Prantl, Arb. d. Bot. Inst. in Würzburg, 1874, Bd. I, pp. 548, 554; Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 292; Fritzsche, l. c., p. 31.

[3] Baranetzsky, l. c., p. 61.

[4] Cf. Wiesner, Die undulirende Nutation d. Internodien, 1878, p. 26 (Repr. from Sitzungsb. d. Wien. Akad., Bd. LXXVII, Abth. I).

[5] Frank (Beiträge zur Pflanzenphysiol., 1868, p. 62) showed that the nutation of peduncles was due to growth. Hofmeister (Pflanzenzelle, 1867, p. 324) also concluded that growth was in part responsible for the movements. Cf. also Winkler, Krümmungsbewegungen bei *Spirogyra*, 1902.

[6] Pfeffer, Periodische Bewegungen, 1875, pp. 88, 156.

increase, and the same would also occur if one side only performed an active contraction or expansion, the other being passively stretched or compressed[1]. Pfeffer has shown that in the latter case the force of expansion in an active half of the pulvinus of *Trifolium* would lie between 0·6 to 2 atmospheres.

PART II

TWINERS AND CLIMBERS

SECTION 8. **General.**

According to the mode of climbing we may distinguish between (*a*) twiners, like the hop, which wind their slender stems around supports, (*b*) tendril-climbers which use special coiling attaching organs for this purpose, (*c*) root-climbers which attach themselves by means of aerial roots, (*d*) scramblers, like the bramble or Goosegrass which support themselves by means of the asperities or hooks upon the stem, or by the unfolding of the leaves after the stem has grown through a bush. No hard and fast distinction can be drawn between the different groups, however, since the tendrils of the Virginian creeper, for instance, attach themselves by means of sucking-disks, while the attaching roots of *Vanilla* are able to coil around supports. Typical root-climbers are *Hedera helix*, *Ficus stipulata*, and *Tecoma*, which are able to attach themselves to walls or to the trunks of trees.

In the case of scramblers no phenomena of special physiological interest are shown, the stem grows upwards in virtue of its heliotropism[2] so long as it receives support, while the unsupported ends trail downwards owing to their own weight. The stems of root-climbers are negatively heliotropic and negatively geotropic, so that they strive to grow erect but avoid light, hence pressing themselves against walls or the trunks of trees. In this way the required conditions for the formation of aerial attaching roots are produced, namely shade, moisture, and possibly contact also in many cases.

The twining stems of *Cuscuta* are not only irritable to contact like tendrils, but also form parasitic roots, while the twining stems of *Hoya* develop attaching roots. Many hook-climbers possess hooks which grow

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[1] [The rigidity depends upon the magnitude of the opposing forces, and therefore is ultimately dependent upon the hydrostatic pressure within the cells. An 'active' contraction produced by a fall of the osmotic pressure allowing the stretched cell-walls to contract on the 'active' side, will allow the cell-walls on the 'passive' convex side to be more expanded by their internal pressure. The increase of volume involving an absorption of water results in a fall of osmotic pressure on this side also. Hence the antagonizing forces decrease on both sides, and the rigidity does not increase but diminishes.]

[2] Schenck, l. c., pp. 7, 134, 156; Darwin, l. c.

in strength and size when attached, and function as most efficient attaching organs, lasting in some cases for several seasons. Certain Bignonias have twining stems in addition to tendrils or coiling leaf-stalks, while in a few species shoots are even formed which develop attaching roots[1]. The tendrils themselves may also not only coil but attach themselves at their tips by special disks produced under the stimulus of contact[2]. Certain plants only develop the climbing habit under special conditions, for instance, most twiners lose the power of twining when the action of gravity is eliminated, while *Polygonum aviculare* and *Galium Mollugo* develop scrambling stems in moist shady rich localities, but short erect or creeping stems in dry exposed situations.

The climbing habit enables the plant to reach light and air without spending a large amount of material in forming a stout erect stem. For this reason their growth in length is especially rapid, the stem of a hop for instance often becoming twelve metres in length during the summer. The conducting tissues need to be especially well developed in the thin stems of climbers. The wood-vessels for instance may be above one to three metres in length, and over half a millimetre in diameter, in this way the resistance to the unusually rapid flow of sap being reduced to a minimum[3].

Twiners are specially adapted for climbing up single thin supports, whereas tendril-climbers grow best when numerous points of attachment are presented, as in bushes or hedges. Root-climbers again are adapted to cling to rough erect surfaces such as walls, rocks or tree-trunks, which is only possible to tendril-climbers possessing attaching disks such as *Ampelopsis hederacea*, or claw-like grappling-hooks such as *Bignonia unguis*. All climbers are not equally well adapted, and in general tendril-climbers exhibit the most striking instances of special adaptation.

The young stem of a climber usually attains a certain length before climbing begins. Thus a seedling scarlet-runner develops at first a stout erect stem with a pair of simple foliage leaves, and only after a period of nutritive preparation produces the slender actively circumnutating twining stem with its trifoliate foliage leaves. In all cases if the stem fails to reach a support, it grows prostrate along the surface of the ground, until by accident, aided by movements arising spontaneously or produced by the wind, it comes into contact with a support. Climbers have no power of seeking out supports, and even the negative heliotropism of the ivy only comes into play when the stem is already quite near to the wall. Circumnutation naturally aids the plant in finding a support, and it is

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[1] Darwin, Climbing Plants, 1875, pp. 93, 101, 135.

[2] Darwin, l. c.; Cohn, Bot. Ztg., 1878, p. 27. Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, T. xv, p. 208 seq.

[3] Cf. Ewart, On the ascent of water in Trees, Phil. Trans., 1904, p. 65. [The longest vessel, 564 cms., was found in *Wistaria chinensis*.]

not only shown by twiners but also by the apices of many tendril-climbers and by the tendrils themselves. Furthermore the periodic daily movements of leaves bearing tendrils may aid the latter in reaching a support[1].

SECTION 9. **The Twining of Stems.**

The obliquely ascending coils formed by a twining stem around a support do not result from the tip being closely applied to it and growing along a continuous spiral path. They are instead the result of complicated movements of the free circumnutating tip, which is pressed closely against the support at one part of its revolution but stands out away from it at another[2] (Figs. 6 and 7). It appears that the coiling is not the result of a contact stimulus as in tendrils, but that the support merely acts as

FIG. 6. Twining stem of *Convolvulus arvensis*.

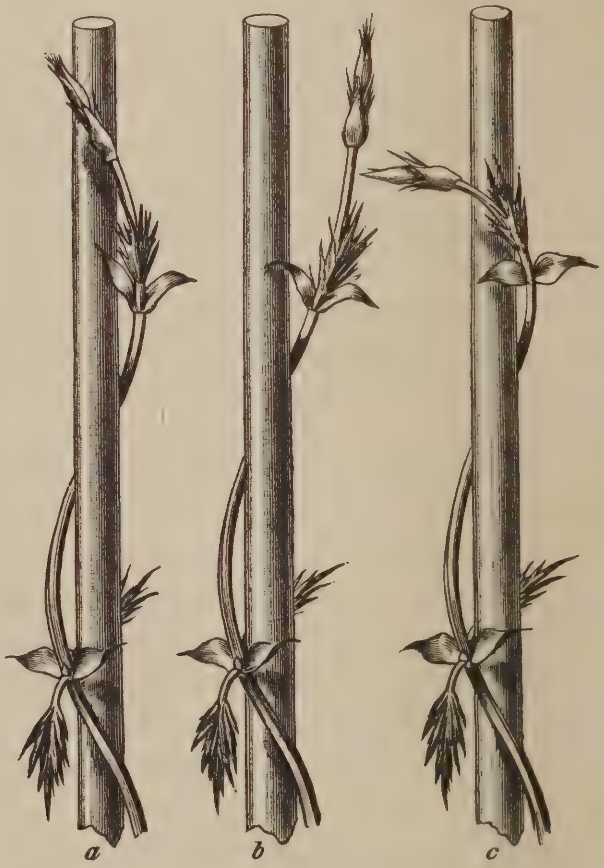

FIG. 7 *a b c*. Twining stem-apex of *Humulus Lupulus* in successive phases (*a*, *b*, *c*) of movement.

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[1] As in the case of *Mutisia Clematis* quoted by Darwin (l. c., p. 90).

[2] For details see Darwin, Climbing Plants; de Vries, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 326; Schwendener (1881), Gesammelte bot. Mitth., Bd. I, p. 405; Baranetzsky, Die kreisförmige Nutation und das Winden der Stengel, 1883, p. 54; Schenck, Beiträge z. Biol. u. Anat. d. Lianen, 1892, p. 115.

a mechanical obstacle determining the production and nature of the permanent coils formed by the growing circumnutating apex.

In the absence of distinct circumnutation no twining is possible and hence the seedling stem of the scarlet-runner, the shoots developed from the rhizome of the hop, and in general all the branches of twiners which are unable to circumnutate sufficiently are also unable to twine[1]. Hence also etiolated stems of *Tropaeolum majus*, and of *Polygonum fagopyrum* gain the power of circumnutating and of twining at the same time.

Circumnutation, and with it twining, cease when a twiner is rotated upon a klinostat so that the action of gravity is eliminated, while as the result of the plant's orthotropism the coiled younger portions may untwine and straighten[1]. It still remains possible, however, that gravity may act directly upon the process of twining, as well as indirectly by influencing circumnutation. At the same time it is evident that the contact with the support exerts no stimulus capable of preventing the uncoiling of the young shoot on a klinostat.

Under such circumstances, however, the stem of *Cuscuta* loses not only its power of circumnutation, but also the contact irritability which it exhibits under normal conditions. Rubbing the stems of *Cuscuta* and *Lophospermum scandens* with a solid body suffices to produce an irritable curvature, but not in the case of the stem of *Phaseolus* or of other twining plants. The same negative result is also obtained when one side of the shoot is repeatedly rubbed, or when permanent contact against an edge of wood is assured (Darwin), or when the circumnutating shoot presses against a rod attached to an appropriate turn-table (de Vries[2]).

The normal symmetric circumnutation is not sufficient to produce twining, for if it were, the horizontal or sloping free end when attached to a support at its base would continue to circumnutate and coil around a horizontal or inclined ideal axis (Baranetzsky's asymmetric circumnutation[3]). By attaching a piece of india-rubber tube to a retort-stand it is easy to show that in this way no twining about an erect support could be produced. It is evident, therefore, that sure and regular coiling involves a regulation of the growth and circumnutation of the growing apex.

According to Schwendener[4] this is produced by grasping movements,

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[1] *Bowiea volubilis* twines when horizontally rotated on a klinostat, according to W. Voss (Bot. Ztg., 1902, Originale, p. 231), if illuminated from the apical side. This plant is more strongly heliotropic than other climbers, and its circumnutation is dependent upon illumination.

[2] H. Mohl (l. c., p. 112) considered twining to be the result of contact irritability, but Palm (Ueber d. Winden d. Pflanzen, 1827, pp. 20, 97) of rotary nutation. Darwin (l. c., 1875, pp. 16, 39) and later de Vries (l. c., p. 321) showed the absence of any contact irritability, which has, however, again been brought forward by F. G. Kohl (Jahrb. f. wiss. Bot., 1884, Bd. XV, p. 327). Ambronn (Zur Mechanik des Windens, 1884, I, p. 32, Repr. from Sitzungsb. d. sächs. Ges. d. Wiss.) has shown that Kohl's experiments are inconclusive.

[3] Baranetzsky, l. c., pp. 11, 16, distinguishes between symmetric and asymmetric nutation.

[4] Schwendener, Gesammelte bot. Mitth., Bd. I (1881), p. 405; (1886), p. 441.

which occur every time the circumnutating apex presses itself against the support and drags upon the portion of the stem below, tightening the coils, and drawing the stem over and around the surface of the support. A pull of this kind is actually exercised every time the apex is pressed against the support, and the periodic changes of tension set up in the coiled but still growing parts by the movements of the free apex act in the same way. Although these factors must aid in twining, it is not certain whether they are the only ones acting. Baranetzsky in fact found that *Dioscorea Batatas* was able to twine in their absence. It is, however, readily possible that regulatory actions come into play of such character as always to cause the side of the stem which is not in contact to grow more actively, so producing the coiling around the support [1]. A regulation of this kind is in fact essential to maintain a homodromous curvature of the free apex, that is a curvature in the direction of twining [2], for as the result of circumnutation the permanently concave anterior side is continually changing. Even according to Schwendener's theory twining is a physiological manifestation produced by the plant exercising a definite power of movement.

We have no grounds for assuming that the factors inducing circumnutation are quite unaffected by the commencement and continuance of twining, and indeed the contrary is indicated by the fact that circumnutation is not performed during all stages of development. Similarly, it is uncertain whether the changes of tone which produce circumnutation continue on a klinostat, on which *Cuscuta* loses its contact irritability. The normal twining of this plant indeed involves a periodic inhibition of the contact irritability.

Sachs [3] observed that growth was often distinctly retarded in the free ends hanging beyond the support, or in shoots which were unable to climb. According to Raciborski [4], many tropical climbers which fail to reach a support either throw off their leaves or show a retarded development, followed ultimately by the death of the growing point. Baranetzsky found that the duration of growth was decreased in the twining portion of the stem and the circumnutation diminished [5].

Unfavourable conditions, or the abscission or fixation of the free apex, tend to cause a production of free coils (Fig. 8). Coiling of this kind is often shown under natural

FIG. 8. Free coiling of *Humulus Lupulus*.

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[1] Baranetzsky, l. c., p. 38; Noll, Sitzungsb. d. Niederrhein. Ges. f. Natur- u. Heilkunde, 4. Febr. 1895; Strasburger's Lehrb. d. Botanik, 1898, 3. Aufl., p. 225.

[2] De Vries, l. c., pp. 336, 341; Darwin, l. c., p. 19; Baranetzsky, l. c., pp. 16, 65; Schwendener, l. c. (1882), p. 436; Kolkwitz, Ber. d. bot. Ges., 1895, p. 513.

[3] Sachs, Lectures on Physiology.

[4] Raciborski, Flora, 1900, p. 2. These shoots have no contact irritability.

[5] Baranetzsky, l. c., p. 61 seq.

conditions by many plants, such as *Akebia quinata*, *Menispermum canadense*, and *Humulus Lupulus*, which have no support or have grown beyond it. The fixation of the shoot a little below the apex often causes free coiling, although this may be but slight[1]. It is possible that this physiological tendency to coiling may be directly or indirectly awakened by contact with a support, and may aid in twining. The fact that the free coils are often straightened again shows nothing, for the same happens when a stick is withdrawn from the coils just made around it.

The factors which determine the permanent homodromous curvature of the asymmetrically nutating free apex are uncertain. It is possible that the epinastic growth of the side becoming convex during winding is more pronounced as the internode approaches the adult condition, hence causing the permanent winding of the stem. Although the apex is curved, the stem remains physiologically radial, and the curvature passes in turn from side to side of the stem as the latter circumnutates. In the same way the contact line of an adult twiner follows usually a more or less spiral path around its stem[2].

The homodromous curvature of the apex is probably partly due to autonomic and aitionomic variations of tone in which the external world and the progress of twining act as directive stimuli. Baranetzsky and Noll[3], on insufficient grounds, assume the existence of a diageotropic irritability in the apex inducing paranasty. Ambronn ascribes the homodromous curvature to the conjoint action of circumnutation and negative geotropism, a conclusion which Schwendener disputes[4]. The latter erroneously regards circumnutation and geotropism as factors of constant magnitude, and forgets that the circumnutation and the klinotropic position of the shoot caused by it are themselves the result of regulated geotropic reactions. De Vries supposed the curvature to be due to the torsion produced by the weight of the free portion of the apex, but this has been shown to be untrue by various investigators[5].

The causes of twining are therefore unknown, but the very fact that regular coils sloping at a definite angle are produced in each individual case suffices to show that the position, thickness, and resistance of the support act as directive agencies upon coiling or regulate the internal tendencies responsible for twining. It is quite possible that the coiling is in one case produced by grasping movements, but in another by an active curvature of the internodes. The stems of *Cuscuta* and *Lophospermum* are able to twine partly as the result of their irritability to contact, which in tendrils is the main factor in producing coiling. Although most twiners seem to

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[1] De Vries, l. c., pp. 324, 339; Baranetzsky, l. c., p. 42; Sachs, l. c., p. 707. Pfeffer has observed in a culture of *Phycomyces nitens* that most of the sporangiophores were spirally twisted, and the shoots of some varieties, as for instance *Juncus effusus*, var. *spiralis*, always show a spiral coiling.

[2] De Vries, l. c., p. 329. Circumnutation is the result of a changeable or labile induction of a physiological dorsiventrality.

[3] Baranetzsky, l. c., p. 38; Noll, Sitzungsb. d. Niederrhein. Ges. f. Natur- u. Heilkunde, 4. Febr. 1895; Strasburger, Lehrb. d. Botanik, 1898, 3. Aufl., p. 225; Noll, Sitzungsb. d. Niederrhein. Ges., 8. Juli 1901. That centrifugal force should act similarly to gravity is not surprising.

[4] Ambronn, Zur Mechanik d. Windens, 1885, 2. Thl., pp. 19, 47 (Repr. from Sitzungsb. d. sächs. Ges. d. Wiss.); Ber. d. bot. Ges., 1887, p. 105; Schwendener (1886), Gesammelte bot. Mitth., Bd. I, p. 452.

[5] De Vries, l. c., p. 337; Baranetzsky, l. c., p. 69; Schwendener, 1881, l. c., pp. 403, 416; Ambronn, l. c., 1885, p. 25.

have no special contact irritability, it remains possible that the pressure against the support, or the curvature which this maintains, may play a certain part in twining, which like circumnutation appears to result from the co-operation of various stimuli.

SECTION 10. **Twining Plants** (*continued*).

In certain climbers special long shoots are adapted for twining[1], while some of the less active climbers may only develop the twining habit in moist shady situations where long weak stems are produced. This applies to such occasional twiners as *Solanum Dulcamara* and *Cynanchum vincetoxicum*[2], but the causes of the non-twining of *Polygonum convolvulus* during certain seasons are uncertain[3]. Darwin[4] mentions that *Ipomoea argyroides* and two species of *Ceropegia* develop in England as twiners, but not in the dry South African regions to which they are indigenous. Furthermore various cultivated varieties of *Phaseolus multiflorus* have lost the power of twining in correspondence with their dwarfed habit. Twining is shown more especially by the aerial stems of flowering plants, but in *Lygodium scandens* and *Blechnum volubile* we have instances of twining leaves[5]. It is, however, uncertain whether the twining occasionally shown by rhizomes and by roots in air, water, and even soil, is produced by the aid of circumnutation or by contact stimulation[6]. The same applies to the filaments of Algae which sometimes twine around supports[7], and to the rhizoids of *Catharinea undulata* which may coil around each other[8].

In all the cases hitherto observed circumnutation and twining take place in the same direction. Usually the direction is against that of the hands of a watch, as for instance in the stems of *Convolvulus* (Fig. 6, p. 34), *Phaseolus*, *Ipomoea purpurea*, *Menispermum canadense*, *Aristolochia sipho*, *Periploca graeca*. On the other hand the stems of *Humulus Lupulus* (Fig. 7, p. 34), *Polygonum convolvulus*, *Lonicera caprifolium*, *Testudinaria elephantipes* twine to the right in the opposite direction. Usually the direction of twining is constant, but in the cases of *Polygonum complexum*, *Testudinaria sylvatica*, and *Solanum Dulcamara* it sometimes happens that

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[1] For details see Schenck, Beitr. z. Biol. u. Anat. der Lianen, 1892, p. 115; Goebel, Organography, 1902; Darwin, Climbing Plants, 1875, p. 41; Voss, Bot. Ztg., 1902, p. 249 (Celastraceae).

[2] Darwin, l. c.; Schenck, l. c., p. 128.

[3] Palm, Ueber d. Winden d. Pflanzen, 1827, pp. 43, 94.

[4] Darwin, l. c.

[5] Cf. Schenck, l. c., p. 113.

[6] Hochreutiner, Rev. gén. de Bot., 1896, T. VIII, p. 92.

[7] Palm, l. c., p. 44.

[8] Schimper, Rech. s. l. mousses, 1848, Plate IV, Figs. 15, 16. Groups of filaments of *Spirogyra* projecting into moist air may show coiling. Hofmeister, Jahreshefte d. Vereins f. vaterländ. Naturk. in Württemberg, 1847, Jahrg. 30, p. 226; Winkler, Krümmungsbewegungen von *Spirogyra*, 1902.

different individuals, or different shoots on the same individual, twine in opposite directions. In *Loasa aurantiaca, Scyphantus elegans, Blumenbachia lateritia*, *Tropaeolum tricolorum*, *Ipomoea jucunda*, and *Hibbertia dentata* the twining may even be reversed on the same shoot[1].

Unless the growth is considerably diminished during the reversal of circumnutation the youngest coils may untwine, and if the reversal occurred frequently no permanent twining would be possible, as is the case when the plant is rotated horizontally on a klinostat. If, however, only a portion of the coils are untwined permanent coiling may continue, but more slowly than usual. Homodromous twining may even take place, if the reversal of circumnutation is only temporary and ceases before any permanent coils have been formed. This was actually observed by Darwin to occur in *Hibbertia dentata*[2]. Indeed in the normal progress of circumnutation the later coils may be partially unwound.

There is no definite relationship between the number of coils and the number of circumnutations, the latter being performed more frequently than the former are produced. Darwin[3] observed that *Ceropegia* circumnutated once in six hours, but only formed a coil in nine and a quarter hours. The same was the case with *Aristolochia gigas*, except that a circumnutation was completed in five hours instead of six. Naturally twining is only produced by definitely regulated circumnutation, and it can be artificially induced by causing a growing apex to slowly follow a tropic stimulus around a support.

If the support is of appropriate thickness the coils are closely applied to it, but around thread, fine wire, or string, loose coils are often formed. These are often subsequently closely pressed to the thinnest supports by the elongation of the stem, for the same reason that the diameter of a spiral spring decreases when the spring is considerably stretched[4]. This elongation is in part autotropic, but is also due to the increased geotropism of the stem inducing the younger coils to straighten more or less[5]. This tendency may cause the straightening of the younger coils formed around a thick support if this is removed, whereas the older coils are permanent, owing to the fact that the power of growth rapidly disappears after coiling. Owing to the same tendency a considerable pressure may be exercised upon the support, sufficient to crush in a hollow paper cylinder[6], to partially strangulate a soft fleshy stem, to compress a leaf or petal, or

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[1] For further details see Darwin, l. c.; Schenck, l. c., p. 123, and the literature there quoted.

[2] L. c., p. 47.

[3] L. c., p. 13.

[4] De Vries, l. c., p. 326; Baranetzsky, l. c., p. 58; Schwendener, l. c., 1881, p. 419; Ambronn, l. c., I, p. 5; II, p. 35.

[5] Baranetzsky, l. c.

[6] Mohl (Ranken- u. Schlingpflanzen, 1827, p. 118) deduced the existence of this pressure from the curvatures produced in a string round which coiling occurs. De Vries (l. c., p. 327) found that the coils at once narrow when the support is removed.

to keep a flower of *Convolvulus* closed. In this way, aided by roughnesses on the stem and support, and often by special climbing-hairs as in *Humulus* and *Phaseolus*, the fixation is rendered more secure [1].

From what has already been said as to the mode of coiling, it is hardly surprising that a good climber should form an extremely regular spiral curve around a cylindrical support, and the slope of the coils is in many cases not appreciably altered by moderate changes in the diameter of the support. With thinner and thinner supports the coils become steeper until a limit is reached which is about that which the coils show when the stem partially straightens after loosely coiling upon a thin support.

As the result of the circumnutation about a vertical axis, the stem is unable to twine around horizontal, or nearly horizontal, supports, and the younger coils may untwine when the support is placed in a horizontal position. Mohl [2] found that a string inclined at an angle of 20° to the horizon was no longer twined round by the stem of *Ipomoea purpurea*, and one at an angle of 40° by *Phaseolus* [3].

The thickness of support a twiner can grasp is determined mainly by the length of the circumnutating apex, and when this attains a considerable length, as in certain tropical Lianas, twining is possible around supports up to 40 cms. in diameter. Scarlet-runners and Hops may twine around sticks of 8 to 15 cms. in diameter, whereas *Convolvulus arvensis* and *Polygonum convolvulus* are usually unable to coil around stems thicker than 3–4 cms.[4] Since the length of the circumnutating apex and other conditions also may vary in the same plant, it is not surprising that de Vries should find plants of *Wistaria chinensis* twining around supports 16 cms. in diameter, whereas Darwin found potted specimens unable to coil around supports of slightly less diameter.

It depends upon these relationships whether a stem twines around a single or several supports when these are grouped near together. That stems should be able to pass from one support to another, sometimes reascending after hanging downwards, is hardly surprising, or that branches may twine around each other. The form of the support is of some importance, thin stems being able to apply themselves more closely to flat supports than thicker stems can, but the material of the support is only of value from a purely mechanical point of view, the older ideas as to the attraction

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[1] Cf. Schenck, l. c., p. 131.

[2] L. c., p. 132.

[3] Voss (Bot. Ztg., 1902, Orig., p. 231) finds that *Bowiea volubilis* will twine around much-inclined supports if the strongly heliotropic shoots are illuminated on one side.

[4] See Mohl, l. c., p. 134; Darwin, l. c., p. 29; Baranetzsky, l. c., p. 56; Schwendener, l. c., p. 418; Schenck, l. c., p. 121. When woody twiners coil around trees, the latter may be slowly strangulated, the twining stem being often deeply imbedded in the secondary wood. Cf. Schenck, l. c., p. 122.

exercised by the support having long ago been shown to be erroneous by Mohl.

Torsion. Circumnutation does not involve torsion, but the latter is usually shown very strongly by the older internodes of stems which have not twined. The torsion is indicated by the twisting of ridges on the stem and by the displacement of the phyllotaxis, and follows the same direction as the circumnutation and twining. It arises, however, from internal causes and hence persists when circumnutation and twining are arrested by rotation on a klinostat [1].

Stems twined around a support usually show antidromous torsion resulting from the twining, and which, owing to the fixation of the coils to the support, has been incapable of removal by the plant's tendency to homodromous torsion. If portions of the support are cut away the latter comes into play over these regions and the antidromous torsion is wholly or partly removed. The same takes place when the coils are loose or unattached, and hence it is hardly surprising that the torsions observed in a climbing stem should vary considerably, and even be in some cases antidromous, in others homodromous [2].

Mohl supposed that circumnutation and twining were produced by the torsion of the stem, but Palm and, more especially, Darwin and de Vries have shown that this was an error. The two latter authors recognized the dissimilar origins of antidromous and homodromous torsions, and their mode of action. Schwendener, and at a later date Baranetzsky, Ambronn, and Kolkwitz, showed in detail how the antidromous torsion was the mechanical result of coiling. If an india-rubber tube bearing a longitudinal stripe is coiled around a support without hindering its tendency to twist around its own longitudinal axis, the spiral twisting of the stripe will show the antidromous torsion resulting from coiling. To keep the stripe on the convex side the tube must be twisted during coiling, and if the end is partially freed the tube will tend to twist back to the original condition. In a stem capable of growth the forcible torsion might become partially or entirely fixed [3], just as is the antidromous torsion produced by twining when tight coils are formed. The homodromous torsion attempted in the attached coils has the effect of fixing the stem more firmly to the support by tightening up loose coils [4].

Heliotropism and twining. According to Mohl, Dutrochet, Darwin, and Baranetzsky [5] the circumnutating shoots of climbers are usually positively heliotropic, but this irritability is so weak as merely to somewhat accelerate circumnutation when

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[1] Baranetzsky, l. c., p. 31.

[2] For details see Kolkwitz, Ber. d. bot. Ges., 1895, p. 497; Schwendener (1881), Gesammelte bot. Mitth., p. 420; Ambronn, Zur Mechanik d. Windens, 1884, I; 1885, II (Repr. from Sitzungsb. d. sächs. Ges. d. Wiss.); Baranetzsky, Die kreisförmige Nutation und das Winden d. Stengel, 1883, p. 66; De Vries, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 330; Darwin, Climbing Plants, 1875.

[3] Cf. Kolkwitz, l. c., p. 505.

[4] Cf. Id., p. 512.

[5] Darwin, The Power of Movement in Plants, 1880, p. 449.

the stimulus is applied so as to aid the autonomic movement, and to slightly retard the latter when acting against it. Baranetzsky found that during the symmetric nutation of *Ipomoea purpurea* the half of the orbit towards the light was performed in 45 minutes and that away from it in 55 minutes. Similar differences were observed in *Ipomoea sibirica* and *Polygonum Convolvulus*. The heliotropic action is weakened during symmetric nutation by the fact that the anterior side is continually changing, whereas since the latter takes place to a less degree during asymmetric circumnutation, the heliotropic action would naturally be somewhat stronger, being more prolonged on the respective sides.

Baranetzsky observed that an asymmetrically nutating apex of *Ipomoea sibirica* performed the half of the orbit towards the light and downwards in 35 minutes, that away from the light in 75 to 85 minutes.

The positive heliotropism of the apex is unfavourable to twining rather than an aid to it, but it is of some advantage that the coiled parts should become negatively heliotropic, for this causes them to curve towards the shaded side and hence towards the support. Baranetzsky[1] found this negative heliotropism to be very pronounced in the shoots of *Ipomoea purpurea*, *Polygonum Convolvulus*, and *Dioscorea sinuata*, whereas it was weaker in the stems of *Dioscorea Batatas*, and was not developed at all in the stems of *Boussingaultia baselloides* and *Menispermum dahuricum*[2].

SECTION II. **Tendril-climbers.**

Tendril-climbers show much more varied special adaptations than twiners, and they may be classed in different groups according to the type of irritable attaching organ they possess[3].

Under tendril-climbers we include all such plants as *Bryonia* and other Cucurbitaceae, *Passiflora*, *Pisum*, *Lathyrus*, *Cobaea scandens*, *Bignonia*, *Eccremocarpus*, *Vitis*, *Cardiospermum Halicacabum* which possess filamentous coiling attaching organs which are irritable to contact (Fig. 9). The tendrils are continually produced at the growing apex, and radiate and attach themselves in all directions. The spiral coiling of the portion between the stem and the support acts like a spring against the tearing effect of violent shocks of wind or rain, and also draws the plant nearer to the support and by the antagonistic action of different tendrils affords more rigid support. The same applies when the tendril itself is branched,

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[1] Baranetzsky, l. c., p. 21. Cf. also Wiesner, Die heliotropischen Erscheinungen, 1880, II, p. 38; Voss, Bot. Ztg., 1902, Orig., p. 238.

[2] Mohl, l. c., p. 120, observed that certain twiners succeed in coiling around a support if they meet it while growing away from the light, but not if they are growing towards it. It is, however, not certain whether this is due to negative heliotropism.

[3] For details see Darwin, Climbing Plants, 1875; Schenck, Beiträge z. Biol. u. Anat. d. Lianen, 1892, I, p. 135; Ludwig, Lehrb. d. Biol. d. Pflanzen, 1895, p. 126; Goebel, Organography, 1900. The physiologist has to deal with the tendril as a functional organ without regard to its morphological origin. Hence Schenck's classification has no value here.

as in *Pisum* or *Lathyrus*, or when, as in the case of *Cobaea scandens*, the tips of the branches are furnished with curved claws which aid not only in maintaining contact until coiling has taken place, but also act as permanent attaching organs.

FIG. 9. *Bryonia dioica.* *a*, young spirally coiled tendril; *b*, expanded and irritable tendril; *c*, tendril which has grasped a support; *d*, tendril which has not grasped a support, and has undergone the old-age coiling.

The last-named plants afford instances of the development of a portion (*Cobaea*, *Lathyrus*), or of the whole (*Lathyrus aphaca*), of the leaf into a typical tendril. In leaf-climbers the leaf or some portion of it acts as the attaching organ without losing its general character. The petioles of

Solanum jasminoides are, for instance, able to coil around a support (Fig. 13), while in *Fumaria officinalis*, var. *Wirtgeni*, the slender leaf-segments act in the same way as irritable attaching organs. The more or less tendril-like leaf-tips of *Corydalis claviculata*, *Gloriosa superba*, *Flagellaria indica*, and *Littonia* form coiling attaching organs and show a transition from typical leaf-climbers to typical tendril-climbers, the first-named plant possessing tendrils which approximate in character to those of *Lathyrus*.

FIG. 10. Tendrils of *Cobaea scandens*. A young branch (*a*) and an older one (*e*), each bearing a leaf (*b*) with three pairs of leaflets, and a branched tendril; (*e*) has grasped and (*a*) is grasping a support (*c*); at (*d*) the claw-like ends are shown slightly magnified.

Among petiole-climbers are *Solanum jasminoides*, *Clematis vitalba*, *Atragene*, *Tropaeolum* and *Lophospermum scandens*, in which the petiole bears a normal leaf lamina, although it may have coiled around a support. The tropical *Dalbergia linga* (Boerlage) is of interest since in this plant the basal pulvini of

FIG. 11. *Dalbergia linga*. *a*, young stem and leaves; *b*, young leaf with the curved terminal pair of pulvini; *c*, older leaf (reduced) with one pulvinus attached and its leaflets thrown off (after Ewart).

the terminal pair of leaf-pinnae are long, backwardly curved, and irritable to contact. After coiling, which begins in five minutes and is usually completed in a day, to the extent of one to four coils according to the thickness of the support, the wood-cylinder becomes within a week more than double the thickness of that of an unattached pulvinus, while very often the terminal pinnae with their leaflets are thrown off at the articulation to the pulvinus so that the tendril character is fully established[1].

FIG. 12. *Gloriosa superba.* Two leaf-tips have grasped a grass haulm.

FIG. 13. *Solanum jasminoides* (after Darwin). The petiole (*b*) has twisted around a support (*s*).

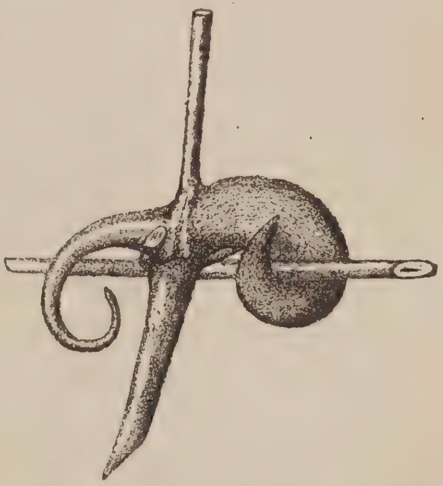

FIG. 14. *Uncaria ovalifolia.* Nat. size (after Treub). The hook (*a*) attached to a support has thickened considerably.

Many tropical plants possess leafy branches, or specially shaped ones which act as irritable attaching organs. In Europe only certain comparatively inefficient climbers belonging to the genus *Antirrhinum* are branch-climbers, and among these *Cuscuta* may be included, since its stem not only twines but is also sensitive to contact. Tropical countries also possess in *Uncaria* (Fig. 14), '*Olax*' (*Roucheria*), *Artabotrys*, and *Strychnos*[2], shrubby climbers provided with attaching hooks or hook-like tendrils, which are either branch-thorns (*Uncaria*) or inflorescence stalks (*Artabotrys*), and which in all cases undergo more

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[1] Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, Vol. XV, 1, p. 227. Most of the climbing *Dalbergias* are branch-climbers. Cf. Schenck, l. c.

[2] Cf. Treub, Ann. du Jard. bot. de Buitenzorg, 1882, Vol. III, p. 1; Ewart, ibid., 1898, Vol. XV, p. 187

or less marked secondary thickening as the result of contact. In the case of *Uncaria* and *Artabotrys* no coiling occurs, but a slight one in *Roucheria* and *Ancistrocladus*, while the hook-like tendrils of *Strychnos* and *Bauhinia* are able to form one or more complete coils around a suitable support[1]. These latter forms show a transition to the watch-spring tendrils whose coiled apices grasp supports and then twine around them.

A feeble contact irritability is shown by various organs. Thus the aerial roots of *Vanilla* and of a few other plants are irritable enough to function as root-tendrils, from three days to a week being, however, required to produce a complete coil, and the coiling often not being completed until after the lapse of three weeks[2]. Both terrestrial and aquatic roots, as well as the rhizoids of *Catharina*, have been observed to coil around foreign bodies, but it is not certain whether this is or is not the result of contact stimulation. Presumably, however, certain special branches of *Cystoclonium purpurascens*, of *Hypnea musciformis*, of *Nitophyllum uncinatum*, and of a few other marine algae, are able to coil like tendrils[3], which power is also possessed according to Zopf[4], by the curved hyphae of *Arthrobotrys oligospora*, and by the hyphae of a few other fungi[5]. In addition Wortmann[6] observed a strong sporophore of *Phycomyces nitens* coiling around a weaker one.

The stimulus of contact not only hastens the coiling of a tendril but also causes its strength to increase. In some cases, as in *Bauhinia tomentosa* and *Amphilobium mutisii* the tendril undergoes a secondary increase in thickness, such as is shown to a marked degree in the tendril-hooks of *Strychnos*, *Roucheria*, and in the non-coiling hooks of *Uncaria* and *Artabotrys*[7]. Similarly the petioles of leaf-climbers may double in thickness at the point of contact (cf. Fig. 13, p. 45), while an attached twining pulvinus of *Dalbergia linga* may attain double the diameter of an unattached one, owing mainly to the very rapid growth of the wood-cylinder and partly to the enlargement of the cortical cells[8]. Similarly the secondary growth of the wood in the petiole of *Solanum jasminoides* leads to the

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[1] Cf. Ewart, l. c., p. 239.

[2] Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, Vol. XV, p. 233. The attaching roots were noticed by Mohl, Ranken- und Schlingpflanzen, 1827, p. 24; and Darwin, l. c., p. 144. These and other aerial roots apply themselves closely to the trunk and walls as the result of their negative heliotropism, and become attached by their root-hairs. A root of *Vanilla* attached in this way to the smooth surface of another leaf was able to support a weight of 250 grams (Ewart, l. c., p. 234). On the roots of the potato developed in moist air, see Sachs, Flora, 1893, p. 8.

[3] Wille, Bot. Jahrb. f. System. u. Pflanzengeographie, 1886, Bd. VII, p. 21; Nordhausen, Jahrb. f. wiss. Bot., 1899, Bd. XXXIV, p. 236.

[4] Zopf, Nova Acta d. Leopold. Carolin. Akad., 1888, Bd. LII, p. 325.

[5] Boudier, Bull. de la Soc. bot. de France, 1894, p. 371; Ludwig, Bot. Centralbl., 1899, Bd. XXXVII, p. 359.

[6] Wortmann, Bot. Ztg., 1887, p. 806.

[7] Ewart, l. c., pp. 189, 208, 218, 222.

[8] Ibid., p. 228.

production of a complete cylinder of wood[1], while the stimulus acts as far as the base of the tendril of *Bauhinia* causing its originally flattened outline to become more or less circular[2].

The stimulus of contact causes the development of the disks by which the tendrils of various species of *Ampelopsis* (Fig. 15), *Bignonia capreolata*, *B. littoralis*, *Hanburya mexicana*, *Cissus pauliniaefolia* attach themselves to rocks, walls, or the bark of trees[3]. These disks may attain a considerable size, those of *Amphilobium mutisii* often being 12 to 14 mm. in diameter, and 4 to 6 mm. thick at the centre[4]. The tendrils of this plant and of *Ampelopsis quinquefolia* may also twine around supports.

FIG. 15. *Ampelopsis quinquefolia*. The tendril (*a*) has formed attaching disks, and has become spirally coiled.

The disks or suckers are usually formed by outgrowths from the epidermal cells and subjacent parenchyma, but those of *Amphilobium mutisii*[5] contain vascular tissue, and often also an annular air-space around the margin of the disk. By the aid of a sticky secretion, or by growing into the irregularities of the supporting surface, so firm an attachment is often produced that the tendril breaks before the disk is torn away. In the tendrils of *Ampelopsis Veitchii*, *Vitis inconstans*, and *Cissus paulinaefolia* the suckers are preformed structures present as small swellings at the tips of the branched tendril and are simply excited to further development by contact, but no such rudiments are present on the tendrils of *Ampelopsis quinquefolia* and *Amphilobium mutisii*. The suckers may be formed at various points on the tendril, but in *Ampelopsis* usually, and in *Amphilobium* always, at the tip of one or all of the branches if these are in contact with the support. The three-armed tendril of *Amphilobium* is able to coil around a smooth glass rod, but not to form suckers even where the tips of the branches touch the glass[6]. When in contact with a rough surface the disks may become perceptible in two or three days, but the full development of the large disks of *Amphilobium* may take from one to two months. The tendrils of most Cucurbitaceae show a certain proliferation of the epidermal

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[1] For details on petiole-climbers cf. Derschau, Einfluss von Contact u. Zug auf rankende Blattstiele, Leipziger Dissert., 1893.

[2] Ewart, l. c., p. 222.

[3] Mohl, Ranken- u. Schlingpflanzen, 1827, p. 70; Darwin, Climbing Plants; Pfeffer, Arb. d. bot. Inst. in Würzburg, 1871, Bd. 1, p. 95; Lengerken, Bot. Ztg., 1885, p. 408; Schenck, Beiträge z. Biol. u. Anat. d. Lianen, 1892, 1, p. 240.

[4] Ewart, l. c., p. 219.

[5] Id., l. c., pp. 219–20.

[6] Id., l. c.

and cortical cells at the point of contact, and in *Sicyos angulatus* and a few other Cucurbitaceae the fixation is aided by a viscid secretion[1].

The physiologically radial stems of *Cuscuta europaea*, *C. epilinum*, and of *Cassytha* twine like typical climbers, and in addition coil and produce haustoria as the result of contact[2]. When this has occurred and a few close coils with haustoria have been formed, the acropetal portion of the stem loses its contact irritability for a time, and a few much steeper coils are formed by circumnutatory coiling. These coils are often loose and form no haustoria. If, however, no support is found, the new growths of the stem of *Cuscuta* remain continually sensitive to contact, which shows that it is the satisfaction of the desire for contact which causes the periodic inhibition of the contact irritability.

FIG. 16. *Cuscuta epilinum* on *Impatiens parviflora*. At (*a*) are close coils with haustoria, at (*b*) steep coils without haustoria.

In addition the stimulus of gravity is necessary to maintain the irritability of *Cuscuta*, for on a horizontally rotated klinostat not only the circumnutation but also the power of responding to contact disappear, while after three days' rotation the irritability only returns after twenty-four hours' rest under normal conditions[3].

It is uncertain whether in other cases the stimulus of gravity may be necessary to maintain contact irritability, for typical tendrils as well as the hyphae of *Phycomyces* appear to remain irritable when rotated on a klinostat. Whether this also applies to the feebly irritable stems of the petiole-climber *Lophospermum scandens*, which rarely coils in nature, is unknown[4], although many instances have been found in which the sensitivity and power of reaction are more or less dependent upon geotropic induction.

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[1] Müller, Cohn's Beiträge z. Biol., 1887, Bd. IV, pp. 107, 123, &c.; Schenck, l. c., p. 200.

[2] First observed by Mohl (Ranken- u. Schlingpflanzen, 1817, p. 131); further studied by Koch (Hanstein's bot. Abhandl., 1874, Bd. II, p. 121; Die Kleeseide, 1880), and fully explained by Peirce (Annals of Botany, 1894, Vol. VIII, p. 53).

[3] Darwin's statement (l. c., p. 100) that the tendril of *Echinocystis lobata* becomes straight and non-sensitive when there is danger of contact with its own shoot requires further proof. The power of discrimination by which Darwin supposed certain tendrils to be able to avoid coiling around one another does not actually exist, the absence of such coiling being due to the slenderness, pliability, and smoothness of the tendrils, combined with their circumnutation movements. (Cf. Ewart, l. c., pp. 224–7; and Pfeffer, Unters. aus dem bot. Inst. zu Tübingen, 1885, Bd. I, p. 495.)

[4] Darwin, Climbing Plants.

The periodic inhibition of the contact irritability at the apex of *Cuscuta* affords a good instance of the influence of a realized activity upon subsequent development, and it has the importance of allowing the plant to spread from one host to a neighbouring one, and of enabling more rapid extension over a single host. The persistence of the irritability in the absence of a support gives a better chance of one being immediately utilized when reached by the circumnutation of the elongating apex.

Since *Cuscuta* usually gains a support by the aid of its circumnutation, the coiling follows the direction of circumnutation[1], but it is uncertain whether the contact irritability suffices by itself to produce definite coiling. Since coiling takes place around a rod of moist gelatine which exercises no contact stimulation, it is evident that circumnutation alone produces fairly good coiling. *Cuscuta*, like other twiners, usually produces no further coils around a support laid horizontally. This is owing to the fact that during the phase when the apex is non-sensitive to contact, the terminal internodes free themselves from the support and strive to become erect[2].

A rod of any material suffices to produce the coiling of *Cuscuta* and the formation of haustoria, which however only attain their full development when they penetrate an appropriate host-plant. Since the production of haustoria is dependent upon the stimulus of contact, they are only formed on the side pressed against the support, although all sides of the stem are capable of producing them.

Heliotropism. The negative heliotropism of certain tendrils aids them in acquiring a support. This applies to the tendrils of *Vitis vinifera*, *Ampelopsis hederacea*[3], *Bignonia capreolata*, *Eccremocarpus scaber*[4], as well as to the root-tendrils of *Vanilla planifolia*[5]. The tendril of *Smilax aspera*[6] possesses very weak negative heliotropism, which causes it to circumnutate somewhat more rapidly away from the light than towards it. The reverse is the case in the feebly positively heliotropic tendrils of *Passiflora*[7], whereas Darwin could detect no heliotropism at all in the tendrils of *Pisum*[8]. Tendrils, like the stems of twiners, are therefore only feebly heliotropic. This also applies to the stems of *Cuscuta*, although when they have been rotated horizontally for some time on a klinostat they become distinctly positively

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[1] Peirce (l. c.) observed no coiling in the opposite direction, but Koch (l. c., 1874, p. 124) found this to occur occasionally.

[2] Peirce, l. c., p. 115. According to Koch (l. c., p. 124), *Cuscuta* is also able to twine around a horizontal support.

[3] Knight, Phil. Trans., 1812, p. 314; Mohl, Ranken- und Schlingpflanzen, 1827, p. 76; Darwin, Climbing Plants, 1875, p. 144; Wiesner, Die heliotropischen Erscheinungen, 1880, Th. II, p. 38.

[4] Darwin, l. c., pp. 86, 103. Beccari (Bot. Jahrb., 1884, I, p. 27) observed that the tendrils of *Cissus* do not apply themselves to strips of mica, possibly because of the negatively heliotropic action of the reflected light.

[5] Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, Vol. XV, p. 237.

[6] Darwin, l. c., pp. 118, 184.

[7] Id., l. c., p. 153.

[8] Id., l. c., p. 112. Wiesner (l. c., p. 38) finds that the tendrils of *Pisum* are positively heliotropic in weak light, negatively heliotropic in strong light. Derschau (Einfluss von Contact und Zug auf rankende Blattstiele, 1893, p. 12) finds the petioles of *Lophospermum scandens* to be fairly strongly positively heliotropic.

heliotropic[1]. It may also be remarked that the tendrils of *Bryonia* remain irritable even when developed in darkness[2], and that the absence of light exerts no perceptible influence upon the development of the haustoria of *Cuscuta*[3].

SECTION 12. **The Special Irritability of Tendril-climbers.**

The contact of a tendril against a support induces a greater activity of growth on the free side, and hence produces coiling. Since the irritability is only attained at a certain stage of development, and gradually disappears as the tendril grows old and loses the power of growth, the effect produced by a stimulus depends not only upon its intensity but also upon the age of the tendril. Ordinary tendrils only become sensitive to contact when fully unfolded, and either at or after the commencement of circumnutation. The irritability usually persists until growth has entirely ceased, which occurs after the circumnutation has become imperceptible[4].

All parts of the tendril are not equally irritable, the basal portion in many cases responding feebly or not at all to contact. Usually only one side responds to contact, but the tendrils of *Cobaea scandens*, *Cissus discolor*, *Smilax aspera*, *Actinostemma paniculatum*[5], and the pulvinar tendrils of *Dalbergia linga*[6] are able to coil around an object touching any side. The tendril of the last-named plant has the proximal surface concave when young, but when older one of the other surfaces becomes convex, and the slightly greater irritability of the original concave side is transferred to the new one[7]. A physiologically dorsiventral tendril remains unstimulated, and moves away from a support which touches one of its non-irritable flanks. In such tendrils the irritability usually appears to decrease from the irritable flank towards the sides, which are however usually sufficiently irritable to commence coiling, and then a slight twist

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[1] Peirce, l. c., pp. 87, 116.

[2] Sachs, Bot. Ztg., 1863, Beilage, p. 12.

[3] Peirce, l. c., p. 88.

[4] For facts see Darwin, Climbing Plants, 1875; Wortmann, Bot. Ztg., 1887, p. 53; Schenck, Beitr. z. Biol. u. Anat. d. Lianen, 1892, I, pp. 141, 154; Fitting, Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 554. On leaf-tendrils and hooks cf. Schenck, l. c.; Derschau, Einfluss von Contact und Zug auf rankende Blattstiele, 1893, p. 12; Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, Vol. XV, p. 188. On the distribution of growth in developing tendrils cf. Macdougal, Annals of Botany, 1896, Vol. X, p. 379; Fitting, l. c., p. 547. Mohl (Ranken- u. Schlingpflanzen, 1827, p. 65) incorrectly supposed that the irritability only appeared when growth in length had ceased. In many cases growth may be re-awakened and a curvature be produced after the tendril has ceased to elongate. Cf. Fitting, Jahrb. f. wiss. Bot., l. c., p. 554.

[5] Darwin, l. c.; Schenck, l. c., p. 141; Derschau, l. c., p. 13; Fitting, l. c, p. 551. The decision is made according to the presence or absence of a curvature after contact on each flank. Even in dorsiventral tendrils, the side on which contact produces no response is actually sensitive in a special way, for contact on this side may prevent simultaneous contact on the irritable side from producing any response.

[6] Buitenzorg garden name, not given in Kew Index.

[7] Ewart, l. c., p. 229

commonly brings the most irritable side against the support. It is rarely the case that a tendril is physiologically perfectly radial, and numerous transitions occur between isotropic and anisotropic tendrils. Contact applied to the convex surface of the hook-tendril of *Strychnos* causes, for instance, a slight increase of thickening but no coiling[1]. Kohl[2] found tendrils of *Pisum sativum* to be occasionally irritable on all sides instead of on one only as is usually the case. The branches of the tendril of *Bignonia venusta* are anisotropic, but the peduncular portion is able to coil towards any side[3].

Among leaf-climbers the tip of the leaf of *Flagellaria indica* is irritable on the upper side, but in all others the under side is the sensitive one[4]. Darwin found the petioles of leaf-climbers to be irritable on all sides, but according to Derschau[5] not to the same degree. Usually only the concave side of an attaching hook is pronouncedly irritable, the back and sides being less so or almost insensitive to contact. In the case of *Artabotrys* the median portion of the hook (*b*, Fig. 17) is much more irritable than either the terminal or basal joints[6]. In the case of the tendril of *Ampelopsis Veitchii* only a particular point at the tip of each branch is irritable, whereas the stems of *Cuscuta* are physiologically radial to contact stimuli. In most cases anisotropic tendrils are morphologically and anatomically dorsiventral, while isotropic tendrils which undergo secondary growth may become very pronouncedly bilateral as the result of contact stimuli. The same stimulus may cause a flattened tendril to become more or less circular in outline[7]. Anatomical and physiological dorsiventrality are not necessary postulates of each other, and in fact various dorsiventral petioles are irritable on all sides. The anatomical structure affords no direct evidence as to the distribution of irritability, and hence requires no discussion[8].

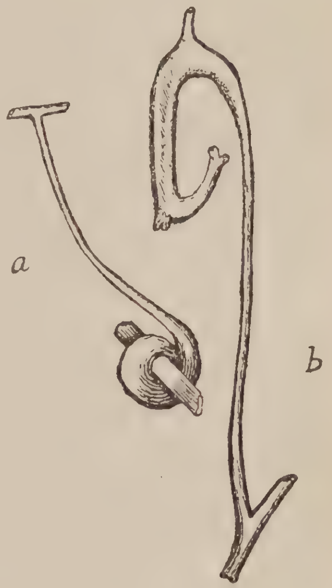

FIG. 17. *a*, coiled and thickened hook-tendril of *Strychnos laurina*; *b*, attaching hook of *Artabotrys Blumei*. (After Ewart.)

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[1] Ewart, l. c., p. 212. [2] Mohl, l. c., p. 65. [3] Schenck, l. c., p. 189; Fitting, l. c.

[4] Schenck, l. c., p. 179. The tendril-leaves of *Adlumia cirrhosa* are irritable on all sides. Cf. Pfeffer, Unters. d. bot. Inst. zu Tübingen, 1885, Bd. I, p. 485.

[5] L. c., p. 13.

[6] Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, Vol. XV, pp. 193, 202, 204, 242.

[7] Ewart, l. c., pp. 218, 222.

[8] On anatomical relationships cf. Worgitzky, Flora, 1887, p. 2; Leclerc du Sablon, Ann. sci. nat., 1887, 7^{e} sér., T. V, p. 5; Müller, Cohn's Beitr. z. Biol., 1887, Bd. IV, p. 97; Derschau, Einfluss von Contact und Zug auf rankende Blattstiele, 1893; Borzi, Rend. Acad. dei Lincei, 1901, 5^{a} ser., T. X, p. 395; Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, Vol. XV, p. 187; Fitting, l. c., p. 600; Schenck, Beitr. z. Biol. u. Anat. d. Lianen, 1892, I, p. 146; Macdougal, Annals of Botany, 1896, Vol. X, p. 394; and the literature quoted by these authors.

In all these cases the attaching organs are stimulated by contact with or rubbing against any solid body. Contact with air or liquids such as a stream of water or mercury produces no effect, whereas in *Mimosa* and similar plants any shaking or disturbance may act as a stimulus if sufficiently intense. This difference is due to the existence of a special contact irritability in the attaching organs, which may also be termed haptotropism or thigmotropism, and which is excited by differences of pressure or variations of pressure in contiguous or neighbouring regions[1]. Hence smearing a tendril with stiff gum-arabic exercises no stimulatory effect, and similarly a glass rod covered with moist but solid 10 per cent. gelatine produces no excitation even when strongly pressed and rubbed against the most sensitive tendrils. Coated glass rods may therefore be used to handle tendrils without stimulating them, or the tendril may be placed upon a glass dish coated with the solidified gelatine. Naturally contact with a rough body exerts a greater stimulus than contact with a very smooth one. Hence smooth and slender tendrils, since they can exert but little pressure on one another, and usually remain in contact for a short time only, rarely coil around each other[2]. Stouter and stiffer tendrils like those of *Bauhinia* and *Smilax* naturally respond to self-contact more readily. The absence of any response to wind and rain is obviously of great use to the plant.

The tendrils of *Sicyos angulatus*, *Cyclanthera pedata*, and *Passiflora gracilis* are especially sensitive, the tendril of the first-named plant being perceptibly stimulated by the contact of a thread of cotton weighing 0·00025 of a milligram laid upon the tendril[3]. The tendril is therefore more sensitive than the human skin, which receives no impression when a thread of this weight moves gently upon it[4]. A worsted thread of 1 to 10 mgm. weight stimulates the less sensitive tendrils as well as many irritable petioles, but a stronger stimulus is required for the tendrils of *Vitis*. A bamboo fibre 1 mm. diameter and weighing 0·1 gram is just able to produce a curvature and slight but perceptible thickening in the pulvinar tendril of *Dalbergia linga* and in the hook tendril of *Strychnos*,

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[1] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. I, p. 483. A detailed list of cases in which contact irritability has been established is given here. This form of irritability was later detected by Peirce (l. c., p. 66) in *Cuscuta*, and by Ewart (l. c., pp. 196, 203) in the irritable hooks of tropical climbers, although in these the stresses and strains set up in the attached hook influence the ultimate amount of thickening.

[2] Pfeffer, l. c., p. 495.

[3] Id., l. c., p. 506; Darwin, l. c., pp. 110, 131, 405; Climbing Plants, 1875, pp. 153, 171, 197.

[4] Exact determination is difficult, since the excitation depends upon the extent of surface in contact, the degree of roughness, and the rapidity of movement. Cf. Frey u. Kiesow, Zeitschr. f. Psychologie u. Physiologie der Sinnesorgane, 1899, Bd. XX, p. 153. Kemmler (Hermann's Handbuch d. Physiologie, 1888, Bd. III, Kap. 2, p. 325) states that the minimal stimulus for sensitive skin is that due to the gentle movement of a weight of 0·002 of a milligram.

whereas a piece of wood less than 2 mm. diameter and 0·1 gram weight acts as a sub-minimal stimulus to *Bauhinia tomentosa*. The irritable hooks of *Uncaria*, *Artabotrys*, and *Roucheria* require the attachment of weights of 100 to 1,000 milligrams according to whether a rough bamboo fibre or hard twine, or a smooth copper wire or glass thread is used[1]. The most sensitive tendrils may curve five to twenty seconds after stimulation, whereas less sensitive ones may take one or more hours to respond perceptibly[2]. The tendrils of *Dalbergia linga* begin to curve in five minutes, those of *Vitis discolor* in one hour, those of *Strychnos* in twelve hours, the root-tendrils of *Vanilla planifolia* in twenty-four hours, whereas no increase of thickness resulting from stimulation can be detected until after the lapse of one or more days[3].

The stimulus usually needs to act for some time to produce a response, but in very sensitive tendrils a single strong contact is sufficient to produce a slight curvature. This as well as more pronounced curvature is followed by a straightening due to orthotropism if the contact stimulus no longer acts[4]. Since the tendril remains irritable, Darwin was able to stimulate the tendril of *Passiflora gracilis* twenty-one times in fifty-four hours, each time the tendril being allowed to straighten after forming a hook-like curvature.

When a weak continuous stimulus is applied, the tendril first bends beyond the ultimate curvature resulting from the antagonism between its orthotropism and the applied stimulus[5]. Although we may say that the tendril accommodates itself to the stimulus, it is not certain whether this is due to the gradual awakening of opposing reactions, or to the decrease of the excitability, or to a combination of factors. No decisive conclusion can be made from the fact that the satisfaction of the contact irritability of *Cuscuta* produces a periodic inhibition of this irritability.

The minimal stimulus needs to be surpassed in order to cause the tendril to coil completely around the support, and to maintain the coiling until growth has ceased and the coils are permanent. The stimulus exercised by a support is usually sufficient for this, and in fact slender sensitive tendrils are able to form close coils around a thin thread. The less sensitive and thicker tendrils of *Vitis*[6] are, however, only able to form loose coils around supports less than 2 or 3 mm. diameter, while the hooks of tropical climbers are usually unable to become firmly attached to

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[1] Ewart, l. c., pp. 211, 223, 231.

[2] Darwin, l. c., p. 172; Pfeffer, l. c., p. 486; Müller, l. c., p. 109.

[3] Ewart, l. c., pp. 209, 223, 229, 236.

[4] Darwin, l. c.; de Vries, Arb. d. bot. Inst. in Würzburg, 1873, Bd. 1, p. 306; Fitting, l. c., p. 611. This straightening was first observed by Gray, Edinburgh New Phil. Journ., 1859, Vol. x, p. 307.

[5] Pfeffer, l. c., p. 507; Darwin, l. c., p. 132.

[6] Sachs, Lehrb. d. Bot., 4. Aufl., p. 872; de Vries, l. c., p. 307.

supports of less than 3 to 5 mm. diameter, and the hooks of *Strychnos* and *Roucheria* are unable to coil around supports more than 7 to 10 mm. diameter[1]. The less actively curving and less irritable tendrils are unable to apply themselves closely to the sides of a flattened support, whereas a thin sensitive tendril may come into close contact with both sides of a thin strip of sheet zinc[2]. If the tendril undergoes secondary growth on attachment, the coils of thick tendrils often become extremely closely applied even to irregular supports[3].

Similarly, if a tendril strives to tighten its coils it may exert pressure upon the support, and either roll up a leaf around which coiling has occurred or diminish the diameter of a paper cylinder slit along one side[4]. Hence, on withdrawing a solid support, the coils usually tend to narrow, and de Vries found that a tendril of the cucumber which had formed five and a half coils around a support 6 mm. thick showed eight narrower coils when the support was removed.

When a tendril is in contact at one point only, the main curvature is produced here, but the stimulus is perceptibly propagated in both directions to a distance of 5 to 10 millimetres[5]. Similarly, the secondary thickening which tropical tendrils such as those of *Bauhinia* and *Strychnos* undergo takes place mainly at the point of contact, the effect of the stimulus ceasing to be perceptible at a distance of 1 to 3 cms.[6] The continued curvature of the tendril usually brings fresh acropetal surfaces in contact with the support until the whole terminal portion has coiled. The same tendency to coil takes place basipetally, but is prevented by the tension existing in the free portion between the plant and the support. If the tendril is allowed to coil around a light paper shell a few coils may be formed basipetally from the original point of contact, and this causes the shell to be drawn towards the plant.

Tendrils may not only coil around horizontal supports or loose objects, but may coil in different directions, so that either left- or right-hand coiling may be shown by the tendrils of the same plant[7]. The coils are usually somewhat inclined, and though near together are not superimposed. Tendrils are unable to coil around thick supports, since, if the stimulated part cannot form a sufficient curvature, it is drawn away by the old-age coiling[8]. By the aid of this coiling long tendrils may sometimes succeed

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[1] Ewart, l. c., pp. 189, 214.

[2] Mohl, Ranken- u. Schlingpflanzen, 1827, p. 82.

[3] Ewart, l. c.

[4] Mohl, l. c., p. 63; de Vries, l. c., p. 307. Cf. Macdougal, Ber. d. bot. Ges., 1896, p. 153.

[5] De Vries, Arb. d. bot. Inst. in Würzburg, 1873, Bd. 1, p. 304; Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. 1, p. 509; Fitting, l. c. On petiole-climbers cf. Derschau, Einfluss von Contact u. Zug auf rankende Blattstiele, 1893, p. 13.

[6] Ewart, l. c., pp. 208, 223.

[7] Cf. de Vries, l. c., p. 307.

[8] Mohl, l. c., pp. 80, 142.

in attaching themselves to flat or irregular supports, of as much as 3 or 4 cms. diameter if these are in close proximity.

The contact not only produces the attachment to the support and accelerates the coiling but also induces an increase in the strength of the tendril, and in some cases the formation of special growths such as suckers. It is, however, uncertain whether the increase of strength by lignification, or by secondary growth where this occurs, is directly due to the stimulus of contact or is the result of the mechanical demands made upon the attaching organs. A decision is by no means easy, since an increase of pressure at the point of contact not only increases the contact-stimulus but also the mechanical demands made upon the organ, and, further, the stimulus of contact may be transmitted some distance away from the directly stimulated area. It seems indeed that both factors enter into play, for Ewart observed a slight thickening in hook-tendrils allowed to pull against gelatine-covered rods where little or no stimulus of contact could be exercised, and observed in other cases a thickening caused by contact without any appreciable strain being set up in the organ, and that where a tendril was in contact with two supports the thickening was mainly shown at the points in contact and not in the region between[1]; similarly Derschau found that the petiole of a leaf-climber exhibited a slight secondary thickening after temporary contact with a support too light to exert any appreciable stress upon the petiole[2].

Hegler's statement that tension in general increases the strength of ordinary stems is incorrect, for Ball[3], under similar conditions, and in part with the same plants as those used by Hegler, observed in no case any perceptible increase in the tensile strength. It is possible that positive results may be gained with other plants, but further experiment is necessary to determine whether the increase in the tensile strength of attached tendrils without any secondary growth is due to the stimulus of tension, of contact, or to other causes.

The acceleration of the ultimate coiling of the tendril due to contact is sometimes very pronounced. Thus Darwin found that an attached tendril of *Passiflora quadrangularis* coiled as much in two days as an unattached one in twelve. The tendrils of *Vitis vinifera*, *Ampelopsis hederacea* (*quinquefolia*), and of various species of *Cissus*, only coil when in contact with a support[4]. The same applies to the hook tendrils of *Strychnos* and to the branches of the tendril of *Amphilobium mutisii* which are thrown off in the absence of a contact-stimulus[5].

The coiling of a free tendril usually begins when growth is reduced to

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[1] Ewart, l. c., pp. 193, 215, 222, 227.

[2] Derschau, l. c., p. 30.

[3] Jahrb. f. wiss. Bot., 1903, Bd. XXXIX, p. 305.

[4] Darwin, l. c., p. 125; v. Lengerken, Bot. Ztg., 1885, p. 360; Schenck, l. c., p. 145.

[5] Ewart, l. c., pp. 208, 218.

a minimum, so that the accelerating of coiling produced by contact may be connected with the retardation of growth which usually ensues[1]. This is presumably the result of the correlative stimuli awakened by contact and not of the mechanical tension exercised on the attached tendril. Tension appears usually to slightly retard growth in length, but subsequently to accelerate it. That a free tendril should coil all one way, but that the free portion of an attached one should form two or more reversed spirals is the natural result of the same attempt at coiling combined in the second case with the fixation of the ends of the tendrils[2]. Similar results may be obtained when longitudinal strips of the peduncle of *Taraxacum* which tend to coil spirally are held at both ends, or when a cord attached at both ends is twisted in opposite directions at two points equidistant from its ends[3].

The production of the suckers of *Ampelopsis* and *Amphilobium*, of the haustoria of *Cuscuta*, as well as the thickening of certain tendrils and attaching hooks and of the petioles of leaf-climbers, are undoubtedly due in the first instance to the stimulus of contact. The thickening only attains its full development when permanent contact is assured and when the attaching organ is subjected to increasing tension. The increased pressure at first increases the contact-stimulation but finally retards or inhibits the growth on the applied surface, which usually becomes more or less flattened when the pressure is considerable[4]. The hooks of tropical climbers may attain a considerable increase of strength, in this way their breaking strain often increasing four- or ten-fold, so that they are able to bear weights of 10 to 15 kilogrammes[5]. The same takes place in the tendrils of *Amphilobium* and *Bauhinia* which undergo secondary thickening, while according to Worgitzky[6] the attached lignified tendrils of *Cucurbita* and *Passiflora* become from two to twelve times stronger than unattached ones.

It is uncertain whether it is the absence of a contact-stimulus or of tension which is responsible for the smallness, shrivelling, death, or abscission of the unattached tendrils of certain plants. This was observed by Darwin on the tendril of *Ampelopsis hederacea* (*quinquefolia*) and *Bignonia Tweediana*, by Müller on that of *Cyclanthera pedata*, by Leclerc du Sablon on leaf-tips of *Flagellaria indica*, and by Ewart on the tendrils of *Amphilobium mutisii*[7].

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[1] Fitting, Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, pp. 550, 608. This coiling is associated with a single slight acceleration of growth.

[2] Correctly interpreted by Mohl, l. c., p. 79, and Darwin, l. c., p. 127.

[3] Noll, Flora, 1899, p. 388.

[4] Derschau, l. c., p. 33; Ewart, l. c., pp. 140, 189.

[5] Ewart, l. c., pp. 194, 208.

[6] Worgitzky, Flora, 1887, p. 40. On the tensions to which tendrils are exposed cf. Macdougal, Ber. d. bot. Ges., 1896, p. 153.

[7] Darwin, l. c., pp. 69, 113, 355; v. Lengerken, l. c., p. 360; Müller, Cohn's Beitr. z. Biologie, 1887, Bd. IV, p. 108; Ewart, l. c., p. 219; Leclerc du Sablon, Ann. sci. nat., 1887, 7e sér., T. V, p. 28. The attachment of the coiling portion of the leaf of *Nepenthes* favours the development of the pitcher according to Goebel, Pflanzenbiol. Schilderungen, 1891, II, p. 98.

If two of the branches of the trifid tendril of this plant become attached the other one usually persists also, but remains thinner and slightly shorter than the attached ones.

On the other hand the coiling of the long pulvinus of the terminal pair of leaf-segments of *Dalbergia linga* around a support often leads to the leaflets being thrown off, but this may also occur spontaneously without apparent cause[1].

SECTION 13. **The Influence of Contact upon the Growth and Curvature of Tendrils.**

Since we are dealing with growth-curvatures it is only natural that a response should only be possible in organisms still capable of growth, or in which the stimulus reawakens the power of growth. This applies not only to the curvature of tendrils but also to the haustoria, sucking-disks, and the coiling part of a petiole-climber in which the stimulus of contact excites renewed growth or awakens a special form of productive activity.

According to Fitting the growth of a curving tendril undergoes a pronounced but temporary acceleration persisting during the reaction[2]. This acceleration is especially great when the curvature is rapid, for the median axis may elongate 20 to 100 times, and the convex side 40 to 200 times as rapidly as before stimulation, and also after its effect has passed away. After transitory stimulation the concave side, which either retains the same length or only slightly shortens, begins to grow more actively, and since the convex side has now ceased to elongate, the tendril soon straightens. Similar results were obtained by Fitting with rapidly and

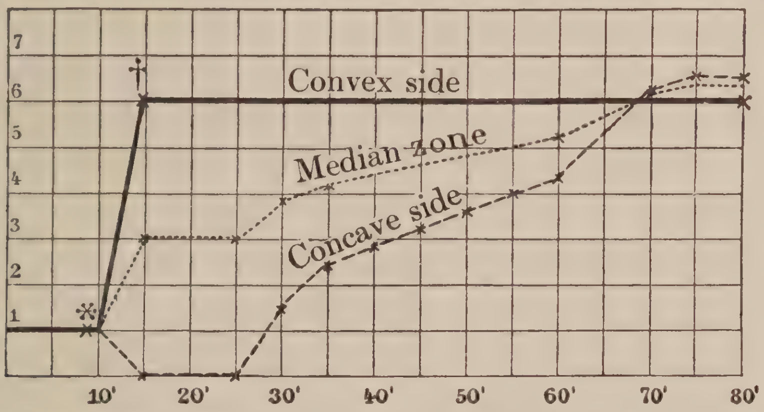

FIG. 18. Curves representing the growth of the convex and concave sides of the tendril of *Pilogyne suavis* after stimulation at *. The curve for the median axis is taken as the mean between those for the concave and convex sides. The horizontal distances give the times in minutes, the vertical distances (1 division = 0·0121 mm.) the growth as indicated by the divisions marked on the tendril previously to stimulation, and which had remained the same distance apart during the previous 20 minutes. (After Fitting.)

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[1] Ewart, l. c., p. 228.

[2] These studies, temporarily interrupted by the untimely death of Ockel, who began them at Pfeffer's instigation, were completed by Fitting, Ber. d. bot. Ges., 1902, p. 373; Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 545.

slowly growing tendrils as well as with those which are irritable on all sides and on one side only[1]. In Fig. 18, curves representing the growth of the different regions of a tendril of *Pilogyne suavis* are given which five minutes after stimulation had curved into an arc of 5 mm. radius. Similar curves were obtained by using marks placed on the sides of the tendrils to determine the elongation of the convex side[2].

Although the exact mode of production of these changes in the rate of growth is uncertain they are undoubtedly the result of the action of the contact-stimulus, and this also applies to the subsequent acceleration of growth in the concave side which causes the tendril to straighten after temporary contact, although it is only an indirect result of the contact stimulation. Fitting[3] found that the accelerations of growth and the tendencies to curvature followed in the same order when curvature was rendered mechanically impossible, so that a realized curvature is not necessary for the production of the secondary acceleration of growth on the concave side. The changes of the tissue-strains produced by the attempted curvatures might, however, act as the exciting cause to the secondary response, for if the tendril is kept straight the growth of the convex side will tend to stretch the concave one. This is shown by the fact that the tendril immediately curves when released, until the concave side is slightly or not at all compressed.

A realized curvature does, however, excite a compensating reaction tending to produce straightening, as is shown by the fact that a tendril to which a plastic curvature is forcibly imparted, has its growth accelerated on the concave side so that it gradually straightens again[4].

It is evident that a chain of reactions is necessary in both radial and dorsiventral tendrils, since the primary acceleration of growth occurs not on the stimulated but on the non-stimulated side. Furthermore, as Fitting[5] found, no curvature occurs if the tendril is rubbed equally strongly on opposite sides or around a circular zone. This applies to both radial and dorsiventral tendrils, neither a curvature nor any acceleration of growth being shown. Contact applied to the convex surface of the tendril of *Strychnos* and of *Bauhinia* is, however, unable to prevent coiling around a support in contact with the concave surface[6]. When the opposed stimuli produce no response it is evident that they are still perceived but mutually antagonize so that no reaction is awakened. The convex surface of many

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[1] Trzebinski (Bull. de l'Acad. de Cracovie, 1902, p. 123) observed that contact produced disturbances in the rapidity of growth of the sporophore and sporangium of *Phycomyces nitens*, but no details are given as to the mode of application of the contact stimulus.

[2] [These observations of Fitting's corroborate the original views of Sachs, Textbook of Botany, 1875, p. 779.]

[3] L. c., p. 588.

[4] Id., pp. 557, 582.

[5] L. c., p. 582.

[6] Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, Vol. XV, pp. 208 seq.

dorsiventral tendrils, though unable when stimulated to produce a curvature, is nevertheless sufficiently irritable to be able to inhibit a response to contact on the concave side, and this action is awakened by contact with a rough surface but not by contact with smooth moist gelatine.

Presumably the compensation begins during perception, so that no attempt at curvature is ever awakened. It is also possible that the two excitations might act simultaneously, but that the power of response might be temporarily lost, or that some essential connecting link between perception and response should be suppressed. The former is however improbable. Fitting[1] observed that the curvatures produced by a change of temperature or by removing the tip of the tendril are inhibited when the back of a dorsiventral tendril is rubbed, and this fact may when further investigated lead to an explanation of the phenomena mentioned. Since this inhibitory action is largely localized, it is possible to keep a portion of a tendril straight while the remainder is performing a thigmotropic, thermonastic or traumotropic curvature.

Continuous contact causes complete and permanent coiling, the continuation of the coiling involving exactly the same stimulatory reaction as is produced by temporary contact. According to Fitting[2] prolonged contact rapidly induces a complete cessation of growth, so that the acceleration of growth on the concave side which produces straightening after temporary contact no longer occurs. Evidently, therefore, the reactions leading to this secondary response are inhibited by continued contact. This applies only when permanent contact is assured, and in fact even sensitive tendrils only partially raise themselves from the support during coiling, partly as the result of accommodation, of orthotropism or of irregularities in the support. Since the free portions usually again come into contact with the support, continue to coil and show an acceleration of growth, they must retain the power of growth for some time. In this way aided by the tendency to curvature of the uncoiled basal portion, the tendril is often able to creep over the surface of a support and increase the number of coils, as was first observed by Darwin[3].

Sachs concluded that changes in the rate of growth on the different sides of the tendril were responsible for its curvature, and this has been confirmed by Fitting. The curvature is therefore not due, as certain authors have assumed, to an active contraction of the concave side[4]. The measurements made by de Vries[5], although not extremely accurate, pointed against this conclusion, but since they were taken after

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[1] L. c., p. 562.

[2] L. c., p. 609.

[3] Climbing Plants, 1875.

[4] Id., 1875, p. 180; Macdougal, Ber. d. bot. Ges., 1896, p. 151; Annals of Botany, 1896, Vol. X, p. 399; Torrey Botanical Club, 1898, Vol. XXV, p. 69. Cf. Fitting, l. c., p. 565; Sachs, Textbook of Botany, 1875, p. 779.

[5] De Vries, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 309.

the completion of the curvature, they failed to reveal the acceleration of growth on the convex side.

De Vries[1] erroneously supposed that contact stimulation produced a rise of turgor in the side becoming convex, the cells of which experienced an elastic stretching, which was subsequently made permanent by growth. The fact that contact accelerates growth is readily shown in slowly-coiling tendrils like those of *Strychnos* and *Bauhinia*, while attached tendrils of *Amphilobium mutisii* usually become about one-sixth longer than unattached ones[2]. Hence the straightening of the curvature produced when the tendril is placed in hot water, or in alcohol and then in water, is not greater than that which other curved objects experience when similarly treated, and it is due to the result of the liberation of the tissue-strains[3]. No straightening at all occurs when a curvature is slowly produced, and sometimes not even when it rapidly follows contact[4].

De Vries erroneously assumed that the straightening of the tendril in strong saline solutions afforded a complete proof of his theory. As a matter of fact the salt solution penetrates so slowly that plasmolysis is only produced after some hours, and in the meantime the continued growth of the tendril causes it to straighten in the usual manner[5].

It is not certain here, any more than in other cases, how the growth of the tendril is produced during curvature. The fact that the cell-walls of tendrils are readily stretched beyond their limit of elasticity affords no proof of their plastic growth[6]. In any case, however, the plastic stretching of the cell-walls would need to be preceded by a preparatory softening physiological action, since the curvature ceases in the absence of oxygen. Regulation would also be necessary if the contact induced a rise of turgor, but the latter is not necessary and has not been proved to exist.

Historical. Our detailed knowledge of tendrils begins with Palm's work in 1827, and also with that of Mohl, who detected the irritability to contact and observed the acceleration of the coiling of the unattached portion produced by contact, but erroneously regarded twining as being due to contact irritability. After Dutrochet[7] had added a few facts our knowledge of climbing plants in general was greatly extended by Darwin. Further additions were made by de Vries and by the other authors mentioned, while Pfeffer explained the inherent character of the sense perception underlying thigmotropic irritability. Sachs showed that the curvature of tendrils was the result of growth, and the fact that the coiling of slowly growing tendrils and tendril-hooks was also the result of growth, and that contact stimulated the growth in length of tendrils was shown by Ewart (1898), while Fitting (1903) studied the mechanics of the growth-curvature of the more irritable tendrils in detail, and determined the changes in the rate of growth which produce curvature and straightening.

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[1] De Vries, Bot. Ztg., 1879, p. 835; Landw. Jahrb., 1880, p. 509. A similar conclusion is given by Leclerc du Sablon, Ann. sci. nat., 1887, 7e sér., T. XXV, p. 38. De Vries attempted to explain the changes in the rate of growth involved in other movements in the same way.

[2] Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, Vol. XV, pp. 208, 218.

[3] Fitting, l. c., 1903, p. 598.

[4] Ewart, l. c., pp. 210, 219, 221, 229, 236.

[5] Fitting, l. c., p. 595.

[6] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. I, p. 489.

[7] Dutrochet, Ann. sci. nat., 1844, 3e sér., T. II, p. 156.

PART III

MOVEMENTS PRODUCED BY MECHANICAL AND CHEMICAL STIMULI

SECTION 14. **The Irritability to Contact and to Mechanical Shocks.**

Mechanical agencies, such as pressure, blows, or shaking, produce movements in many cases, including the pronounced variation movements shown by plants possessing motile pulvini, as in the Papilionaceae, Mimoseae, and Oxalidaceae. (Cf. Figs. 19–24.) The response to stimulation is especially rapid in the leaves of *Mimosa pudica*, and of *Desmanthus plenus*. The leaves of the first-named plant rapidly pass from the unstimulated (Fig. 19, *A*) to the stimulated condition (Fig. 19, *B*) when

FIG. 19. Stem and leaves of *Mimosa pudica*. The leaf *A* is fully expanded, whereas the leaf *B* has been stimulated; *p* = primary pulvinus, *s* = secondary pulvini; the tertiary pulvini at the bases of the leaflets are not shown.

the plant is shaken, the main petiole sinking, the secondary petioles becoming less spreading, and the leaflets folding up in pairs. If the tip of a single leaflet is cut off, the stimulus first affects its pulvinus, but then spreads down the leaf-segments, the leaflets folding up in pairs, and then to the other segments and to the main pulvinus until the whole leaf is in the stimulated condition. The leaves of *Biophytum sensitivum* also respond readily, whereas repeated strong shaking is necessary to produce a complete sinking of the leaves of *Oxalis acetosella* (Fig. 20). The leaflets of *Robinia pseudacacia* are still less sensitive, and the strongest shaking only produces a slight movement in the leaflets of *Acacia lophantha*, although in the Tropics the sensitiveness may approach that of *Mimosa*[1].

The power of response varies much among the stamens of different Cynareae, those of *Centaurea jacea* and *Cynara scolymus* suddenly drawing together when stimulated by contact and at the same time becoming 10 to 30 per cent. shorter. The similar movement of all five filaments pulls down the anther tube in which the pollen lies and causes the style to push out pollen and protrude at the apex. In this case stimulation produces a shortening as in a muscle, but when the active tissue is appropriately joined to inactive or elastic tissue a curvature may be produced as in *Mimosa*. The active region need not always be swollen like a pulvinus, and indeed the irritable stamens of Berberidaceae (Fig. 22), of Cistaceae, and of *Sparmannia*, as well as the stigmas of *Mimulus*

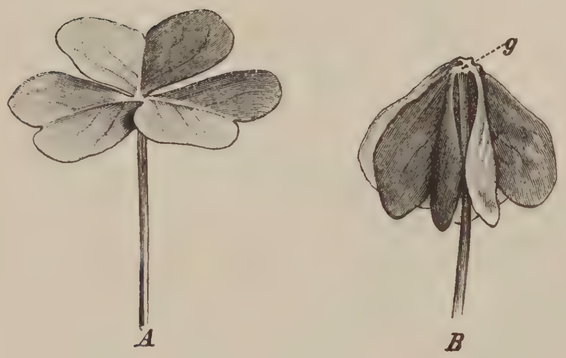

FIG. 20. Trifoliate leaf of *Oxalis acetosella*. *A*, unstimulated; *B*, after repeated strong shaking. The pulvini are shown at *g*.

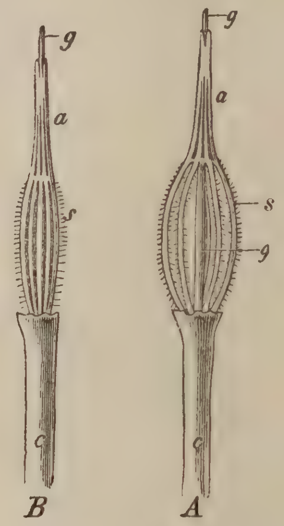

FIG. 21. Flower of *Centaurea jacea* after the removal of the corolla. The stamens are shown at *A* in the unstimulated, at *B* in the stimulated condition (magnified). *c* = corolla tube; *s* = filaments; *a* = anther tube; *g* = stigma.

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[1] Ewart, Annals of Botany, 1897, Vol. XI, p. 455.

(Fig. 23), of *Martynia* and of *Bignonia* show no external structural sign of their power of rapid movement on stimulation. Furthermore the sudden closure of the leaf of *Dionaea muscipula* (Fig. 24) and of *Aldrovanda* is produced by the influence of contact acting on the midrib and lamina.

In all these cases the responding organ is also the percipient one, but in *Masdevallia muscosa*, according to Oliver, the movement of the labellum is produced by touching the neighbouring part of the flower and not by touching the motile zone[1].

The above-named plants respond to any sufficiently intense mechanical shock or disturbance, whether produced by wind, rain, contact with solid bodies, or vibrations propagated through the soil. They may hence be said to possess a seismonic irritability as distinguished from the sense of touch (contact or thigmotropic irritability) shown by tendrils, by certain algae and fungi, as well as by the tentacles of *Drosera*. In these cases a response is produced only by contact with a solid body, whereas the strongest bending or shaking caused by wind, water, or the impact of a thread of mercury, as well as rubbing with a wet rod covered with 10 or 15 per cent. gelatine, fail to awaken any irritable response. At the same time sensitive tendrils respond to the lightest contact with a solid body, such as fails to awaken any response in the highly irritable leaflets of *Mimosa*. The tentacles of *Drosera* are almost as sensitive as tendrils, the head of the tentacle perceiving the stimulus to which the stalk responds by bending[2].

FIG. 22. A flower of *Berberis vulgaris* after the removal of the anterior petals and stamens (magnified). The stamen (*a*) is unstimulated, but contact has caused the stamen (*b*) to curve over and apply itself to the stigma (*g*).

FIG. 23. Longitudinal sections of the flower of *Mimulus luteus*. In *A* the stigmas (*n*) are unstimulated, in *B* a touch has caused them to close together.

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[1] Oliver, Annals of Botany, 1888, Vol. 1, p. 244.

[2] For details see Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. 1, p. 483.

By means of rubbing with a wet rod covered with gelatine, and with an ordinary wooden one, it can easily be determined whether an organ shows contact or seismonic irritability, for we are dealing here with as distinct types of irritability as in the geotropism or heliotropism of a root or stem. The distinction would still be justified even if subsequently the two forms of irritability should be found to be closely related, for we are dealing here with collective terms for types of response varying as regards their character and mode of production. Since, however, the distinction is primarily based upon the perception or non-perception of the exciting agency, it is immaterial whether the response is rapid or slow, and whether it takes the form of a curvature, of a secondary thickening, or of a production of haustoria or other attaching organs.

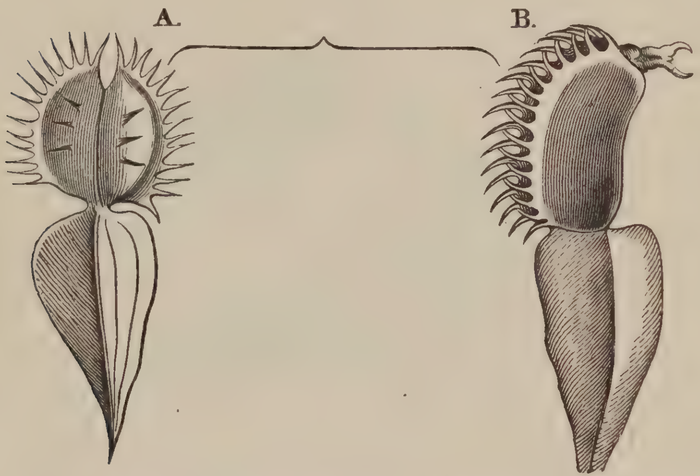

FIG. 24. Leaves of *Dionaea muscipula*, *A* unstimulated and showing the three sensitive hairs on each leaf-lobe, *B* stimulated leaf which has closed and captured an earwig.

Although the details of the mode of perception are still unexplained, it is impossible to deny that the sensation of contact is produced under similar conditions in both plants and animals[1]. In both cases a stimulation is only exercised when unequal pressure is exerted at different points, so that local variations of pressure are produced. It is not the statical pressure but the rubbing against the solid body which acts as a stimulus, but changing local variations of pressure produced without lateral movement may also act as an excitation, as in the hooks of tropical climbers, or when a weighted cork stuck full of pins is allowed to rest upon the skin and its centre of gravity laterally displaced. A tickling sensation

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[1] Cf. Pfeffer, l. c., p. 499. On the sensation of contact in man cf. Tigerstedt, Physiologie d. Menschen, 1898, Bd. II, p. 71; Frey u. Kiesow, Zeitschr. f. Psychologie und Physiol. d. Sinnesorgane, 1899, Bd. XX, p. 126. In plants direct contact with the cell-wall is necessary, and hence no stimulus is exercised when direct contact is prevented by the interposition of a layer of gelatine or mucilage. Cf. Pfeffer, l. c., p. 513.

[The anatomical studies of Haberlandt (Sinnesorgane im Pflanzenreich, 1901, p. 117) have brought nothing essentially new to light. The statement (l. c., p. 122) that only a tangential stretching of the ectoplasmic membrane of the protoplasm is capable of producing an excitation is not supported by the facts. Thus sudden and pronounced curvatures produced by the aid of gelatine-covered rods do not exercise any stimulating action on tendrils, whereas the gentle movement of a thread weighing 0·00025 of a milligram does so and can obviously produce only a minimal amount of tangential stretching. The fact that sharp local inward bending of the outwardly curving epidermal walls may produce a stimulatory response has already been pointed out by Pfeffer.]

is awakened in the epidermis of man and of tendrils by weak induction shocks, and furthermore, rubbing against a rough body acts in both cases as a stronger excitation than rubbing with similar pressure against a smooth one. In general the intensity of the excitation depends upon the amount of surface in contact, upon the magnitude of the local variations of pressure, and upon the rapidity with which they alter. The determination of the numerical relations between these factors and the strength of the excitation affords, however, no explanation of the actual nature of the sensation of contact.

In any case the deformations produced by varying local pressure in the outer cell-walls of the epidermis create the conditions for an excitation of the irritable protoplasm, which does not come into contact with the object exercising pressure any more than in the case of the touch-corpuscles in the skin of animals. The structure of the cell and cell-wall may therefore aid considerably in the perception of the stimulus, although an excitation is only possible when the protoplasm is endowed with this special form of irritability. The pits which occur in the outer walls of the epidermis in the tendrils of Cucurbitaceae and a few other plants undoubtedly act in this way. Since, however, similar pits are present in the non-sensitive portion of the tendril of *Bryonia*, it is evident that their presence does not confer this special form of irritability upon the protoplasm of all cells possessing them. Furthermore no pits are present in the epidermal walls of the very sensitive tendrils of *Passiflora* and *Cobaea*[1], and in some motile organisms only a portion of the cilia are sensitive to contact, although here the sensitive protoplasmic organs come into direct contact with foreign bodies.

It is, however, uncertain whether differences of pressure in the protoplasm act as the exciting stimuli, and also whether the entire protoplasm or only the peripheral membrane, or only portions of the latter are able to perceive contact stimuli. Even in the latter case, however, it is hardly to be expected that so high a differentiation should be reached as in the Pacinian or touch-corpuscles of vertebrate animals. A knowledge of the nature and position of the percipient organs does not, however, reveal the mode of perception of the stimulus.

An organ having seismonic irritability responds to every variation of pressure if sufficiently intense, quite independently of its origin. Certain highly sensitive plants even respond to sudden variations in the atmospheric pressure, or to sudden changes of temperature, or to rapid alterations of transpiration and to the resulting water-currents[2]. The stimulus may

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[1] Pfeffer, l. c., p. 524. Haberlandt, Physiol. Anat., 2. Aufl., 1896, p. 478; Haberlandt, Sinnesorgane im Pflanzenreich, 1901, p. 126; Strasburger, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 515.

[2] Long known in the case of *Mimosa pudica*. Munk (Die elektrischen- und Bewegungserscheinungen am Blatte von *Dionaea*, 1876, p. 105) observed that a sudden increase of transpiration acted

apparently be perceived in the internal living cells as well as in the peripheral ones, and possibly many plants may exist in which the epidermal cells are quite insensitive to seismonic stimulation. Even in the case of tendrils it is uncertain whether the subjacent cortex is able to perceive contact-stimuli as well as the epidermis, or whether the latter only has this special form of irritability. A contact-stimulus may easily be localized in the epidermal cells as regards its application, but a blow or shaking almost unavoidably affects the cortical cells as well as the epidermis. In every case the change of pressure must be rapid even though transitory, for statical pressure as well as gradual changes of pressure or tension are inoperative as stimuli. In this respect seismonic irritability agrees with contact-irritability, which requires for its excitation special pressure relationships. Hence it is hardly surprising that tendrils should not be stimulated by the strongest bending or twisting, so long as the latter fail to produce the localized pressure-gradients required for excitation.

Both seismonic and contact irritability may, like geotropism and heliotropism, be developed in the same organ, and this may possibly be the case in the leaf of *Dionaea muscipula*. The flaccidity and the transitory disturbances of growth produced by mechanical agencies may be regarded as the result of seismonic stimulation, and in this sense this special form of irritability is possessed to a limited degree by all growing organs including tendrils. It is difficult to decide whether *Mimosa pudica* has a feeble contact-irritability, since every mechanical agency of any intensity excites the usual seismonic response.

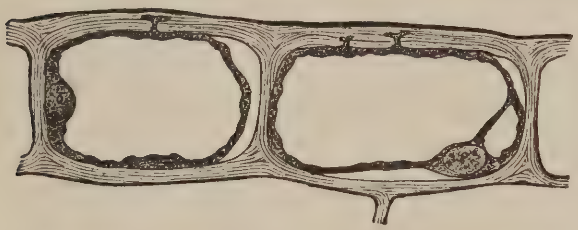

FIG. 25. Epidermal cells from a longitudinal section of the tendril of *Cucumis sativus*, showing the pits in the outer walls.

Mechanical agencies probably awaken more or less feeble reactions in all plants, and it has already been mentioned that in addition to the special seismonic irritability, other forms of sensitivity to mechanical agencies may be developed. Indeed, all stimulation resulting from movements of water, or from other forms of movement in the plant, may be termed mechanical, while if geotropic irritability is awakened by the changes in the position of the denser particles of the cell it becomes closely related in character to a form of internal contact-irritability. The manner in which currents of water exercise a rheotropic stimulus is quite uncertain, but it also is probably akin to a form of contact-stimulation.

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as a stimulus to the leaf of *Dionaea muscipula*. [The streaming-cells of *Chara* and *Nitella* possess very pronounced seismonic irritability, although here the response is not a movement but a cessation of movement. Less pronounced seismonic irritability is shown by streaming-cells in general. Cf. Ewart, Protoplasmic Streaming in Plants, 1903, p. 72.]

The shape and relationships of the cell and cell-wall, as well as the way in which the cells are joined and arranged in the tissues, may render the perception of the stimulus more readily possible at particular points, but do not produce this special form of irritability. The production and activity of the response are, however, dependent in a much greater degree upon the structure of the organ, but the primary perception always takes place in the sensitive protoplasm. The impermeability of the cell-wall or of an intervening tissue may render it difficult or impossible for a substance to exert any chemical stimulation, or may restrict its action largely or entirely to those points where the substance is able to penetrate. Differences in the transparency of the tissues must act in the same way in regard to light stimuli, and hence it arises that a seedling performs a heliotropic curvature in diffuse light if one side is covered with indian ink. Similarly the presence of thick walls, or of resistant tissues, may render the sensitive cells beneath less responsive or not responsive at all to blows or pressure. Furthermore, the arrangement of the tissues may be such that pressure and tension exercise different stimulatory actions, or may cause contact at a particular region to produce a response especially readily as in the case of the sensitive hairs of *Dionaea*. This is probably because pressure at these points is more readily transmitted to the sensitive cells beneath [1]. The best knowledge of the structure of an irritable organ will not reveal the nature of irritability, and in fact organs with a pronounced similarity of structure may possess widely dissimilar irritabilities, while the same sensitivity may be shown by organs differing widely in structure. Furthermore, various special irritabilities may reside in cells and tissues which differ in no anatomical features from ordinary indifferent cells and tissues [2]. It is also easy to see that the coarser anatomical structure can more readily favour the perception of mechanical stimuli, than of thermal or photic stimuli; and the observed facts bear out this conclusion. It must, however, be remembered that the mere enumeration of all the observed cases in which the anatomical structure shows a biological adaptation for the reception of stimuli leads one to attach undue importance to structure, and as a matter of fact in most cases the structure shows no perceptible adaptation for sensory perception. In any case physiology is only concerned with structure in so far as it affects functional activity [3].

SECTION 15 (*continued*).

Since the distinction between seismonic and contact irritability is purely a matter of special sensitivity, it remains an open question whether both forms of stimuli involve similar or dissimilar primary reactions. Seismonic stimulation usually produces variation movements, but contact-

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[1] The first interactions may be purely physical or chemical, and may act as a preparation for the subsequent physiological perception. When purely mechanical transmission is performed by hairs or the like, Haberlandt (Sinnesorgane im Pflanzenreich, 1901, p. 9) terms the intermediary structures 'stimulators.'

[2] All cells and organs capable of perceiving stimuli may be termed sense-organs, whether they show any special anatomical structure or not.

[3] On problems of this kind see Haberlandt, l. c., 1901.

stimulation growth curvatures. The closure of the leaf of *Dionaea*, however, due to seismonic stimulation is partly produced by growth[1]. On the other hand, the disturbances of growth in growing shoots produced by shaking are to be regarded as the result of seismonic stimulation. Although at present only nutation curvatures are known to result from contact-stimulation, it is hardly to be expected that the potential powers of the plant should find expression in this direction alone, and in fact we have in the secondary thickening of the hooks and tendrils of many tropical climbers induced by contact a special response which may or may not be accompanied by curvature. Furthermore, the movements produced in the cilia of certain organisms by contact-stimuli are not due to growth, but are the result of contractility, just as the movements of an animal produced by a tickling sensation are due to muscular contraction.

In regard to sensitivity, the duration of the latent period, and the rapidity of the reaction, no definite line of demarcation can be drawn between seismonic and contact-stimulation. It is true that the latter never produces so rapid a reaction as occurs in the leaf of *Mimosa pudica*, in which under favourable conditions the latent period may be less than a second, while the sinking of the primary petiole and the folding of a pair of leaflets may be performed in two to five seconds. The stamens of *Centaurea jacea* and the leaves of *Dionaea muscipula* move with about the same rapidity. Burdon-Sanderson[2] found that at 20° C., when the leaves of the latter plant are moderately responsive, the latent period after mechanical stimulation was about one second, and the closure of the leaf-lobes required five to six seconds. Sensitive tendrils may, however, begin to curve five to twenty seconds after contact-stimulation, so that the reaction is more rapid than the movements produced by seismonic stimulation in less sensitive plants such as *Robinia*, *Oxalis*, and *Acacia lophantha*. Since the sensitivity and power of reaction are largely dependent upon the stage of development and upon the external conditions, their precise determination is of subordinate interest and importance. It is however worthy of note, that under special conditions *Mimosa pudica* may show only a slow and feeble power of reaction, while when the plant has been kept for some time at a low temperature, such as 5° to 10° C., it temporarily or permanently loses the power of response to seismonic stimuli.

In the case of the leaves of *Mimosa pudica* and the stamens of Cynareae and *Berberis* every successful stimulation excites the full amplitude of movement. This is however not always the case, for even the strongest mechanical stimulation only produces a partial folding or drooping of the

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[1] How far the curvature of the pulvini of *Mimosa pudica* is a matter of growth is uncertain, but the latter does appear to take part in the performance of many sleep movements.

[2] Burdon-Sanderson, Phil. Trans., 1882, Pt. I (p. 48 of reprint); Biol. Centralbl., 1882, Bd. II, p. 497.

leaves of *Robinia* or of *Oxalis*. A strong blow also acts as a submaximal excitation upon the leaves of *Mimosa pudica* when their irritability has been diminished by keeping the plant at a low temperature[1].

It is obviously advantageous that the response should be more marked when the stimulus is more intense or prolonged, or is increased by repetition and summation. This applies more especially to organs endowed with contact-irritability, for in this way they are enabled to a certain extent to so adapt their response as to perform their special function in the best possible manner. A few touches usually suffice to produce a distinct reaction, although in very sensitive tendrils a single contact, if sufficiently intense, will produce a response, while three or four touches are required to produce a curvature in the highly-sensitive tendrils of *Drosera*[2]. Even a single contact, however, may represent a series of local variations of pressure, and it cannot be denied that a sudden maximal explosive movement is better attained by the release of strains previously prepared, than by changes in the rate of growth.

As in other cases the result of a transitory mechanical stimulation may gradually disappear, whereas when the stimulus is continuous the new position of equilibrium assumed will depend upon the intensity of the stimulus, upon the awakened counter-actions, and upon the accommodation of the plant to the stimulus, which is mainly due to its depressed excitability. So long as the plant maintains the position induced by stimulation and reacts to a rise in the intensity of the same stimulus, no accommodation other than that involved in a certain depression of the excitability can take place. This latter appears to be of general occurrence; and in many cases, as, for example, in the leaves of *Mimosa pudica*, it goes so far that the stimulated organ in spite of the continued application of mechanical or of weak induction shocks returns to its original position and is no longer responsive to mechanical excitation[3]. If the return to the original position has taken place during the continued application of gentle shaking, the sensibility is only weakened and an increase in the intensity of the mechanical shocks brings about the usual movement. It is owing to these facts that some authors have found that continually-shaken plants of

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[1] Pfeffer, Physiol. Unters., 1873, p. 69; Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. I, p. 520; Macfarlane, Biological lectures, 1894, p. 190. According to G. Haberlandt (Ann. du Jard. bot. de Buitenzorg, 1898, Suppl. II, p. 35) gentle rubbing excites a sub-maximal movement in the leaves of *Biophytum sensitivum*. In such circumstances the movement may be produced by repeated stimulation as in the case of tendrils, although single stimuli may be ineffective. According to Burdon-Sanderson (Proceedings of the Royal Society, 1877, Vol. XXV, p. 411) the sudden maximal movement of the leaves of *Dionaea muscipula* may be excited by the summation of the action of repeated gentle blows. Cf. also Darwin, Insectivorous Plants. Macfarlane's statement (l. c., p. 187) that at least two blows are required to produce a response in *Dionaea muscipula* appears only to apply under special conditions.

[2] Darwin, Insectivorous Plants, 1875, p. 19.

[3] Pfeffer, Physiol. Unters., 1873, p. 56; Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. I, p. 521.

Mimosa were irresponsive to blows, whereas others found that they remained sensitive[1].

A single stimulation of the pulvinus of *Mimosa* causes its irritability to be transitorily suppressed during the return movement, and it is only gradually restored after the return-movement has been completed. Hence the same stimulus induces at first a feeble, and later a pronounced response[2], and if gentle blows are struck on the primary pulvinus at intervals of three to five minutes, the irritability is sufficiently restored during the intervals to enable each stimulus to produce a moderate response. During the period of insensitivity following mechanical stimulation, the pulvinus of *Mimosa* remains irritable to photonastic, heliotropic, and other stimuli, so that the absence of a response to mechanical stimuli is due to the temporary inhibition of the power of perceiving such stimuli, and not to the motor-mechanism being temporarily ineffective. Nothing is, however, known as to the way in which this special sensitivity is suppressed and restored.

It is hardly to be expected that all sensitive plants should react in this respect in a precisely similar fashion to *Mimosa*, but in general any sudden explosive stimulatory reaction appears often to be followed by a more or less transitory diminution of excitability. This applies to the stamens of Cynareae, although here the excitability soon returns, and is partly restored before the stamens have re-expanded[3]. A complete suppression of excitability does not always follow as the result of stimulation, for Pfeffer[4] has shown that the leaves of *Oxalis* remain excitable during the return movement. In the same way the voluntary muscles of animals can be kept permanently contracted in a condition of tetanus by rapidly repeated stimuli.

On the other hand, *Cuscuta* affords an instance in which stimulation induces a periodic inhibition of the contact-irritability. The tentacles of *Drosera*, however, remain permanently irritable, although the sensitivity is so far decreased by stimulation, that a weak continuous stimulus is unable to produce a permanent curvature, the tentacles gradually straightening again[5]. It is highly probable that further specific peculiarities will be discovered, and investigations in this direction are likely to throw light upon the phenomena of irritability in general.

Both the stimulatory and the return movements begin slowly, increase to a maximum and then gradually cease, while not only in the case of *Mimosa*, but also where the movement is slow, the response to stimulation takes place more rapidly than the return movement. The occurrence of

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[1] The literature is given by Pfeffer, l. c., 1873, p. 56.

[2] Pfeffer, l. c., 1873, p. 60.

[3] Cohn, Abhdlg. d. schles. Ges. f. vaterl. Cultur, 1861, Heft 1, p. 16.

[4] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. 1, p. 521.

[5] Cf. Pfeffer, l. c., 1885, p. 514.

oscillations during movement is partly the result of the nature of the motor-mechanism, and is partly due to the induction of opposed reactions by the realized movement. The extent of the maximal movement in *Mimosa* is determined by the diminution of the energy of contraction and the increase of the mechanical resistance as the curvature progresses. Similarly, in tendrils under sub-maximal stimulation, the curvature ceases as soon as the stimulation is balanced by the counter-actions, although an additional curvature is possible when the stimulus is increased.

Few detailed observations upon the progress of movement have been made. Bert[1] found, for instance, that the end of the primary petiole of *Mimosa* had sunk 22 mm. 7 seconds after stimulation, but that on the commencement of the return movement it rose 4 mm. in the first minute, 4·5 mm. in the second, 3 mm. in each of the third, fourth, and fifth minutes, 2 mm. in the sixth, 1 mm. in the eighth, and 0·5 mm. in the ninth minute.

Uses. The importance of the movements of tendrils for purposes of attachment does not need to be emphasized. The movements of stamens and stigmas induced by seismonic stimuli are usually for the purpose of ensuring the transference or reception of pollen, while in carnivorous plants the responses to seismonic, chemical and contact-stimuli are especially connected with the capture and digestion of insects. The extremely readily induced movements of *Mimosa pudica* and similar plants probably aid in keeping off large browsing animals such as goats and camels, and may also be of use in warding off the attacks of injurious insects. One can often see how goats, after the first tug at a bush of *Mimosa,* seek less bewildering pasturage, and how a surprised fly hastens from a leaf on which his descent has excited a movement[2]. The folded leaflets and drooping leaves of *Mimosa pudica* are less readily injured by rain and hail, while the re-expansion on continued stimulation aids in avoiding a prolonged derangement of the functional activity of the leaf.

It is uncertain whether the slow response of the leaflets of *Oxalis* to mechanical stimuli has any biological utility, for the leaves are not more readily injured by mechanical agencies than other non-irritable ones.

SECTION 16. **Movements produced by Mechanical Stimuli.**

The mechanism of movement has been studied most in the cases of the stamens of Cynareae and the pulvini of *Mimosa*, and as far as we know similar mechanisms are employed in other motile organs which

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[1] Bert, Mém. de l'Acad. de Bordeaux, 1870, T. VII, p. 41. A similar progress was observed by Cohn (Abhdlg. d. schles. Ges. f. vaterl. Cultur, 1861, Heft 1, p. 13) in the stamens of Cynareae, and by Burdon-Sanderson (Proc. of the Royal Society, 1877, Vol. XXV, p. 416; Phil. Trans., 1882, p. 48 of the reprint) in the leaf of *Dionaea muscipula.*

[2] See Johow, Kosmos, 1884, Bd. II, p. 124; G. Haberlandt, Tropenreise, 1893, p. 36; Ewart, Annals of Botany, 1897, Vol. XI, p. 339 (Protective movements of leaflets); Burgerstein, Wiener illustrirte Gartenzeitung, März 1898.

respond to mechanical stimuli. Actual experiment is required, however, in each case before any final conclusion can be made, since similar movements may be produced in various ways. Although the movement of the leaf of *Dionaea* appears to be accompanied by growth, it is nevertheless possible that the cell-mechanism may be the same as in the irritable stamens of Cynareae and in the pulvini of *Mimosa pudica.* It is indeed possible that every movement of the young pulvinus may be accompanied by growth-changes, whereas when adult pure movements of variation may take place. As was shown by Pfeffer[1], the movements both of the leaves of *Mimosa pudica* and of the stamens of Cynareae result from the fact that stimulation induces a sudden fall of turgor, and hence a sudden equilibration of the elastic stresses in the motile organ, which are gradually reproduced as the original turgor is restored. The phenomenon can best be followed in the stamens of Cynareae, of which those of *Centaurea jacea* shorten by 10 to 30 per cent., and those of *Cynara scolymus* by 8 to 20 per cent. of their length when stimulated by a touch. The whole length of the filament takes an equal part in this contraction, with the exception of the two extremities where less shortening is shown. An isolated stamen remains capable of contraction, and when stimulated performs lateral curvatures or convolutions.

The construction of the filament from longitudinal rows of cylindrical cells symmetrically disposed around the central vascular bundles results in a close correspondence between the degree of contraction of the individual cells and of the whole filament. Direct measurements have established the fact that the epidermal and neighbouring parenchyma cells do actually shorten, but retain their original transverse diameter and experience no lateral curvature. The fall of turgor in the cells by lessening the tangential stretching compensates for and prevents the broadening which would otherwise result from the shortening of the cell[2]. Hence when the filament shortens by 20 per cent. of its length, the individual cells also become one-fifth shorter and hence correspondingly decrease in volume. This involves an escape of water from the cells into the intercellular spaces, the displaced air streaming away through the communicating intercellular spaces so that its compression is avoided. If the filament is injected with water, a drop of liquid exudes from the cut end when the stamen shortens on excitation, although the shortening is less than before. This water appears to escape from the intercellular spaces of the parenchyma, and hence it is easy to understand how the stamens of *Centaurea jacea* and of *Cynara scolymus* are able to shorten without increasing in diameter[3]. It is,

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[1] Pfeffer, Physiol. Unters., 1873; Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, p. 325.

[2] Pfeffer, l. c., 1873, p. 96.

[3] Pfeffer, l. c., 1873, p. 89. The methods of measurement of other authors and a criticism of them is given in this work. The matter is in no wise altered by the apparently somewhat

however, always possible that the contraction of other stamens may involve a decrease or increase in diameter. These facts, together with the absence of any active contraction of the protoplasts, and of any transitory increase in the elasticity of the stretched cell-walls, suffice to show that the shortening is due to a fall of turgor, and the subsequent re-expansion to its gradual restoration. The energy of contraction as determined by comparing the maximal load with the area of cross-section of the filament amounts to as much as 1 or 3 atmospheres. Hence it cannot possibly be produced by an active contraction of a viscous fluid like the protoplasm[1], and the diameters of the cells are too great to enable changes in the peripheral surface tension to have much effect.

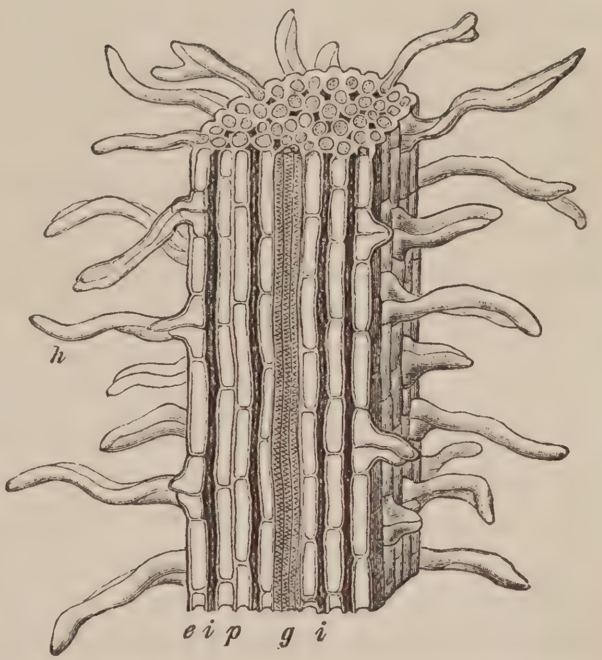

FIG. 26. A portion of the longitudinal half of a filament of *Centaurea montana* (magnified). *g* = vascular bundle, *p* = parenchyma, *e* = epidermis, *i* = intercellular spaces, *h* = hairs.

The filament when contracted possesses the same elasticity as when expanded and rendered non-irritable by chloroform. Further, the same weight which is required to stretch a contracted filament to its original length also suffices to prevent any contraction. Hence it is obvious that no increase in the elasticity of the cell-walls occurs during contraction, although by raising the pressure exerted by the cell-wall against the internal osmotic pressure this might produce a contraction of the cell accompanied by an outward filtration of water under pressure[2]. It is evident therefore that changes in the osmotic pressure are solely responsible for the contraction, although, since these are only temporary in character, they cannot be detected by plasmolytic methods[3].'

The reason for the pronounced contraction resulting from a fall of turgor lies in the fact that the cell-walls are as extensible as india-rubber, and when not under any permanent tension can be stretched to double their length without their limit of elasticity being passed, that is, without undergoing any permanent stretching. Even when fully turgid the cell-

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careless experiments of Schenkemeyer, Ueber die Contraction der Filamente von *Centaurea*, Breslauer Dissertation, 1877.

[1] Pfeffer, Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, pp. 326, 329.

[2] Pfeffer, Physiol. Unters., 1873, pp. 110, 117; also l. c., 1890, p. 327.

[3] Pfeffer, l. c., 1890, p. 327.

walls are not stretched to this extent, and hence a chloroformed filament undergoes a considerable elastic elongation when weights are attached to it. On the other hand, when a contracted filament is suddenly killed by dropping it into boiling water, it undergoes an additional shortening of 10 to 40 per cent. of its length, owing to the fact that the previous stimulation caused a fall of turgor but not its entire removal. This naturally applies only when the filament is highly irritable and before the fall of turgor which precedes death has begun. A shortening corresponding to that produced by excitation results from the action of an injected solution of 0·5 to 1 per cent. potassium nitrate, which diminishes the osmotic pressure in the cell by 1·7 to 3·5 atmospheres.

These general considerations are not affected by the fact that the realized movement of the filament results from the interaction of dissimilar cells, for the association of the active cells with passive ones merely acts like an increase in the thickness of the cell-wall and not only diminishes the extent of the contraction produced by the available energy, but also lessens the elastic stretching produced when turgor is restored. Presumably not only the parenchyma, but also the epidermal cells and possibly also the living cells of the vascular bundles are all active agents in producing the contraction[1]. If this were not the case and only a limited number of cells were active, we could hardly have so pronounced an energy of contraction per unit area as is actually shown. The fact that the epidermis and vascular bundles are under tension both in the contracted and uncontracted conditions is the direct result of the fact that only a diminution and not a removal of turgor is involved. In fact a further fall or an entire removal of turgor causes a longitudinal compression of the vascular bundle, and allows the walls of the parenchyma cells to show wavy bulgings[2].

The fall of turgor allows the stretched cell-wall to contract until the decreasing tension of the wall is balanced by the internal osmotic pressure, which rises somewhat as water escapes and the sap becomes consequently more concentrated. A renewed production of osmotic materials causes the extruded water to be again absorbed and the cell to be once more distended and ready to respond to excitation. The mechanism can therefore be compared to an india-rubber tube in whose walls a spiral wire is imbedded, so that on forcing in water under pressure the tube is distended longitudinally but not transversely, and shortens when some of the water is allowed to escape. The cell-walls do actually permit of the rapid filtration through them of water under pressure, required to allow sudden contraction.

Since a perceptible diminution in the size of a cell can only be

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[1] Pfeffer, l. c., pp. 102, 112. An excitation is produced not only by touching the hairs, but also the epidermal cells free from hairs. See also Haberlandt, Sinnesorgane im Pflanzenreich, 1901, p. 35.

[2] Pfeffer, l. c., p. 114.

produced by a fall of turgor when the cell-wall was previously stretched sufficiently, it is possible that in certain cases no response may be shown although the cells react as in the filaments of Cynareae. This special irritability is, however, certainly not a general phenomenon, and the stamens of *Helianthus annuus*, for instance, have no seismonic irritability although the cell-walls undergo a considerable elastic stretching when the cells are fully turgid[1].

The protoplast remains closely pressed against the cell-wall of a stimulated cell, and this is still the case, even when a stimulated staminal filament is loaded with a weight sufficient to prevent any contraction. The retraction of the protoplasm from the cell-wall, such as occurs during rejuvenescence, necessitates that the centrally-directed pressure exercised by the protoplasm should be greater than the osmotic pressure of the cell-sap, which cannot therefore be very great. This must also be the case when, as Schütt and also Benecke found, the protoplast of a Diatom subjected to mechanical and other stimuli contracts away from the cell-wall[2]. It is possible that this stimulatory plasmolysis may be the result of a sudden change of permeability in the plasmatic membranes allowing the osmotic materials in the cell to escape.

Stimulation also causes a fall of turgor in the under half of the dorsiventral primary pulvinus of *Mimosa pudica*. The change of inclination of the petiole is so great as to need a pronounced curvature of the pulvinus. This, though aided by the mechanical moment exercised by the leaf-segments, is mainly produced by an active contraction of the cells in the under stimulated side, which cells are compressed by the expansion of the upper turgid half of the pulvinus until equilibrium is restored. The original condition of turgor is then gradually reproduced in the lower half of the pulvinus which expands, raising the leaf and producing the compression of the upper half of the pulvinus which aids in the rapid curvature of the stimulated pulvinus[3].

After the upper half of the pulvinus has been carefully removed no movement is produced by stimulation, whereas when the lower half is

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[1] Pfeffer, l. c., p. 107.

[2] Schütt, Die Peridineen der Planktonexpedition, 1895, p. 110; Benecke, Jahrb. f. wiss. Bot., 1901, Bd. XXXV, p. 554. According to Nägeli (Pflanzenphysiol. Unters., 1855, Heft 1, p. 13) mechanical pressure causes in *Spirogyra*, and according to Hofmeister (Pflanzenzelle, 1867, p. 303) in *Nitella*, a withdrawal of the protoplasm from the cell-wall. It remains, however, to be seen whether we are dealing here with stimulatory functions or with the results of mechanical injury, and the observations of Schütt and Benecke require further proof.

[3] For details concerning the structure and mechanics of the pulvinus of *Mimosa* see Pfeffer, Physiol. Unters., 1873, p. 9; Haberlandt, Das reizleitende Gewebesystem der Sinnpflanze, 1890, p. 23; Physiol. Anat., 2. Aufl., 1896, p. 475; Sinnesorgane im Pflanzenreich, 1901, p. 38; Schwendener, 1897, Gesammelte Abhandlungen, Bd. II, p. 211. On the structure and mechanics of the pulvini of the leaflets cf. Schwendener, l. c., p. 236.

absent a weakened power of movement is retained[1]. Since, however, the operation undoubtedly affects the irritability, it is impossible to determine from such experiments the exact part played by the active contraction of the lower half of the pulvinus. Nor is it certain whether all the different cells and tissues of this zone are equally excitable. The parenchyma cells around the vascular bundles appear in fact to be of primary importance, but the epidermal cells may also take part in the contraction, although their tangential tension is converted into a tangential pressure, that is, they are compressed instead of being stretched where a strong curvature is produced. The way in which stimuli may be conducted from one pulvinus to another, as well as the fact that the pulvinus may perceptibly react after the epidermis has been removed, suffice to show that the cortical cells may be stimulated without the aid of the epidermis. The latter may also receive an excitation[2], and contact with the hairs alone is able to excite a response in the pulvinus. The hairs probably only act by readily transmitting the pressures to the cells beneath, and hence behave as 'stimulators' in Haberlandt's sense of the term. The fact that gentle direct contact on the under half of the pulvinus may act as an excitation points to the direct excitability of the epidermal cells, for a much greater pressure must be applied or a more violent blow struck upon the upper epidermis of the pulvinus in order to produce an excitation of the under half.

The contraction and diminution of volume of the pulvinar cells of *Mimosa* cannot be directly observed, but they are indicated by the escape of water from the reacting cells, as in the stamens of Cynareae. This water partly fills the intercellular spaces and is partly conducted into the neighbouring tissues of the stem and petiole[3], and possibly also a little may pass into the vascular bundles. If the leaf-stalk is separated from the pulvinus by a sharp cut, and the still attached pulvinus kept in moist air, on stimulation water escapes from the cut surface, and at first from the inner, but not from the inmost layers of parenchyma in the lower half of the pulvinus. A little later some water also escapes from corresponding cells in the upper half of the pulvinus.

This displacement of air and water causes the under half of a stimulated pulvinus to increase in volume as determined by micrometer measurements,

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[1] The observations of Pfeffer and of other observers are given in full in Pfeffer's Physiol. Unters., 1873.

[2] The researches of Borzi (L'apparato di moto delle sensitive, 1899, p. 17, reprint from Rivista di Scienze Biologiche, Vol. IV) fail to reveal the distribution of sensitivity in the tissues. Cf. Haberlandt, l. c., 1901, p. 79. The latter author (p. 88) concludes that in the case of *Biophytum sensitivum* the hairs on the pulvini directly perceive stimuli.

[3] Hence arises the fact that Bonnier (Revue générale de bot., 1892, T. IV, p. 512) observed slight variations of the air pressure during a stimulatory movement, when a manometer was inserted in the stem of *Mimosa pudica* near to the origin of the pulvinus.

whereas the elongating upper half slightly decreases in volume[1]. The displacement of the intercellular air by water is also shown by the sudden darkening following stimulation, just as occurs when the pulvinus is injected with water, and as is also shown in the under half of the pulvinus when the movement is mechanically arrested[2]. The presence of intercellular spaces in the inner layers of parenchyma facilitates the rapid extension and removal of water, but nevertheless the outer layers may also give off water with sufficient rapidity, although no system of communicating air-spaces exists between them[3]. The anatomy of the tissues does not therefore enable us to conclude that the outer layers of parenchyma are inactive or less active than the inner layers.

Additional and important evidence to show that the movement is produced by a fall of turgor is given by the fact that the stimulated pulvinus is more flaccid and less rigid than the unstimulated one. This can be shown by determining in each case the deviation of the angles between the stem and petiole in the normal and inverted positions. Brücke[4] observed the angles of deviation in the stimulated pulvinus to be two or three times greater than in unstimulated ones. Similar relationships were determined by Hofmeister[5] to exist in the case of stimulated and unstimulated stamens of Cynareae. These facts show that the water is not pressed out by an increase in the elasticity of the cell-wall increasing the pressure on the cell-sap, for in that case the rigidity of the cells and tissues would be increased. From the load required to prevent movement it can be calculated that the energy of movement in the pulvinus represents a fall of turgor of two to five atmospheres[6]. Hence it is obvious that the movement cannot be due to an active contraction of the protoplast.

The fact that the rigidity of a stimulated pulvinus of *Oxalis acetosella* decreases[7] and that water escapes under favourable circumstances from the stamens of *Berberis vulgaris* when a curvature is produced by irritation[8],

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[1] Pfeffer, l. c., p. 23,

[2] Pfeffer, l. c., p. 35. The fact that this change of coloration, first observed by Lindsay in 1827, should not always be distinctly shown probably depends upon the fact that the air which is always only partially displaced may in some cases be displaced but little or not at all. It is therefore quite possible that Schwendener (l. c., p. 212) worked with plants which did not show any change of colour, but the latter has been recently observed by Macfarlane (Biological lectures, 1894, p. 205) in various species of *Mimosa*, and more especially in *Mimosa sensitiva*.

[3] Pfeffer, l. c., p. 11; Schwendener, l. c., p. 212.

[4] Brücke, Müllers Archiv f. Physiologie, 1848, p. 40. It has not yet been determined why the rigidity rises after chloroforming and also when the irritability is suppressed by repeated shaking. Pfeffer, Physiol. Unters., 1873, p. 65.

[5] Hofmeister, Pflanzenzelle, 1867, p. 311; Pfeffer, l. c., p. 145.

[6] Pfeffer, Periodische Bewegungen, 1875, p. 111.

[7] Pfeffer, Physiol. Unters., 1873, p. 74.

[8] Pfeffer, l. c., p. 158. Intercellular spaces are usually present in the stamens of *Berberis*. Cf. Pfeffer, Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, p. 326, footnote 2.

seems to indicate that the same mechanism is involved as in the pulvini of *Mimosa* and the stamens of Cynareae.

SECTION 17 (*continued*).

The mode in which the fall of turgor is produced in the cell-sap[1] is uncertain and need not always be the same. The rapidity with which this occurs affords little evidence as to its character, for a rapid fall of turgor can be produced in various ways. The escape of water is the natural result of the pressure exerted by the stretched cell-wall when allowed to contract, combined with the permeability of the walls of the cells and tissues concerned[2].

Hitherto no visible changes in the cells have been observed which might throw light upon the stimulatory movement. Stimulation does not, for instance, affect the protoplasmic streaming of the stamens of Cynareae, whether the movement takes place or is mechanically prevented[3]. In case any visible reactions should be detected, it would still remain to be determined whether they were directly connected with this stimulatory response or were due to some simultaneously awakened activity. The protoplasmic aggregations shown in stimulated cells of *Drosera* and *Dionaea* are partly or entirely connected with the induced secretory activity. Changes in the shape of the protoplast and in the position of the chloroplastids may be produced without any change of turgor, and hence can hardly be responsible for its induction[4]. The same is still the case even when stimulation causes the protoplast to retract from the cell-wall[5].

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[1] For details see Pfeffer, l. c., 1890, p. 333.

[2] Cf. Pfeffer, l. c., 1890, p. 329. Vines (Arb. d. bot. Inst. in Würzburg, 1878, Bd. II, p. 146) and Gardiner (Annals of Botany, 1887–8, Vol. I, p. 366) assumed that an active contraction of the protoplasm was responsible for the movement, without bringing any real arguments forward, and without explaining how the high energy of contraction could be developed in this way. Pfeffer has further shown that the fall of turgor is not produced by any active pumping action, and that the escape of water is not the result of a local tearing in the protoplasm, such as occurs in many contracting vacuoles. It hardly needs to be mentioned that so long as no exosmosis of dissolved materials occurs, an increase in the permeability of the protoplasm or cell-wall cannot produce any fall of turgor.

[3] Pfeffer, Physiol. Unters., 1873, p. 138; Bot. Ztg., 1875, p. 290, footnote.

[4] Borzi (L'apparato di moto delle sensitive, Rivista di Scienze Biologiche, 1899) does not pay sufficient attention to the principles indicated here. The same applies to the studies of Chauveaud (Compt. rend., 1894, T. CXIX, p. 103) and Heckel on the stamens of *Berberis*. Cf. the criticism of this work in the Bot. Ztg., 1875, p. 289, and 1876, p. 9. Heckel has, in fact, in part regarded the appearances produced by plasmolysis or death as being the result of stimulation.

[5] Hitherto the changes in the electrical currents as well as in the production of heat have not been used to throw light upon the phenomena of stimulation and response. Bert (Mém. de l'Acad. de Bordeaux, 1870, T. VIII, p. 43; Compt. rend., 1889, T. LXIX, p. 895) observed by means of thermoelectric needles that the primary pulvinus of *Mimosa pudica* is somewhat cooler than the petiole and stem, and remains so in spite of the slight rise of temperature on stimulation. According to Kraus (Wasservertheilung i. d. Pflanze, 1880, II, p. 68) the percentage of sugar increases in continually

Although we may safely assume that the perception of the stimulus takes place in the protoplasm, nothing further is known concerning it. We may, however, in general conclude that a mechanical stimulus produces in a sensitive plant some explosive disturbance in the protoplasm involving a sudden release of energy, and that the gradual storage of energy required for the restoration of the original labile condition of equilibrium takes place independently of the processes of stimulation and perception. The latter is shown by the fact that the organ returns to its original position even when its irritability is permanently suppressed by chloroforming or continual shaking. We do not, however, know whether the return of irritability is due to the formation of a substance capable of explosive decomposition, or is a matter of structural rearrangement in the protoplasm, or involves other changes[1]. In many cases the power of movement may be retained, although the irritability has been suppressed, and this appears to occur more readily in the case of seismonic than of other forms of irritability[2].

Historical. The cellular mechanism of movement in the pulvini of *Mimosa* and the stamens of Cynareae was revealed in the manner stated above by Pfeffer[3], for although Brücke[4] in his historical researches recognized that the curvature of the pulvinus of *Mimosa pudica* was connected with the flaccidity of the responsive half of the pulvinus produced by the escape of water, he did not further investigate the cell-mechanism, and left it uncertain where the stimulation induced a change in the cell-walls, in the protoplasm, or in the cell-sap. Cohn, and also Unger[5], erroneously assumed that the movement of the stamens of Cynareae is produced by a change in shape of the cells of the filament without any escape of water[6]. The former author inclined to the conclusion that the movement was due to an active contraction of the protoplasm, a view adopted at a later date by Vines and Gardiner, but one which is totally incapable of explaining the high energy of contraction. Hofmeister's[7] conclusion that the cell-wall was the responsive part of the cell was also based upon incorrect or nebulous arguments.

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shaken growing shoots while the percentage of acid often decreases. Niklewski, however, working at Pfeffer's instigation, found no increase in the percentage of sugar under these circumstances.

[1] Cf. Pfeffer, Physiol. Unters., 1873, p. 143; Osmot. Unters., 1877, p. 192. An attempt to stimulate the stamens of Cynareae by sound-waves was without success.

[2] Irritability is not regained by sections of the stamens of Cynareae or of the pulvinus of *Mimosa pudica*.

[3] Pfeffer, Physiol. Unters., 1873; a few complementary details are given in the Osmot. Unters., 1877, p. 188. The older view that the spiral vessels were the contractile parts is given in the former work. Ray (Historia Plantarum, 1686, p. 1) was perhaps the first who attempted a mechanical explanation. A few experiments were also performed by Hooke (Micrographia, 1767, p. 119). Cf. also Sach's History of Botany, 1890, p. 535.

[4] Brücke, Archiv f. Physiologie, 1848, p. 443.

[5] Cohn, Abhandlg. d. schles. Ges. f. vaterl. Cultur, 1861, Heft 1, p. 28. Cohn (Zeitschr. f. wiss. Zoologie von Siebold u. Kölliker, 1863, Bd. XII, p. 366) at a later date compared the contractile cells to muscle-fibres.

[6] Unger, Bot. Ztg., 1862, p. 112; 1863, p. 350.

[7] Hofmeister, Pflanzenzelle, 1867, p. 300. Cf. also Flora, 1862, p. 502 and Pfeffer, Physiol. Unters., 1873, p. 6, 128.

Our knowledge as to how the movement of the pulvinus of *Mimosa pudica* is produced by the antagonism of the upper and under halves has developed gradually[1]. Lindsay in 1790 considered the fall of the petiole to be due to the expansion of the upper half of the pulvinus, whereas Burnett and Mayo[2] recognized that only the under half of the pulvinus of *Mimosa* is irritable, but failed to gain a correct view of the entire mechanism. After Dutrochet, Treviranus and Mohl had collected definite facts in regard to the strains between the distended parenchyma and the vascular bundles, Brücke definitely established the fact that the curvature is the result of the under half of the pulvinus becoming flaccid[3].

The varying grades of irritability in the leaves of Mimoseae, Papilionaceae, and Oxalidaceae have already been discussed[4]. Meyen[5] observed that the leaves of *Gleditschia triacantha* possessed a feeble seismonic irritability, and Mohl[6] observed the same in the leaves of *Robinia pseudacacia*, *R. viscosa*, and *R. hispida*. In many cases even the cotyledons are irritable, as was shown by A. P. de Candolle[7] in the case of *Mimosa pudica*, and by Darwin[8] in those of *Oxalis sensitiva*, *Smithia sensitiva*, and a few species of the genus *Cassia*, *Dionaea*, and *Aldrovanda*. When the leaf of *Dionaea muscipula* is stimulated the two halves of the leaf fold sharply together and become at the same time somewhat concave, so that the marginal teeth interlock[9] (cf. Fig. 57, p. 378, Vol. I). Apart from the marginal zone, the whole leaf seems to take an active part in the movement. According to Batalin's measurements, the most pronounced curvature takes place along a zone on each side parallel to the midrib, while the midrib itself takes little or no part in the movement. Darwin[10], however, found that a pronounced movement occurs along the midrib. Batalin[11] considered the movement to be mainly the result of growth, but it is not certain whether young and old leaves behave alike in this respect. The observations and discussion of Darwin and of Munk fail to definitely decide whether the movements of *Dionaea* are wholly or partially due to a similar cell-mechanism as that which exists in the pulvinus of *Mimosa pudica*.

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[1] Pfeffer, Physiol. Unters., p. 3.

[2] Burnett and Mayo, Quarterly Journal of Science, Literature and Arts, 1827, Vol. XXIV, p. 79; 1828, Vol. XXV, p. 434.

[3] Cunningham (Annals of the Royal Botanical Garden of Calcutta, 1895, Vol. VI, p. 1) goes so far as to doubt whether the movements of *Mimosa pudica* are irritable movements at all, but this somewhat voluminous work is without value.

[4] An enumeration of the sensitive plants is given by Hansgirg, Physiol. und phycophytolog. Unters., 1893, p. 118; Neue Unters. üb. d. Gamo- und Karpotropismus, 1896, p. 102 (reprint from Sitzungsb. d. böhm. Ges. d. Wiss.). Numerous cases were given by Dassen, in Wiegmann's Archiv f. Naturgeschichte, 1838, Bd. I, p. 347; Meyen, Physiologie, 1839, Bd. III, p. 539.

[5] Meyen, l. c., p. 540.

[6] Mohl, Vermischte Schriften, 1845, p. 372.

[7] A. P. de Candolle, Physiologie, a German translation by Röper, 1835, Bd. II, p. 647.

[8] Darwin, The Power of Movement in Plants.

[9] Ibid.

[10] For details see Darwin, Insectivorous Plants; Munk, Die elektrischen- und Bewegungserscheinungen am Blatte von *Dionaea muscipula*, 1876, p. 97; Batalin, Flora, 1877, p. 105; Burdon-Sanderson, Proceedings of the Royal Society, 1877, Vol. XXV, p. 411; Phil. Trans., 1882, p. 48 of the reprint; Goebel, Pflanzenbiol. Schilderungen, 1891, II, p. 68; 1893, II, p. 201; Macfarlane, Contributions from the Biological Laboratory of Pennsylvania, 1892, Vol. I, p. 7; Biological Lectures, 1894, p. 187. See more especially Haberlandt, Sinnesorgane im Pflanzenreich, 1901, p. 108.

[11] l. c.

The whole of the inner side of the leaf is irritable, but the three large hairs found on the upper side of each half of the leaf are especially sensitive (cf. Fig. 24, p. 64). This is, according to Munk, simply because, owing to the structural arrangements, pressure applied to the hair is transmitted with increased intensity by leverage to the irritable parenchyma cells at the base of the hair. The cells at the tip of the hair appear to be insensitive, since they can be cut away without producing an excitation [1], but the cells at the base of the hair appear to become flaccid when the leaf is stimulated. This is of importance in that it aids in the bending of the basal joint of each hair, enabling it to lie flat against the leaf when the latter closes.

The leaf is not sufficiently sensitive to be excited by the impact of a single raindrop [2], but responds to that of a jet of water, and also when the irritable hairs are touched with a moistened gelatine-covered rod [3]. It is not, however, certain whether the leaf possesses contact-irritability in addition to seismonic irritability.

The mechanism of movement is apparently similar in the leaf of *Aldrovanda vesiculosa* to that in *Dionaea*, and the hairs on the inner surface of the leaf appear to produce an excitation with especial readiness when touched. The leaves of this plant only open when the temperature is fairly high, and very feeble contact is then sufficient to excite them [4].

Stamens. All members of the Cynareae appear to possess more or less irritable filaments, and the same is also the case with a few species from the other sub-orders of the Compositae, such as *Cichorium intybus* and *Telekia speciosa.* On the other hand, all stamens whose cell-walls are readily extensible are not capable of perceptible irritable movements [5].

The mechanism of movement of the stamens of *Berberis* [6] and of *Mahonia* appears to be similar in character to that of the pulvinus of *Mimosa.*

The movements of the stamens of other plants [7] which cause them to approach or recede from the stigma appear to indicate a power of response to seismonic stimuli [8]. Apparently, it is owing to the anatomical structure and distribution of the irritable tissues that the stamens of *Helianthemum* and of other Cistaceae, as well as of *Mesembryanthemum*, always move in the same direction wherever they may be touched,

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[1] Munk, l. c., p. 103.

[2] Darwin, l. c., p. 273.

[3] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. I, p. 518.

[4] For details see Stein, Bot. Ztg., 1874, p. 389; Cohn, Beiträge z. Biol., 1875, I, Heft 3, p. 71; Darwin, Insectivorous Plants; Goebel, Pflanzenbiol. Schilderungen, 1893, Bd. II, p. 70; Haberlandt, Physiol. Pflanzenanat., 2. Aufl., 1896, p. 480; Biol. Centralbl., 1901, Bd. XXI, p. 375; Sinnesorgane im Pflanzenreich, 1901, p. 103.

[5] Cf. Pfeffer, Physiol. Unters., 1873, pp. 107, 151. A detailed enumeration is given by Hansgirg, Physiol. u. Phycophytol. Unters., 1893, p. 141; Neue Unters. üb. d. Gamo- u. Karpotropismus, 1896, p. 106 (reprint from Sitzungsb. d. böhm. Ges. d. Wiss.).

[6] Pfeffer, Physiol. Unters., 1873, pp. 127, 158. At a later date (Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, p. 326, footnote) Pfeffer showed that intercellular spaces are normally present in the active tissues. A summary of the literature is given by Usteri, Bot. Centralbl., 1900, Bd. LXXXIV, p. 228. According to Haberlandt (l. c. 1901, p. 24), the papillose part of the inner surface of the stamens of *Berberis* and *Mahonia* is especially irritable.

[7] Facts and literature are given by Hansgirg, l. c., 1893 and 1896; Beihefte zum bot. Centralbl., 1902, Bd. XII, p. 273; Haberlandt, l. c., 1901, pp. 17, 21, 32, 46, 51.

[8] Cf. also Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. I, p. 518.

whereas the stamens of *Opuntia* and *Cereus*, and to a less degree those of *Sparmannia*, and certain members of the Tiliaceae and Portulaceae, always bend towards the side stimulated.

Irritable stigmas, which close together when touched, are possessed by *Mimulus*, *Martynia*, *Bignonia*, and *Goldfussia*[1]. In addition the style of *Glossostigma elatinoides*[2], and also of *Arctotis*[3], curves in response to contact.

Except in the case of *Berberis*, it is not known in the case of a single one of these irritable stamens, stigmas, and styles whether the movement is produced by growth or by elastic contraction, and the same applies to the movement of the irritable labellums of certain orchids[4]. Hence it is impossible to say whether the cell-mechanism is the same as in the pulvini of *Mimosa* and the stamens of Cynareae. The rapid movements of *Stylidium* and of other objects are, however, due to the sudden release of a mechanical resistance to an attempted growth-curvature[5].

SECTION 18. **Movements produced by Contact-stimulation.**

No contact-irritability can be detected in ordinary growing stems and leaves, and, according to Newcombe[6], the same applies to the radicles of seedlings, for the feeble curvatures which Sachs[7] observed as the result of rubbing the growing zone strongly were traumotropic in character. Since, however, the roots of *Vanilla*, and of a few other plants, possess distinct thigmotropic irritability, it is possible that other roots may be found to be more or less irritable to contact.

Strong contact-irritability is shown by the sporangiophore of *Phycomyces nitens*, for when the tip is rubbed on one side a curvature of the growing zone begins in a few minutes[8]. Since no reaction is produced by contact below the growing zone, either the power of perception is restricted

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[1] For additional instances see Hansgirg, l. c., 1893 and 1896. Cf. also W. Oliver, Ber. d. bot. Ges., 1887, p. 112; Miyoshi, Journal of the College of Science, Japan, 1891, Vol. IV, p. 205; Haberlandt, l. c., 1901, pp. 55, 58. According to Burk (Bot. Centralbl., 1902, Bd. LXXXIX, p. 645) the stigmas of *Mimulus* and of *Torenia* close when pollinated owing to the withdrawal of water by the swelling pollen-grains.

[2] Quoted by Hansgirg, l. c., 1893, p. 149.

[3] Minden, Flora, 1901, p. 238; Haberlandt, l. c., 1901, p. 60.

[4] For additional literature see Oliver and Hansgirg, l. c., 1893, p. 150.

[5] Many such instances are given by Hansgirg, l. c., 1893, p. 149.

[6] Newcombe, Beihefte zum bot. Centralbl., 1902, Bd. XII, p. 242.

[7] Sachs, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 437; Darwin, The Power of Movement in Plants. Darwin (l. c., pp. 109–71) erroneously ascribed a power of contact-irritability to the root-tip, which enabled the root to curve away from solid bodies, whereas the observed curvatures appear to have been traumatic in origin.

[8] Errera, Bot. Ztg., 1884, p. 653; Wortmann, Bot. Ztg., 1887, p. 803; Steyer, Reizkrümmungen bei *Phycomyces nitens*, 1901, p. 19. That only solid bodies act as stimuli was shown by Wortmann. The sporangiophore of *Phycomyces* responds most actively during the period of stretching growth, but the weak power of reaction present just before the formation of the sporangium disappears with the cessation of growth.

to this zone or, if all regions are capable of receiving a stimulus, little or no power of transmitting stimuli is possessed by the protoplasm. The hyphae of this fungus have indeed no perceptible contact-irritability, and the same applies to *Mucor mucedo* and *M. stolonifer*, whose sporangiophores behave similarly to those of *Phycomyces*. On the other hand, the conidiophores of *Aspergillus* and *Penicillium*, as well as pollen-tubes and apparently also root-hairs, seem to be devoid of this form of irritability[1], for the partial enclosure of particles of soil by the root-hairs appears to be produced in a purely mechanical manner.

In all the above-mentioned plants the reaction only takes place at the point stimulated, whereas the leaf-tentacles of various species of *Drosera* afford good instances of the transmission of stimuli from the receptive to the responding regions[2]. Contact and also chemical stimuli are only perceived by the head of the tentacle, whereas the curvature occurs at the base and median portion of the stalk. When an insect alights on the leaf and adheres to it, both kinds of stimuli co-operate, but similar results are produced when either acts separately. Since, however, the chemical stimuli are more active, a partial recovery from the original curvature occurs more readily during prolonged contact than during the continued application of a chemical stimulus[3]. Thus the presence of a fragment of glass on the tentacles is only able to keep them fully curved for a few hours to a day, whereas the body of an insect may cause them to remain curved for one or more weeks, that is until all the soluble proteids have been digested and absorbed so that further chemical stimulation ceases[4].

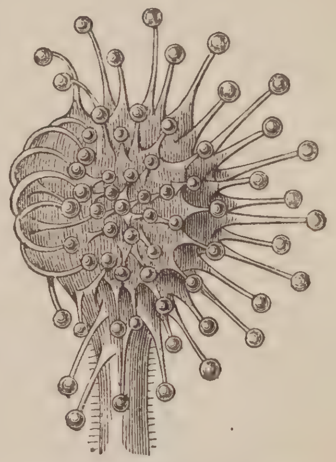

FIG. 27. Leaf of *Drosera rotundifolia* (magnified). The tentacles on the left are curving as the result of stimulation.

Darwin showed that a curvature was only produced when the head of the tentacle was mechanically or chemically stimulated, and not when the stimuli were directly applied to the stalk or to the lamina of the leaf. Hence when the head of a tentacle is cut off the latter can be excited to a curvature by the transmission of a stimulus from a neighbouring tentacle, but not by direct excitation. The effect of strong chemical and

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[1] Kny, Sitzungsb. d. bot. Vereins v. Brandenburg, 12. Juni, 1881; Dietz, Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. II, p. 482; Miyoshi, Flora, 1894, p. 86.

[2] For details see Darwin, Insectivorous Plants, 1875; Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. I, p. 511. For anatomical details see Haberlandt, Physiol. Anat., 2. Aufl., 1896, p. 397; Rosenberg, Physiol.-Cytol. Unters. über *Drosera rotundiflora*, 1899, p. 42; Haberlandt, Sinnesorgane im Pflanzenreich, 1901, p. 94.

[3] Cf. Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. I, p. 514.

[4] Darwin, l. c., pp. 13, 21, 92 seq., 22, 117; Goebel, Pflanzenbiol. Schilderungen, 1893, Bd. II, p. 203.

mechanical stimuli is not restricted to a single tentacle but spreads through the leaf-lamina to neighbouring tentacles not directly excited.

The small tentacles at the centre can perceive stimuli and transmit them to the larger marginal ones which curve towards the centre of the leaf, whereas the small central tentacles themselves do not curve. The dorsi-ventrality of the stalk of the tentacle leads to the curvature being always to the centre of the leaf, but does not prevent a slight lateral bending when a tentacle at the side is radiating a strong orienting stimulus. By varying the intensity and duration of the stimulus, an excitation may either be confined to the stimulated tentacle, or may be caused to spread to neighbouring ones or even to all the tentacles on a leaf. Strong stimulation, especially if chemical, may cause the lamina of *Drosera rotundifolia* to become more or less concave, or may lead to an inrolling of the margin of the elongated leaf of *Drosera longifolia* and *D. intermedia*, which may sometimes be so pronounced as to completely enclose a captured insect.

The irritable movements of the tentacles and lamina of *Drosera rotundifolia* were first noted by Roth[1]. Nitschke[2] gave an account of the movements and their propagation which was in the main correct, but our knowledge was greatly increased by the historical researches of Darwin. Among other important points Darwin showed that the power of perception was localized in the heads of the tentacles. Pfeffer established definitely the fact that the tentacles possessed contact-irritability, although Darwin had previously shown that drops of rain did not act as stimuli, and that a solid body only acts as a stimulus when it is pushed through the slimy excretion into direct contact with the head of the tentacle.

The sensitivity to contact-stimulation depends upon the stage of development and other conditions, but under favourable circumstances is nearly as great as that of the most sensitive tendrils, since Darwin found that a perceptible result was produced by rubbing a hair weighing 0·000822 of a milligram upon the head of a tentacle of *Drosera rotundifolia*. A single touch hardly produces any result, whereas repeated strong contact causes a curvature to begin in 10 to 20 seconds, and in 10 to 20 minutes the heads of the tentacles are pressed against the middle of the leaf.

The lamina of the leaves of *Pinguicula vulgaris*, *P. lusitanica*, and *P. alpina*[3] rolls inwards when subjected to mechanical and chemical stimuli. The excitation spreads to a certain distance from the point of application of the stimulus, but the leaf is only moderately sensitive, and it has not been determined whether the stimulus is perceived by the lamina or by the heads of the numerous small stalked glands present on the under surface.

The mechanics of the movement. The curvature of a tendril produced by contact

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[1] Roth, Beiträge z. Botanik, 1782, T. 1, p. 60.

[2] Nitschke, Bot. Ztg., 1860, p. 229; 1861, pp. 224, 234, 253.

[3] Darwin, l. c., p. 374; Pfeffer, l. c., p. 516. Cf. also Klein, Cohn's Beitr. z. Biologie, 1883, Bd. III, p. 163; Goebel, l. c., p. 186.

has already been shown to be connected with a transitory acceleration of growth, and the bending of the sporangiophores of Mucorineae is also a growth-curvature. Batalin's[1] measurements, though not fully satisfactory, indicate the same to be the case for *Drosera*. Here also a transitory acceleration of growth appears to result from stimulation, but further research is required to make this certain. The conclusion that we are dealing with a growth-curvature is supported by Corren's observation that the curvature remains permanent when a stimulated tentacle of *Drosera* is suddenly killed by immersal in boiling water[2].

As in the case of tendrils, the causes inducing the changed rates of growth are unknown. De Vries'[3] supposition that the curvature was in the first instance due to an elastic stretching of the cell-wall by turgor is as inapplicable to the tentacles of *Drosera* as to tendrils, and in any case the curvature of the unicellular sporangiophore of *Phycomyces* could hardly be due to a rise of turgor unless the cell-wall on the convex side became at the same time more extensible.

SECTION 19. **Curvatures produced by Chemical Stimuli.**

We are here concerned primarily with the curvatures due to diffuse chemical stimuli, such as must occur whenever the growth of the opposite sides of a dorsiventral organ is unequally affected. Chemonastic reactions of this kind, like thermonastic responses, are rarely pronounced in character, but the action of chloroform causes a strong curvature in the pulvini of *Mimosa pudica*[4], as well as in tendrils[5], which also respond to treatment with a dilute solution of iodine. In addition, the rarification of the surrounding air causes, when pronounced, a certain alteration in the position of the leaflets of *Mimosa* and of the stigmas of *Mimulus*[6].

This power of chemonastic movement is, however, especially well developed in certain carnivorous plants, and it is shown in response to such substances as proteids, salts of ammonium, and phosphates. The chemonastic movement resembles that produced by contact-stimulation in the case of the tentacles of *Drosera* and the leaves of *Pinguicula*. Contact, however, causes a sudden closure of the leaflets of *Dionaea*, whereas chemical stimulation induces a gradual closure, which may take as long as a day when the stimulus is a feeble one[7]. In addition, after mechanical stimulation the leaves remain hollow so that they enclose a cavity, whereas

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[1] Batalin, Flora, 1877, p. 39.

[2] Correns, Flora, 1892, p. 126.

[3] De Vries, Bot. Ztg., 1886, p. 5.

[4] Pfeffer, Physiol. Unters., 1873, p. 64.

[5] Correns, Bot. Ztg., 1896, p. 16. This author also states that ammoniacal vapours induce a certain curvature in tendrils.

[6] Correns, Flora, 1892, pp. 97, 146, 148. On *Mimosa* cf. also Bonnier, Revue générale de botanique, 1892, T. IV, p. 525.

[7] Darwin, Insectivorous Plants, 1875, p. 297. The progress of the movement was also followed in detail by Darwin (The Power of Movement in Plants, 1880, pp. 239, 241, 261).

chemical stimulation causes them to press closely together, and hence also against the body of a captured insect[1].

Since proteids, ammonium salts, phosphates and other substances act as stimuli, the products of the digestion of a captured insect or of a piece of meat or egg-albumin always induce a chemical excitation. Darwin found that ammonium phosphate was more active than any other substance, for a drop of water containing 0·000423 of a milligram of this substance caused a curvature when placed upon the head of the tentacle. The same result was produced by 0·0025 of a milligram of ammonium nitrate and 0·0675 of a milligram of ammonium carbonate. Darwin also found that phosphates, and to a less degree camphor, a few ethereal oils, and in fact most varied substances acted as stimuli, but not certain alkaloids, so that all substances containing nitrogen are not chemical excitants. Darwin observed that the irritability of the tentacles of *Drosera* was suppressed by the application of small amounts of potassium salts, and this has been confirmed by Correns[2]. The latter author also finds that distilled water produces a feeble curvature, so that it remains an open question to what extent the response or lack of response to particular substances is due to external circumstances or to the presence of traces of potassium salts. It is possible that the stimulating action of distilled water is due to its dissolving away or diluting substances present in the glandular excretion, which by causing a difference of concentration in regard to the cell-sap might induce an excitation. In addition it is not sufficiently certain whether the inactivity of certain substances is or is not due to their non-absorption. Since, however, in general absorption is a preliminary to excitation, one may follow Munk[3] in speaking of absorption stimuli and digestive movements, although this must not be taken to indicate that only nutritive substances act as stimuli.

The association of a mechanical with a chemical irritability is of biological importance to carnivorous plants, although in other cases the one form of irritability may be developed but not the other[4]. Tendrils and the stamens of Cynareae are hardly or not at all responsive to chemical stimuli, but are readily excitable by mechanical ones. Chemical stimuli appear to have a more intense and prolonged action than mechanical ones in the case of the carnivorous plants, and in fact the mechanical excitability is so feeble in *Drosera binata* that it was overlooked by Morren[5]. It

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[1] Darwin, 1876, l. c., p. 307; Batalin, Flora, 1877, p. 134.

[2] Correns, Bot. Ztg., 1896, p. 25.

[3] Munk, Die elektr.- u. Bewegungsersch. an *Dionaea*, Reichert und du Bois-Reymond's Archiv, 1876, p. 98.

[4] Darwin (1875, l. c.) was the first to distinguish between mechanical and chemical excitation. The prolonged closure over insects was observed earlier, but was either unexplained or ascribed to the continuance of the mechanical excitation. This explanation was, in fact, given by Oudemans (Bot. Ztg., 1860, p. 163) in the case of the leaf of *Dionaea*.

[5] Morren, Note sur le *Drosera binata*, 1875, p. 10 (reprint from Bull. de l'Acad. royale de Belgique, 2^{e} sér., T. XL). The mechanical excitability was detected by Darwin, l. c., p. 256, and by Goebel, Pflanzenbiol. Schilderungen, 1893, Bd. II, p. 199. Darwin (l. c., p. 270) also found that the leaf of *Drosera* was still excitable by proteids when almost inexcitable by mechanical stimuli.

is owing to this fact that when all the products of digestion have been absorbed the leaves of *Drosera*, *Dionaea*, and *Aldrovanda* re-expand, although a mechanical excitation may still be exercised by the undigested remains. Since, however, it is entirely a question of specific excitability it is not surprising to find, as was shown by Darwin, that in the case of the leaf of *Pinguicula vulgaris* a chemical excitation does not persist much longer than a mechanical one. Conjoint excitation produces varying results, and although the summation is usually positive, chemical stimulation causes the leaf of *Dionaea* to be less responsive to mechanical stimuli[1].

Both mechanical and chemical stimuli are perceived by the heads of the tentacles of *Drosera*, whereas the hairs on the leaf of *Dionaea* are especially responsive to mechanical stimuli and much less so to chemical excitations. The small gland-hairs of *Dionaea* appear to be the special receptive organs for chemical stimuli, but show little or no mechanical excitability[2]. The motor-mechanism excited by both forms of stimulation may, however, be of similar character, and this applies even when, as in the leaf of *Dionaea*, the movements induced by mechanical excitations are more rapid than those produced by chemical stimuli.

Every vital response produced as the result of the chemical quality of an absorbed substance may be regarded as being due to a chemical excitation. This applies to all chemonastic movements, whether induced by the presentation of some special material or by a quantitative change in the composition of a nutrient medium. The chemical excitation may naturally be transitory in character and need not necessarily produce a permanent alteration. Instances of the former are afforded by the contraction of the stamens of *Berberis* and the closure of the stigmas of *Mimulus* produced by sudden exposure to ammonia vapour, and also by the contraction of the stamens of *Berberis* and *Helianthemum* induced by a sufficiently rapid fall in the partial pressure of the oxygen in the surrounding air[3]. Since, however, in these cases as well as in that of *Mimosa* the movement may be excited by various internal disturbances, it is impossible to say whether a chemical excitant directly awakens a special chemical irritability, or acts indirectly by inducing internal disturbances which operate as the immediate exciting agencies.

The same stimulus may in many cases excite several dissimilar responses simultaneously, and in carnivorous plants stimulation may not only induce movement but may also awaken, modify, or accelerate the

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[1] Darwin, 1875, l. c.; Munk, l. c., p. 99.

[2] Cf. Darwin, l. c., pp. 267, 295.

[3] Correns, Flora, 1892, p. 151. It is worthy of note that it is not every plant which readily responds to seismonic stimuli that can be stimulated in this way. As Correns showed, the excitation is not due to the mechanical disturbances induced by the sudden evacuation of the air. It is further to be expected that many substances may produce a response in *Mimosa* if only they penetrate with sufficient rapidity to produce a 'shock-effect.'

secretory activity of the digestive glands. The secretory activity of the leaf of *Dionaea* is in fact only aroused by stimulation, whereas the glandular heads of the tentacles of *Drosera* continually excrete mucilage and water, but do so more rapidly when chemically and also when mechanically stimulated. At the same time the excretion of acid begins, so that the reaction of the digestive fluid alters much as it does in the stomach of a carnivorous animal[1]. Although the pitchers of *Nepenthes* and the leaves of *Drosophyllum lusitanicum* have no power of independent movement, the secretion of water, mucilage, and enzymes by the glands is awakened or accelerated to a certain extent by chemical stimuli. Chemical excitation, on the other hand, induces both movement and secretion in the case of the leaf of *Dionaea*, whereas mechanical excitation induces movement only[2]. It will without doubt ultimately be found possible to excite excretion without movement even in those cases where both occur together normally; and in fact, according to Darwin, a mechanical stimulus induces movement without secretion in the leaf of *Pinguicula*, whereas ammonium carbonate produces secretion without movement. In certain cases, however, a separation of this kind may not be possible owing to the fact that the excitation of the motor-mechanism may unavoidably awaken changes leading to secretory activity and vice versa.

Various visible changes in the cell-contents are associated with the secretory activity, and these are also shown by the gland-cells of the pitchers of *Nepenthes* and the leaves of *Drosophyllum*, which possess no power of movement. These changes are therefore presumably of secretory origin, although it is possible that other visible changes in the cells may be associated with the response to stimulation by movement. Neither the causes nor the genetic relationship of these changes are, however, satisfactorily known, although it appears as though the waxing and waning of the amount of nuclear chromatin is the direct result of secretory rest and secretory activity respectively.

The intracellular changes have been studied by Darwin on *Drosera rotundifolia* and by Gardiner also on *Drosera dichotoma* (= *Drosera binata*)[3], in which a change of coloration accompanies the aggregation beginning in the head and progressing

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[1] Darwin, Insectivorous Plants, 1875, p. 85. Facts in regard to other plants are also given by Darwin.

[2] According to Macfarlane (Contrib. from the Bot. Lab. of Pennsylvania, 1892, Vol. I, p. 37), a certain secretory activity is awakened in the leaf of *Dionaea* by strong mechanical or electrical excitation.

[3] These changes were first observed by Darwin (l. c., p. 38), who did not, however, distinguish between aggregation and precipitation (granulation), as did Schimper (Bot. Ztg., 1882, p. 231); de Vries (ibid., 1886, p. 1); and, at a later date, Gardiner (Proc. of the Royal Soc. 1886, Vol. XXXIX, p. 229). Huie, Quarterly Journal of Microscopical Science, 1896, Vol. XXXIX, p. 387; 1899, Vol. XLII, p. 203; Rosenberg, Physiol.-Cytol. Unters. über *Drosera rotundifolia*, 1899; and Haberlandt, Sinnesorgane, 1901, p. 94, have paid especial attention to the changes in the gland-cells.

along the stalk of the tentacle[1]. These intracellular aggregations involve in the cells of the tentacle-stalk, according to de Vries, Gardiner, and Schimper, an increase in volume of the protoplasm and a decrease in volume of the cell-sap[2]. At the same time active protoplasmic streaming is excited, and the vacuoles increase in number. The shapes of the vacuoles also alter, and this naturally involves changes of shape in the protoplasm, although Darwin attached undue importance to the latter. A little later a precipitate, the granulation[3], usually appears in the cell-sap when strong chemical stimuli are applied, but it is usually absent after weak mechanical or chemical excitation. The precipitate is usually due to the excretion of tannin into the cell-sap, which finally forms rounded masses, often tinged red owing to the absorption and accumulation by them of the red colouring-matter in the cell-sap[4]. It need not, however, always be tannin which separates out and is precipitated, although similar precipitations are produced by the action of ammonium carbonate, caffein, and other substances in the cell-sap of many other plants which contain tannin.

Hence it is possible that the granulation resulting from stimulation is also due to the production of substances which precipitate the tannin in the same way that ammonium carbonate does when applied to the head of a tentacle. Since mechanical stimulation may influence the secretory activity, it may also lead when sufficiently intense to a sufficient production of the materials responsible for the precipitation.

The intracellular changes have not been followed any further in the living gland-cells at the head of the tentacle of *Drosera*. According to the researches of Huie, and also of Rosenberg, carried out on fixed material, these cells show a decrease in the volume of the protoplasm and an increase in the volume of the cell-sap after stimulation, that is exactly the reverse changes to those occurring in the cells of the stalk. It remains to be seen, however, whether the difference is due to the fact that the observations on the heads of the tentacles were made on fixed material, but those on the stalk-cells upon living material. It is possible that the active excretion of mucilage and other materials from the gland-cells may lead to a diminution in their protoplasmic contents[5], and in fact the amount of chromatin in the nuclei of the gland-cells of animals appears to decrease greatly in amount during active secretion. Both Huie and Rosenberg have found that, especially after long chemical excitation, the nuclei of the gland- and stalk-cells decrease in volume, while their chromatin threads assume an appearance and differentiation resembling the initial stages in mitotic nuclear division.

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[1] Gardiner, l. c.

[2] On the changes of volume in the cell cf. Pfeffer, Plasmahaut u. Vacuolen, 1890, p. 290. According to de Vries (l. c., p. 30) the turgor of the cell as determined by plasmolysis is uninfluenced by the aggregation, whereas Gardiner (l. c., p. 232) assumes on insufficient grounds that a fall of turgor ensues.

[3] The term was suggested by Goebel, Pflanzenbiol. Schilderungen, 1893, Bd. II, p. 198. Darwin (l. c., p. 263) found that aggregation is produced in the leaf of *Dionaea* by chemical but not by mechanical excitation.

[4] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1886, Bd. II, p. 244; Flora, 1889, p. 52.

[5] It is uncertain what the importance of Gardiner's 'rhabdoid' may be (l. c., p. 230). This structure occurs in the cells of *Drosera* and *Dionaea* and, according to Gardiner, increases in size as the result of stimulation, whereas Macfarlane (l. c., p. 36) could detect no such increase of size in the rhabdoid of *Dionaea*.

The aggregation and precipitation produced by stimulation gradually pass away again, not only in the cells of intact tentacles, but also in sections cut from them. In the latter case repeated washing accelerates the solution of the precipitated materials by removing the soluble diosmosing products as fast as they are formed. The precipitation resulting from stimulation can only be regarded as a chemical reaction due to the production of a precipitating substance, whereas the protoplasmic aggregation as well as the changes in shape and differentiation of the nucleus are vital responses[1]. That the aggregation is associated with the secretory activity is shown by the fact that it is produced by nitrogenous and other substances, not only in the cells of the tentacle stalk of *Drosera*, but also in cells of the non-motile glands of *Sarracenia*, *Nepenthes*, and *Drosophyllum*[2], and can apparently be also induced in many cells which have a somewhat analogous power of secretion. It is also known that changes of shape are shown by the nucleus and cytoplasm of a few plant-cells and various animal-cells[3] during active secretion. This is in accord with the fact that many chemical agencies which act fatally when concentrated, induce various changes in the shape and visible structure of the protoplasm when applied in diluted form.

The conduction of the stimuli. The visible nature of the aggregation and precipitation enables the progress of the excitation to be followed from cell to cell. It has, however, not yet been determined by comparison whether the motory and aggregation reactions involve the conduction of a single or of two separate stimulatory processes. Darwin[4] observed that when the head of a tentacle of *Drosera* was moderately strongly stimulated, a neighbouring decapitated tentacle curved but showed no aggregation, whereas aggregation appeared in the head of a neighbouring intact tentacle, and spread in a reflected fashion downwards in the cells of the stalk. Apparently, therefore, a stimulus inducing aggregation was propagated from the head in the reverse direction to the primary stimulus inducing curvature and exciting the head. When the stimulus is more intense, however, the aggregation is directly propagated to a greater distance and spreads to neighbouring decapitated tentacles.

If the stimuli for each reaction are distinct, they are at least conducted along the same path, that is in the parenchyma cells and in the living elements of the vascular bundles. That the parenchyma cells are capable of conduction is shown by an experiment of Darwin's in which the vascular bundles were cut across and yet a stimulus was transferred through the tentacle. In addition the aggregation may be propagated from cell to cell of the epidermis. According to Batalin[5], stimuli travel more rapidly along the vascular bundles than through the parenchyma. This is probably the result of the elongation of the living cells of the vascular bundles,

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[1] Precipitating substances are not present in all secreting cells, even of carnivorous plants, and hence, according to Goebel (l. c., p. 119, footnote), no granulation is produced in the secretory gland-cells of *Utricularia* and *Pinguicula* as the result of stimulation.

[2] Cf. Schimper, l. c., p. 231; Goebel, l. c., p. 199.

[3] For the literature see Rosenberg, l. c., p. 112.

[4] Darwin, Insectivorous Plants, p. 242. [Darwin does not state that the decapitated tentacle showed no aggregation, but that it showed less aggregation, and further, the aggregation disappears first at the base of the tentacle and travels upwards.]

[5] Batalin, Flora, 1877, p. 66. Cf. also Zeigler, Compt. rend., 1874, T. LXXVIII, p. 1417.

for Darwin found that stimuli travelled more rapidly parallel to the long axes of the parenchyma cells than transversely to them. It is for these reasons that stimuli radiate mainly centripetally from the marginal tentacles, and centrifugally from those near the centre, but are only propagated slowly and feebly tangentially.

It appears probable that the conduction of stimuli, at least in *Drosera*, involves a transference of stimulatory materials, either by the diffusion of an absorbed substance or as the result of the formation of stimulatory materials in the secretory cells which diffuse to neighbouring ones and excite aggregation in them. In this case the transference of the stimulus would be merely a matter of translocation, aided possibly by the fact that the secondarily excited cells themselves begin to produce stimulatory materials. The transference of these might take place if they are diffusible, without the aid of any interprotoplasmic connexions, and, in fact, aggregation and granulation may be produced in the cells of the tentacle of *Drosera* by the direct application of ammonium carbonate.

Comparative investigations on other plants will, without doubt, aid in the elucidation of these problems, but so far it is only known that the effects of mechanical stimuli are propagated through the parenchyma of the leaf of *Dionaea*, and more rapidly along the vascular bundles[1]. No aggregation is produced by mechanical stimuli in *Dionaea*, but this change and the chemonastic excitation due to absorbed proteids appear to follow the same path but to travel more slowly. The rapid transference of mechanical stimuli in the leaf of *Aldrovanda* must, however, take place through the parenchyma of the leaf, since in the leaf-lobes no vascular bundles are present.

SECTION 20. **The Propagation of Mechanical and Chemical Stimuli.**

The influence of mechanical and chemical stimuli is often restricted to the region immediately surrounding the point of application, or to the pulvinus when this is the only irritable portion. On the other hand, *Mimosa pudica* affords a well-known and striking instance of the transmission of stimuli, for under favourable conditions burning or cutting off the terminal leaflets of one of the segments of the leaf may cause all the leaves and leaflets to be stimulated in succession. The stimulus is conducted somewhat less readily in *Biophytum sensitivum*[2], while in the trifoliate leaves of *Oxalis acetosella* the reaction is restricted to the leaflet directly stimulated[3].

In the case of the highly irritable stamens of *Berberis* and *Centaurea* the stimulus is not transmitted from an excited stamen to neighbouring

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[1] Darwin, l. c., p. 313; Batalin, l. c., p. 147.

[2] G. Haberlandt, Ann. du Jard. bot. de Buitenzorg, 1898, Suppl. II, p. 33; Sinnesorgane im Pflanzenreich, 1901, p. 88. On *Oxalis dendroides* cf. Macfarlane, Biological Lectures, 1894, p. 194.

[3] Cohn, Verhdlg. d. schles. Ges. f. vaterl. Cultur, 1859, p. 56; Pfeffer, Physiol. Unters., 1873, p. 74.

ones, and no response is aroused when the corolla is cut through above or below the insertion of the stamens[1]. Stimulation of one stigma-lobe of *Martynia lutea*, *M. proboscidea*, and *Mimulus cardinalis* causes the other to move, but not in the case of the stigmas of *Mimulus luteus*[2]. An excitation is propagated with extreme rapidity from one leaf-lobe of *Dionaea* to the other, while in the case of the fairly sensitive stamens of *Sparmannia africana*[3] irritation of one stamen spreads to a limited extent to the neighbouring ones. In the case of *Phycomyces*, on the other hand, no conduction of stimuli appears to take place, whereas a contact-stimulus is rapidly propagated to the outer side of a tendril and also to some extent longitudinally. The leaf of *Drosera* again affords a specially good instance of the conduction of stimuli, for as the result of stimulating the head of a single tentacle all the tentacle-stalks on the leaf may be caused to curve inwards. Here the receptive and motory zones are distinct, and, according to Oliver, the same is the case in the labellum of *Masdevallia muscosa*, which appears to possess seismonic irritability. In all the other cases that have been investigated the motory zone seems also to be capable of perception, for one can hardly ascribe a vital power of perceiving stimuli to the leaf-laminas or stems of *Mimosa* simply because the movement of water produced when they are cut, crushed, or burned acts as a stimulus to the motile pulvini[4].

The above instances suffice to show that a high sensitivity to contact or seismonic stimuli does not necessarily involve a pronounced power of conducting stimuli, and that the transference of the stimuli may either be vital or purely mechanical. The latter is the case in all organs which respond to seismonic stimuli, for the collapse of one stimulated cell excites the next, this the next, and so on. In the case of *Mimosa pudica* the stimulus is propagated by means of a movement of water or hydrostatic pulsation which is able to travel through dead portions of the stem and leaf, and which excites the pulvini on which it impinges. Since this can only occur when a proper connexion is maintained between the conducting channels and the responding organ, it is not surprising that the stamens of *Berberis* and of Cynareae cannot be excited in this way.

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[1] Pfeffer, Jahrb. f. wiss. Bot., 1873–4, Bd. IX, p. 317.

[2] Oliver, Ber. d. bot. Ges., 1887, p. 167; Hansgirg, Physiol. u. Phycophytol. Unters., 1893, p. 47.

[3] Morren, Rech. s. l. mouvement d'étamines du *Sparmannia*, 1841, p. 23 (reprint from Mém. de l'Acad. de Bruxelles, T. XIV).

[4] The movements observed by Darwin (The Power of Movement in Plants, 1880, p. 127) when the laminas of the cotyledons of *Oxalis sensitiva*, and of a few species of Cassia, were strongly rubbed were probably the result of the ensuing movements of water stimulating the motile pulvini. Goebel (Pflanzenbiol. Schilderungen, 1893, Bd. II, p. 201, footnote) observed incidentally that in the case of a feebly irritable leaf of *Dionaea* one leaf-lobe could be excited by stimulation of the other leaf-lobe, but not directly.

It is, however, probable that the conduction of stimuli in the stigmas of *Martynia* and *Mimulus*, in the stamens of *Sparmannia*, and possibly in the labellum of *Masdevallia* takes place in some other way. Furthermore, the transference of stimuli in organs sensitive to contact-stimuli cannot possibly be due to movements of water, since these organs do not respond to repeated bending with its attendant movements of water. In such cases we may assume that we are dealing either with a vital transmission of stimuli which can only take place through intervening protoplasm, or with a transference of stimulating materials, or of an electrical excitation from cell to cell, for which the existence of living interprotoplasmic connexions is not essential. It is in fact not inconceivable that dissimilar modes of conduction may be excited at the same time. A simple instance of this is afforded when the disturbance due to the response of a single stimulated cell serves for the propagation of the stimulus through the whole of the irritable organs, but not through the intervening non-motile tissue to neighbouring motile organs. In addition, a mechanical disturbance can be transferred so as to excite the rapid closure of the leaf of *Dionaea*, but not the slow movements resulting from chemical stimulation.

According to Oliver[1], the transference of stimuli in the labellum of *Masdevallia* is restricted to the vascular bundles, although it does not appear to be due to a movement of water as in *Mimosa*. Even here, however, a slow vital transmission of stimuli may also be possible, while a transference of stimuli across active parenchyma tissue occurs both in the pulvini of *Mimosa* and in irritable stamens. In addition, stimuli are transferred mainly or entirely through parenchyma cells in the case of the stigmas of *Mimulus* and *Martynia*, according to Oliver[2], when these respond to seismonic stimulation, for the stimulation of one stigma may excite the other after the intervening vascular bundles have been severed. Both mechanical and chemical stimuli appear to be conducted through the parenchyma cells of the tentacles of *Drosera*, but the rate of propagation appears to be more rapid along the vascular bundles.

The transmission of stimuli is in most plants extremely slow, but in *Mimosa pudica* a rate of propagation of 15 mm. per second has been observed[3], and in the pulvinus itself, as well as in the stamens of *Centaurea*, stimuli may travel still more rapidly. On the other hand, the impulse radiating from the chemically or mechanically excited head of a tentacle of *Drosera* does not appear to travel at a much greater rate than 10 mm.

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[1] Oliver, Annals of Botany, 1888, Vol. I, p. 249.

[2] Oliver, Ber. d. bot. Ges., 1887, p. 168.

[3] Dutrochet, Recherch. anat. et physiol., 1824, p. 80; Bert, Mém. de l'Acad. de Bordeaux, 1870, T. VIII, p. 47; Pfeffer, Jahrb. f. wiss. Bot., 1873–4, Bd. IX, p. 325; G. Haberlandt, Das reizleitende Gewebesystem der Sinnpflanze, 1893, p. 69. On the slow rate of propagation of stimuli in *Biophytum sensitivum*, cf. Haberlandt, Ann. du Jard. bot. de Buitenzorg, 1898, Suppl., p. 35.

per minute, for ten or twenty seconds after the head of a tentacle has been strongly stimulated a curvature may be shown in a region of the stalk, distant 2 or 3 mm. from the head. These times, it is true, include the latent periods of perception and reaction, which can only be eliminated by comparing the times at which curvature is shown at varying distances from the head. In most plants, however, stimuli travel still more slowly than in *Drosera*, and in this way plants largely avoid the waste of energy which would be involved in a continual attempt to adjust themselves to transitory variations in the external conditions.

The exact determination of the velocity of propagation of stimuli is difficult, and even when measured by the appearance of a reaction the rate will depend not only upon the specific nature of the plant but also upon the external conditions. A fall of temperature, a decrease of turgidity, and the action of chloroform all lower the rate of transmission of stimuli in *Mimosa* and in other plants, and ultimately produce a complete cessation of conductivity[1]. A result of this kind may be due either to a direct action upon the conductivity, or to an action upon the sensitivity, excitability, or power of response, or may be due to a combination of these factors. The importance of a close study of the influence of the external conditions upon conductivity, excitability, and the power of response cannot be overestimated, and the fact that stimuli may travel through etherized or dead pieces of the stem of *Mimosa* shows that in this case the transmission of seismonic stimuli is not vital in character.

Dutrochet[2] was the first to show that stimuli are conducted through the vascular bundles of *Mimosa pudica*, and he also came to the correct conclusion that the transmission was due to a pulsation of water. Pfeffer[3] subsequently showed that the stimulus was able to travel over chloroformed parts of the stem, and Haberlandt found that dead regions of the stem and leaf retained their conductivity some time after they had been killed[4]. We are, therefore, fully justified in ascribing the transmission of the stimulus to the movements and changes of pressure of the water in the vascular bundles, and when a cut is made in the stem, a stimulus is only exercised when the knife penetrates the vascular bundles and allows the escape of a drop of water. The stimulation of the neighbouring leaves at once follows, and, as the stimulus spreads, all the leaves and leaflets may be in succession excited when the plant is in a highly irritable condition. No stimulation or conduction takes place, however, when the plant's turgidity is so low that no drop of water escapes

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[1] Cf. Pfeffer, l. c., p. 326.

[2] Dutrochet, Recherch. anat. et physiol., 1824, p. 69; Mém. p. servir à l'histoire d. végétaux, Bruxelles, 1837, p. 272.

[3] Pfeffer, Jahrb. f. wiss. Bot., 1873-4, Bd. IX, p. 308.

[4] G. Haberlandt (Das reizleitende Gewebesystem d. Sinnpflanze, 1890, p. 35) observed a propagation of the stimulus over a 10 cm. length of dead stem; Macdougal (Botanical Gazette, 1896, Vol. XXII, p. 296) over as much as 30 cms. The mode of treatment and the maintenance of turgidity are factors of considerable importance.

when an incision is made in the vascular bundles. Similarly the transference of an excitation from one pair of leaflets to another in the intact plant only takes place when it is sufficiently turgid, and may hence safely be assumed to be due to the hydrostatic pulsation aroused by the sudden escape of water from the directly-stimulated cells, possibly aided by the sudden bending of the part of the vascular bundles lying in the pulvinus. Since this pulsation is usually comparatively feeble, it is only natural that the abscission or burning of a leaflet should produce an effect which, being more intense, is propagated to a greater distance than that due to touching a single leaflet.

According to Haberlandt, the conduction of stimuli takes place in the tannin-tubes[1] of the phloem, which transfer positive or negative pressure waves to the pulvini, and these mechanically excite the motile cells. Macdougal, however, denies that the stimuli are transmitted by hydrostatic pulsation in this manner. Haberlandt's conclusion is mainly based upon the fact that the drop of liquid which escapes from an incised vascular bundle is, for the most part, derived from these tannin-sacs. Transmission is, however, also possible in their absence, for Dutrochet[2] found a conduction of stimuli was still possible when incisions were made through all the tissues excepting the wood. Haberlandt has also overlooked the fact that in a dead portion of the stem the conditions for the transference of a pressure wave through the sap-containing tannin-sacs are not fulfilled[3]. In addition Borzi[4] has found that the conduction of stimuli in *Aeschynomene indica* and *Neptunia oleracea* takes place in tissues which do not possess any continuous system of tannin-sacs.

Macdougal found that no stimulation was produced when as large a cut surface as possible of the shoot was submerged in a solution of potassium nitrate, so that a sudden fall of turgor was produced in the exposed tissues, including the tannin-sacs. Negative results were also obtained when the pressure with which water was driven into a cut surface of the stem was suddenly raised by three to eight atmospheres. Macdougal found that the rise of pressure was rapidly transmitted in the xylem vessels, and also in the tannin-sacs, to the furthermost shoots and leaves, so that it is evident that not every movement of water or change of pressure is able to transmit a stimulus to the pulvinus.

[These results of Macdougal's do not necessarily show that the transference of the stimulus is due to a special stimulatory substance, and indeed do not afford conclusive proof that the transference is not due to a hydrostatic pulsation.

The cells of *Chara* and *Nitella*, for instance, respond to seismonic stimulation

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[1] For details concerning these tubes and their contents, cf. Haberlandt, 1890, l. c., Physiol. Anat., 2. Aufl., 1896, p. 482; Baccarini, Bot. Centralbl., 1893, Bd. LIV, p. 171; Borzi, L'apparato di moto delle sensitive, 1899. (A reference is given in the Bot. Centralbl., 1899, Bd. LXXX, p. 351.) Since these tubes occur in other plants, and are primarily together with their contents of metabolic importance, they can only secondarily have developed a power of conducting stimuli in certain plants.

[2] Dutrochet, 1824, l. c., p. 69. Confirmatory results have been obtained by Haberlandt, 1890, l. c.; Macdougal, l. c.

[3] The living portion of the tube shuts itself off from the injured portion, according to Haberlandt, and without this no restoration of turgor would be possible in the tube.

[4] Borzi, l. c., p. 4.

(sudden pressure, or the impact of a falling body) by a temporary stoppage of streaming, and the stimulus may be transferred to a neighbouring cell by a hydrostatic pulsation in the cell-sap. The pulsation must, however, be a sharp one, and changes of pressure produced in the same way as in Macdougal's experiment are ineffective as stimuli even when high pressures are used. A hydrostatic impulse produced by a blow upon a piston-rod does, however, produce a sufficiently intense wave to act as a stimulus to the cell, and to be capable of propagation to the next one[1]. It is evident, therefore, that this question needs further investigation before a definite conclusion can be made. It is in any case by no means improbable that other changes besides the hydrostatic pulsation may co-operate in the transmission of stimuli in *Mimosa*, and it hardly needs to be mentioned that the structure of the pulvinus affords no evidence as to the means by which the stimulus is transferred to the motile cells. The mere existence of inter-protoplasmic communications[2] does not indicate whether these are of fundamental importance in a particular case, and the manner in which stimuli travel from one part to another is dependent upon the course and connexions of the vascular bundles, whether the stimuli travel in the phloem or in the xylem[3].]

Biophytum sensitivum also responds, according to Macdougal[4], to stimuli travelling through a dead portion of the leaf axis, although, according to Haberlandt[5], this is not the case. A peculiarity of the latter plant[6] lies in the fact that the removal of a leaflet acts as a sub-maximal stimulus to the pulvini of the remaining leaflets, and this incomplete movement is repeated several times without any further stimulus being applied. Since this periodicity might be produced in various ways, further research is necessary to reveal its mode of origin. Under appropriate periodic stimulation a periodic movement may be induced in the leaves of *Mimosa pudica*, owing to the gradual recovery or increase of excitability, but it does not follow that the periodic movements of the leaflets of *Biophytum* are produced in a similar way. If we are actually dealing in this case with a prolonged stimulatory action, it can hardly be due to a temporary hydrostatic pulsation or movement of water.

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[1] Ewart, Protoplasmic Streaming in Plants, 1903, p. 72.

[2] Haberlandt's statement (1890, l. c., p. 25) that no interprotoplasmic communications exist between the tannin-sacs, and between the collenchyma cells is incorrect according to Kienitz-Gerloff (Bot. Ztg., 1891, p. 25), but the positive statement of this author may be accepted with some caution.

[3] Cf. Pfeffer, l. c., p. 318; Haberlandt, l. c.

[4] l. c., p. 296.

[5] Haberlandt, Ann. du Jard. bot. de Buitenzorg, 1898, Suppl. II, p. 38. On *Oxalis dendroides* cf. Macfarlane, Biological Lectures, 1894, p. 194.

[6] Haberlandt, l. c., p. 35.

PART IV

PHOTONASTIC, THERMONASTIC, AND HYDRONASTIC CURVATURES

SECTION 21. **General.**

Since the growth of the different cells and tissues of an organ is unequally affected by temperature, light, and the percentage of water, physiologically dorsiventral organs are often caused to perform thermonastic, photonastic, or hydronastic curvatures by variations in one of the above factors. These curvatures, though often trifling in amount, may be in many cases pronounced, as in the case of the daily movements[1] dependent upon variations in the intensity of the light, or upon changes of temperature. Instances of these movements are afforded by those flowers which open and close at definite periods of the day, and by those leaves which perform sleep movements at night when the light is feeble, or at midday when it becomes intense. In such cases the organ assumes a position best suited to the external conditions, and within certain limits the amount of movement corresponds to the degree of change in the external conditions, such as illumination, temperature, or supply of water. At low temperatures or under feeble illumination the peduncles of certain plants curve downwards instead of being erect, while in other cases the foliage or floral leaves remain pressed together, so that the flower of such a plant under these conditions becomes cleistogamous and never opens. Such flowers may be said to be facultatively cleistogamic.

It often happens that during these aitionastic movements the curvature is at first excessive, so that the ultimate position of equilibrium is only attained after a few oscillations. Thus a sudden rise of temperature causes the flowers of *Crocus* and *Tulipa* to open widely at first, and this is followed by a gradual assumption of the less expanded position which they maintain so long as the new conditions remain unaltered. The same progress of the reaction can be traced when the temperature is lowered, if by removing five of the perianth-segments the remaining one is allowed to perform its full amplitude of movement. When all the segments are present they press against one another, and so prevent any movement in excess of that required to close the flower. Similar results are obtained by illuminating or darkening flowers and foliage-leaves capable of photonastic reaction. Hence it may happen especially in the cases of foliage-leaves that the change from light

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[1] Since the term 'tropism' is reserved for curvatures produced by unilateral stimuli, it becomes necessary to change the term 'nyctitropic' used by Darwin (The Power of Movement in Plants, 1880, p. 281) into that of 'nyctinastic.'

to darkness may produce a pronounced temporary but no permanent curvature, since the leaf gradually returns to approximately the same position that it occupied when illuminated.

The ultimate position is naturally independent of the transitory oscillations, which are due to the fact that the antagonistic tissues attain their new positions of equilibrium in different ways, or at least with unequal rapidity. Hence oscillations are absent when the change in the external conditions takes place gradually, as also are the temporary curvatures shown only when the temperature or illumination is suddenly altered. These considerations have been shown experimentally to apply to the thermonastically-reacting flowers of *Crocus* and *Tulipa*, and to the photonastically-reacting leaves of *Impatiens* and *Robinia*. Nor is it surprising that slowly reacting or comparatively insensitive organs should gradually assume a new position in response to sudden and pronounced changes of temperature or illumination without exhibiting any perceptible transitory oscillations. A good analogy is afforded by two metal rods riveted together, and one of them being surrounded by a non-conductor, for when the system is suddenly warmed a transitory curvature will be produced independently of whether the rods have the same or dissimilar coefficients of expansion, that is independently of whether the rods ultimately straighten again or remain permanently curved.

Obviously the relationships are not quite so simple in a living organism as in this instance, for although the curvatures are primarily due to the unequal growth or expansion of the opposed tissues, the causes which induce these variations of growth, or which cause the tendency to elastic expansion or contraction, are extremely complex in origin. In addition, the realized curvature, like vital reactions in general, excites regulatory stimuli and counteractions, so that the progress of the response and the ultimate position assumed depend upon the conjoint action of these factors with the original stimulus. It has already been mentioned that special conditions may be introduced by accommodation, by changes of excitability, and by alterations in the power of response during excitation, even when the organ remains excitable during response.

Transitory disturbances may frequently be produced by sudden changes as the result of shock. For instance, a sudden change of temperature induces an acceleration of growth in the perianth-segments of *Crocus* and *Tulipa*, while a sudden change of illumination has the same effect upon foliage and floral leaves capable of photonastic reaction. This is of importance in so far as it increases the power and rapidity of response. In addition, owing to the unequal responses of the inner and outer sides of the perianth-segments, a sudden fall of temperature produces a rapid closure of the flower of *Crocus* even when the temperature is so low that growth ultimately almost entirely ceases. A similar transitory acceleration of growth is produced in tendrils by contact-stimulation, and presumably it would not be shown if all shock-effect was avoided by allowing the contact-stimulation to increase gradually from a sub-minimal to an optimal intensity.

Sudden changes in the external conditions probably leave no organism entirely unaffected, although no disturbance of growth or other pronounced reaction may be perceptible. Sudden variations of temperature and of illumination do, however, appear in general to excite feeble transitory disturbances of growth, and these have become especially pronounced in certain cases as the result of biological adaptation, so that, more especially in photonastic plants, a transitory acceleration of growth is produced even by a comparatively slow diminution in the illumination. All plants have not the same power of response, and there are even organs which appear to experience no shock-effect, although they change their position in response to alterations of temperature or illumination. It is even possible that in some cases a sudden change may produce a temporary depression of growth, just as a shock-stimulus causes a transitory fall of turgor in one-half of the pulvinus of *Mimosa pudica*, or a transitory cessation of streaming in a cell of *Chara* or *Nitella*.

The constant daily repetition of the sleep-movements of photonastic leaves induces a periodic rhythm which gradually disappears in darkness or under constant illumination. Under natural conditions the movements in the morning and evening result from the co-operation of the photonastic reaction with the after-effect of the previous ones, the photonastic rhythm being induced and not hereditary.

Aitionastic reactions do not always exert appreciable after-effects, for these are absent from the thigmonastic movements of bilateral tendrils and of the tentacles of *Drosera*. The same appears to apply to thermonastic movements, such as the opening and closing of the flowers of *Crocus* and *Tulipa*. Since, further, the daily variations of temperature are much more irregular than the daily changes of illumination, it is not surprising that the daily opening and closing of thermonastic flowers should be more irregular than the periodic movements of photonastic organs.

Photonastic, thermonastic, and hydronastic movements are often associated together under natural conditions, and may also be coupled with tropic responses due to unilateral stimulation. It is naturally necessary at first to determine the nature of each form of response before studying conjoint actions. Granted that an organ possesses definite properties, the character of its response can largely be predicted from what is known as to the general influence of the external conditions on growth. For instance, an opening movement may be converted into a closing one by an additional rise of temperature, if the temperature optimum for the previously epinastic side is lower than for the opposite more slowly-growing one.

Under constant external conditions only autogenic movements are performed, such as the expansion of the foliage and the opening of the foliage and flower-buds.

Flowers which periodically open and close behave like ephemeral ones under these conditions and open once only. The duration of both ephemeral and periodic flowers may vary considerably[1], and in fact at low temperatures the life of an ephemeral flower may be so prolonged that it is able to perform daily movements.

The flowers of *Crocus* do not open when the temperature is kept low, nor those of *Stellaria media* when the illumination is feeble. This is owing to the fact that at no period of development does the growth of the inner surface of the perianth-segments become active enough, as compared with that on the outer surfaces, to produce a separation of the closely applied leaves. An opening movement is, however, in part attempted during development, as is shown by the fact that if all the perianth segments are removed but one, this may curve at first nearly at right angles to the stalk, but subsequently straightens more or less. At still higher temperatures the segment expands outwards, but the opening of the flower is slower and less pronounced than at the optimal temperature. A sudden rise of temperature produces an opening movement which is temporarily in excess of the ultimate position for this temperature, and this may cause the temporary opening of a flower, when raised to a temperature at which it finally closes again. The same general considerations also apply to photonastic and hydronastic movements.

The uses of the movements. When feeble they are probably accessory reactions without any special biological importance. Moth-pollinated flowers which close in the daytime avoid the visits of useless insects, and economize scent, nectar, and pollen. Flowers which close at night keep the sexual organs protected from dew, and to a certain extent from injurious cooling[2]. The drooping of flower- and inflorescence-stalks, which causes many flowers to be inverted during the night, may be of use in the same way.

The sleep-movements of leaves and leaflets reduce the amount of surface exposed, and hence lessen the radiation of heat during clear nights. Darwin[3] showed that less dew formed on such leaves than on ones which had been fixed in the expanded condition. The latter suffered more than the normally sleeping leaves, and hence Darwin concluded that the nyctinastic movements were for the purpose of lessening temporary cooling during night as far as possible. Stahl[4], however, considers the utility of these movements to lie in the fact that the lessened formation of dew avoids the blocking of the stomata and the consequent hindrance to transpiration. If Stahl's

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[1] Cf. Oltmanns, Bot. Ztg., 1895, pp. 32, 52; Hansgirg, Physiologische u. Phycophytolog. Unters., 1893, p. 15; Kerner (Natural History of Plants, 1895, Vol. II, p. 211). [Hansgirg (l. c., p. 10) suggests the terms thermo-, photo-, and hydrocleistogamy to indicate the main causes which keep a facultatively cleistogamic flower permanently closed. Since the causation may vary at different times, these terms are as unnecessary and superfluous, as it would be to use special terms (mechano-cleistogamy, plaster-of-paris-cleistogamy) for the cleistogamy produced by tying-up a flower or embedding it in plaster-of-paris.]

[2] Hansgirg, l. c., p. 175; Kerner, l. c., Bd. II, p. 112. Die Schutzmittel des Pollens, 1873. Sprengel (Das entdeckte Geheimniss der Natur im Bau u. in d. Befruchtung d. Blumen, 1793, p. 13) considers the closing movements to be for the protection of the nectar.

[3] Darwin, The Power of Movement in Plants, 1880, pp. 286, 413; Bot. Centralbl., 1881, Bd. VIII, p. 77.

[4] Stahl, Bot. Ztg., 1897, p. 81. A detailed discussion of the biological utility of these movements is given by Stahl.

view is correct, the blocking of the stomata is more likely to be a serious matter by preventing the assimilation of carbon dioxide during the early morning hours. Both the avoidance of dew-formation and of cooling may be of importance, and possibly the sleep-movements may have still other biological advantages.

In many cases organs are brought into positions which enable them to utilize the light best or to avoid it when intense, and this may take place by the aid of photonastic reactions, coupled with tropic movements. Although photonastic reactions may often be feeble, there is no reason for restricting the term nyctinastic to pronounced sleep-movements.

SECTION 22. **Instances of Photonastic and Diurnal Movements.**

Pronounced daily movements are performed by the foliage and floral leaves of many plants, and these movements are in some cases induced by the daily changes of illumination, but in other cases by alterations of temperature. Frequently the power of photonastic response is accompanied by a feeble or pronounced capacity for thermonastic reaction. In such cases decreases of temperature or illumination usually induce similar curvatures; and, since the movements produced by increases are also alike, both factors co-operate at morning and evening in producing the awakening or sleep-movements as the case may be.

FIG. 28. Leafy shoot of *Desmodium gyrans*. *A* in the day position, *B* in the night position (after Darwin).

The photonastic sleep-movements are the result either of growth or of variation curvatures, the latter of which are commonly performed wherever motile pulvini are present. These movements are shown by the leaves of most Leguminosae and Oxalidaceae, as well as by the leaves of *Marsilea*, *Porliera*, *Portulaca*, and *Phyllanthus Niruri*. It can be seen from Fig. 28 that *Desmodium gyrans* allows the leaf laminas to droop so that the stalks rise up when night falls, and hence assumes quite a different appearance. The three leaflets of *Oxalis acetosella*[1] droop downwards around and against the petiole, whereas the leaflets of *Trifolium* fold together upwards, and then the upper end of the petiole curves laterally or downwards. In the case of the pinnate leaves of *Amorpha* and *Robinia* the leaflets droop downwards at night and press their under-surfaces together (Fig. 29) whereas those of *Acacia lophantha* and *Mimosa pudica* fold upwards in pairs with the dorsal surfaces together[2]. Since at the same time the main petiole of *Mimosa pudica* sinks, the position assumed resembles closely that produced by a mechanical excitation (Fig. 19, p. 61). If the plant is highly turgid the pulvinus may when mechanically excited during the early hours of the tropical night show an additional curvature and may bend the leaf backwards across the stem and support it for a short time upside down against the action of gravity. This excessive movement is not always shown, and later on the normal drooping position is again assumed[3]. It is only in certain cases that, in addition to its photonastic excitability, the leaf-pulvini

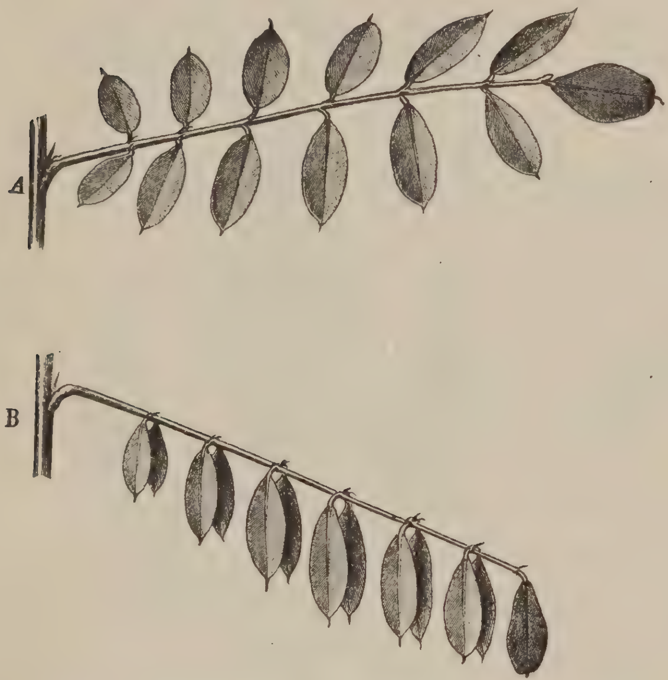

FIG. 29. Leaf of *Amorpha fruticosa*. *A* in day position, *B* in night position.

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[1] The leaflets assume the same position as after mechanical excitation. Cf. Fig. 20, p. 62.

[2] A summary of the plants showing sleep-movements is given by Hansgirg, Physiolog. u. Phycophytolog. Unters., 1893; Neue Unters. über den Gamo- u. Karpotropismus, sowie über Reiz- u. Schlafbewegungen, 1896 (Sitzungsb. d. böhmisch. Ges. d. Wiss.); Beihefte z. botan. Centralbl., 1902, Bd. XII, pp. 267, 272. Cf. also Pfeffer, Periodische Bewegungen d. Blattorgane, 1875, p. 159, and the literature there quoted. Numerous facts and figures are given by Darwin, The Power of Movement in Plants, 1880; Kerner, Natural History of Plants, 1895, p. 534. For additional facts see Popow, Bot. Jahresb., 1880, p. 278 (*Gleditschia*); Brückner, Bot. Centralbl., 1882, Bd. XII, p. 171; Vöchting, Bot. Ztg., 1888, p. 519 (Malvaceae); F. W. Oliver, Bot. Centralbl., 1891, Bd. XLV, p. 52 (*Abrus*); Paoletti, Nuov. giornal. bot. ital., 1892, T. XXIV, p. 65 (*Porliera*); Möbius, Bot. Centralbl., 1894, Bd. XV, p. 8; Jost, Bot. Ztg., 1897, p. 17; Jahrb. f. wiss. Bot., 1898, Bd. XXXI, p. 345; Ewart, Annals of Botany, 1897, Vol. XI, p. 439; Stahl, Bot. Ztg., 1897, p. 85; Linsbauer, Ber. d. bot. Ges., 1903, p. 27.

[3] Ewart, l. c., p. 453.

possess seismonic (*Mimosa*) or contact-irritability (*Dalbergia*), in most cases the pulvini being of value for the performance of sleep-movements.

The nyctinastic variation movements continue usually until the death of the leaf, though often their amplitude decreases, whereas the nyctinastic nutation movements are performed only by the aid of those regions of the petiole and lamina which remain capable of growth. Hence these latter movements are shown for a few days only or for a longer period, and cease when the leaf becomes adult. Usually the daily movements of growing dorsiventral organs are but trifling, but the growing leaves of *Impatiens noli-me-tangere*, *Impatiens parviflora*, *Sigesbeckia orientalis* (Pfeffer), *Myriophyllum proserpinacoides* (Stahl), and of *Stellaria media* (Batalin) raise themselves upwards every evening, whereas those of *Nicotiana rustica*, *Chenopodium album*, and of *Amaranthus* curve distinctly downwards[1].

The flowers of various Oxalidaceae, Mesembryanthemaceae, Nymphaeaceae, and Compositae[2] perform photonastic sleep-movements. Among the last-named the evening closure of the capitulum is due to the inward curvature of the whole of the ligulate florets of *Leontodon* or *Hieracium* (Fig. 30), but only by that of the ray-florets in *Bellis*. In the capitulum of *Chrysanthemum* the spreading ray-florets bend back along the stalk at night, while flowers pollinated by moths open in the evening and close when morning dawns[3].

The leafy shoots of *Mimulus Tilingii*, which are obliquely or horizontally expanded during the daytime, rise upwards in the evening[4] by the aid of a photonastic reaction. It is possible also that the change in the illumination aids in producing the evening sinking of the inflorescences of *Daucus*, *Falcaria*, and *Scabiosa*, and of the flowers of *Viola*, although these movements are mainly produced in response to the change of temperature[5]. According to Morren[6], the stamens of *Sparmannia africana* perform sleep-

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[1] For additional facts see the works of Hansgirg, Darwin, Pfeffer, Stahl, Jost, which have already been quoted. See also Batalin, Flora, 1873, p. 437.

[2] For additional instances see Hansgirg, Pfeffer, Jost, l. c. Also Pfeffer, Physiol. Unters., 1873, pp. 195, 210; Royer, Ann. d. sci. nat., 1868, v^{e} sér., T. IX, p. 355; Kerner, Pflanzenleben, Bd. II, p. 208 (Natural History of Plants, 1895, Vol. II, p. 215); Burgerstein, Ueber die nyctitrop. Beweg. d. Perianthien, 1887; Oesterreich. Bot. Zeitschrift, 1901, Nr. 6; Oltmanns, Bot. Ztg., 1895, p. 31; R. Scott, Annals of Botany, 1903, Vol. XVII, p. 761 (*Sparmannia*).

[3] Cf. Hansgirg, l. c., 1893, p. 12; Oltmanns, l. c., 1895, p. 50.

[4] Vöchting, Ber. d. bot. Ges., 1898, p. 39.

[5] For the literature see Hansgirg, l. c., 1893, p. 88; Vöchting, l. c., 1898, p. 42, and Jahrb. f. wiss. Bot., 1890, Bd. XXI, p. 285; Pfeffer, Period. Beweg., 1875, p. 162; Wittrock, Bot. Centralbl., 1883, Bd. XVI, p. 220; Kerner, Pflanzenleben, Bd. I, p. 494; Bd. II, p. 120; (Natural History of Plants, Vol. I, p. 530; Vol. II, p. 118). According to Knoch (Bibl. Bot., 1899, Heft 47, p. 17) the flower-buds of *Victoria regia* and *Nymphaea blanda* are submerged in the evening by the curvature of the flower-stalk. [The fact that movements of this kind may still be performed in a hothouse at nearly constant temperature points to their being photonastic in character, but direct experiment is necessary to make this certain. The repeated evening closure and partial or complete submersal of the flowers of the Water-lily was known to Linnaeus.]

[6] Cf. Pfeffer, l. c., p. 162.

movements, and it is possible that further research may reveal the existence of such movements among vascular and even non-vascular Cryptogams.

Variation movements are performed by comparatively short pulvini, whereas nutation movements may be derived from growing zones of considerable length. Indeed, in some cases the greater portion of the leaf may be capable of curvature, which may in the case of the floral leaves of *Silene nutans* go so far as to cause a rolling up of the leaf[1]. As growth dies out, the growing and curving zone gradually decreases, so that in *Malva*, for instance, the nyctinastic movements are at first carried out by the whole petiole, but ultimately only by the basal pulvinus[2].

The movement usually takes place in a vertical or oblique plane, but in many cases a complicated curve is traced, and in others a twisting occurs which goes so far in the leaves of *Phyllanthus Niruri* and *Cassia*[3] as to lead the downwardly curving leaflets to apply their dorsal surfaces to one another. These twistings, as well as the feebler ones of *Mimosa pudica*, are determined by the structure of the motile organs, but the twisting of the leaflets of *Mimosa*, and possibly also of *Phyllanthus Niruri*, are not produced by a true torsion in the pulvini, but by its curving along two intersecting planes[4]. As in other cases, the movement may either be spasmodic or regular, but the remarkable spasmodic movements observed by Darwin on the leaves of *Averrhoa Bilimbi* may possibly be in part autonomic in origin[5]. If the further movement of a leaf is prevented by contact with the stem or with another leaf, the tendency to curvature continues, so that the pressure exerted reaches a maximum, and then dies away again as the return movement begins. Hence a leaflet of *Acacia lophantha* or of *Mimosa* curves to a greater extent when the opposite leaflet with its resistance to movement is removed. In this case, as with other free leaves, the return movement begins soon after the attainment of the extreme night position, whereas when the leaflets are in contact they remain for some time pressed together without movement[6].

FIG. 30. *Hieracium pilosella.* *A* in day position, *B* in night position.

Not only are different leaves capable of varied movements, but in addition the different parts of the same leaf may behave dissimilarly. Thus the petioles of the leaves of *Desmodium gyrans* and of *Phaseolus vulgaris* rise up in the evening, whereas the laminas sink downwards. Furthermore, the primary petiole of *Mimosa pudica* and the leaflets move in opposite directions, while the palmate leaflets of some species

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[1] Cf. Hansgirg, l. c., 1893, p. 13.

[2] Vöchting, Bot. Ztg., 1888, p. 519.

[3] Pfeffer, Periodische Bewegungen, 1875, p. 159; Darwin, The Power of Movement in Plants, 1880, pp. 387-8.

[4] Schwendener, Gesammelte bot. Mittheil., 1897, Bd. II, pp. 214, 242.

[5] Darwin, l. c., p. 330. Cf. also Dewèvre and Bordage, Rev. gén. de bot., 1892, T. IV, p. 77.

[6] Pfeffer, l. c., pp. 48, 160.

of *Lupinus* become erect at night-time, and those of other species droop downwards. Darwin also gives instances of plants in which the cotyledons perform different sleep-movements to the foliage-leaves, and mentions that the young cotyledons of *Trifolium strictum*, in addition to the pulvinar movements, show a torsion of the petioles [1]. In addition, the position of the leaf of *Bauhinia* changes at night-time, while the two halves of the leaf fold together along the midrib. (Cf. Fig. 31, p. 107.) In many cases, though not always, the sleep position of the leaves resembles that which they occupied during their early development [2].

Since these daily movements are the result of a photonastic reaction coupled with the after-effect of periodic stimulation, every increase or decrease of illumination produces a more or less pronounced movement corresponding to that occurring at morning and evening respectively. In both cases the movement surpasses the permanent position of equilibrium, and that often to a considerable extent. Hence it arises that periodic flowers are usually most widely open during the early morning hours.

Changes of illumination always affect the position of the leaves more or less. The latter is more especially the case with the leaves and leaflets of *Phaseolus* and *Acacia lophantha*, for when these are placed in darkness, after performing a photonastic movement they return approximately to their original position, and maintain this position, in part at least, for an indefinite length of time in continued darkness. On the other hand, amongst others, the leaves of *Impatiens noli-me-tangere* and of *Chenopodium album* when placed in darkness during the daytime assume a position intermediate between the day and night positions, and one which approaches the former or latter more closely according to the species of plant. Flowers which perform nyctinastic movements show similar peculiarities [3].

Photonastic changes of position are, however, also shown by organs which do not exhibit any pronounced daily sleep-movements, either because they do not react rapidly enough, or not in such fashion as to produce a definite movement. Reactions of this kind take part in and often are mainly responsible for the assumption of the permanent position of dorsiventral organs. Heteronastic, tropic, and other reactions may, however, also co-operate with the photonastic, thermonastic, and hydronastic responses. The leaves of *Taraxacum officinale*, *Plantago media*, and *Primula elatior* assume a more or less erect position in deeply shaded places, but under strong diffuse illumination spread more or less horizontally, so that the rosette of leaves is often closely applied to the ground. Light therefore favours epinastic and darkness hyponastic growth in these leaves, and when

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[1] Darwin, l. c., pp. 309–13.

[2] Cf. Pfeffer, l. c.; Dietz, Flora, 1887, p. 577.

[3] Cf. Pfeffer, l. c., pp. 19, 38, 49. Autonomic changes of position are possible under constant external conditions. Cf. Pfeffer, l. c, p. 49, &c.; Jost, Jahrb. f. wiss. Bot., 1898, Bd. XXXI, p. 382.

the light is withdrawn all the leaves capable of growth gradually assume a more erect position. On the other hand, darkness favours the epinastic growth of the leaves of *Impatiens*, *Helianthus annuus*, *Ceratophyllum*, and *Myriophyllum*, and hence causes a more or less pronounced downward curvature of the leaves[1].

Certain flowers which perform no evident sleep-movements respond to the presence or absence of light. Thus the flowers of *Gagea lutea*, *Gentiana campestris*, *Stellaria media*, *Holosteum umbellatum*, *Veronica alpina*, and *Drosera longifolia* develop and fade without ever opening in darkness[2], and are therefore 'photo-cleistogamic.' The flowers of *Stellaria media* require a considerable intensity of light to induce their expansion, and hence remain closed when grown behind a window facing north.

All these considerations apply only for moderate intensities of light, and leave it an open question whether under sufficiently intense diffuse illumination the reaction would be reversed. The cases in which movements have been observed in the leaves of *Acacia*, *Mimosa*, *Robinia*, &c., in response to strong sunlight falling on one side give no satisfactory answer, since these are heliotropic curvatures towards the light performed by the motile pulvini. In this way the blades of the leaflets are placed parallel to the incident rays. This reaction, sometimes termed midday sleep, was called paraheliotropism by Darwin[3], and is due to the unilateral illumination producing a greater fall of turgor in the more strongly illuminated half of the pulvinus than in the less strongly illuminated one. In this position the chloroplastids are protected, and the transpiration is usually diminished[4]. The leaflets of *Cassia montana*, however, assume positions which tend to increase transpiration, the stomatic ventral surfaces facing outwards or upwards, so that the plant apparently risks a fatal loss of water in order to keep down the insolation temperature[5]. That the response in not due to the localized warming of the exposed side of the pulvinus is shown by the fact that it takes place when the pulvini are submerged under water, and, as in the case

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[1] Frank, Die natürl. wagerechte Richtung von Pflanzentheilen, 1870, p. 46; Detmer, Bot. Ztg., 1882, p. 787; Wiesner, Bot. Ztg., 1884, p. 677; Vines, Annals of Botany, 1889, Vol. III, p. 421; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 272; Möbius, Biolog. Centralbl., 1894, Bd. XV, pp. 8, 14.

[2] Vöchting, Jahrb. f. wiss. Bot., 1893, Bd. XXV, p. 180; Hansgirg, Physiol. u. Phycophytol. Unters., 1893, pp. 27, 45, 53; Beihefte z. bot. Centralbl., 1902, Bd. XII, p. 271; Oltmanns, Bot. Ztg., 1895, p. 31; Leclerc du Sablon, Rev. gén. de bot., 1900, T. XII, p. 305.

[3] The Power of Movement in Plants, 1880, p. 445. Cf. also Pfeffer, Periodische Bewegungen, 1875, p. 62; Hansgirg, 1893, l. c., p. 134; Oltmanns, Flora, 1892, p. 238; Wilson, Contributions from the Botanical Laboratory of the University of Pennsylvania, 1892, Vol. I, p. 66; Ewart, Annals of Botany, 1897, Vol. XI, p. 447; Jost, Jahrb. f. wiss. Bot., 1898, Bd. XXXI, p. 385.

[4] Wiesner, Die natürl. Einrichtungen zum Schutze des Chlorophylls, 1875, p. 62; Stahl, Bot. Ztg., 1897, p. 91.

[5] Ewart, l. c., p. 456.

of other responses to light stimuli, it is mainly produced by the blue and more refrangible rays[1].

[The assumption that the 'paraheliotropic' position is the result of a heliotropic response is hardly justified, any more than is the assumption that the pulvini of the main and secondary petioles possess the same irritability and mode of response as those of the leaflets. The main pulvinus of *Mimosa pudica*, and to a less degree those of the secondary petioles, are, for instance, heliotropic and curve or twist under unilateral illumination even when comparatively intense, so as to place the general surface of the leaf more or less at right angles to the incident rays. The folding-up of the leaflets in strong sunlight is, however, performed in whatever position the leaf may be, and takes place also when the leaves are illuminated from beneath by a beam of light thrown upon one or more of the pulvini of the leaflets, each pulvinus reacting separately. The relationships are somewhat complicated by the fact that the pulvini of the leaflets also appear to possess a weak heliotropic irritability; but sufficiently strong illumination, whatever its direction, always causes the same response, the leaflets folding together owing to the reversal of their previous photonastic response. In regard to the leaves of other Leguminosae, both the nyctinastic and the paranastic (paraheliotropic) positions of the leaflets are produced, not in response to the direction of the illumination, but to its

FIG. 31. *Bauhinia tomentosa.* A plant climbing by hook-tendrils, and whose leaves show photonastic movements. (*a*) A leaf expanded owing to the pulvinus being covered with tinfoil; (*b*) the same but the pulvinus being shaded by another leaf; (*c*) young leaf which has not yet unfolded; (*d*) folded leaves with pulvini exposed to sunlight and showing that the folding is independent of the direction of the incident light. (From a photograph. After Ewart.)

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[1] Ewart, l. c., pp. 451, 480; Macfarlane, Bot. Centralbl., 1895, Bd. LXI, p. 136.

intensity. If the movement of the leaflets causes the pulvini to be shaded it may cease when a certain inclination is reached, which sometimes gives the appearance of a heliotropic curvature. In addition, the old leaves of *Bauhinia* (Fig. 31) are unable to fold together as completely as do the young leaves, owing to the increased rigidity of the tissues [1].]

In any case sufficiently strong diffuse illumination produces a sinking of the leaflets of *Oxalis* [2], while Ewart (l. c.) has shown that in the case of a variety of leaves that perform variation movements a reversal of the photonastic response is produced by an increase in the intensity of diffuse light above the optimum. It is presumably also owing to a reversal of the previous heteronastic growth that, as Oltmanns found [3], the flowers of *Tragopogon brevirostris* close not only when the illumination decreases to a minimum but also when it increases beyond a certain intensity.

SECTION 23. **The Origin of the Daily Photonastic Periodicity.**

The photonastic reactions of responsive organs are enhanced by the periodicity induced by repeated previous stimulation. Hence when the plant is kept in continuous constant illumination or in darkness the daily movements are still performed for a certain time, but with gradually decreasing amplitude. The periodic movements are at first pronounced both in constant light and in darkness in the case of the leaves of *Acacia lophantha*, *Mimosa pudica*, *Impatiens noli-me-tangere*, and *Sigesbeckia orientalis*, and they continue to be perceptible until after the lapse of four to eight days. On the other hand, the daily movements of the flowers of *Oxalis rosea* cease after being for three to four days in darkness, and the same happens in the capitulums of *Bellis perennis* after one or two days [4].

After the cessation of the daily periodicity, the leaves assume positions corresponding to the illumination and to other factors, while under constant external conditions all movements cease except those of autonomic origin. When the external conditions are favourable such leaves retain fully their irritability and power of response, so that a plant whose daily periodicity has been removed by continuous illumination retains its photonastic irritability, and responds by the usual sleep-movement when placed in darkness. This was found by Pfeffer to take forty-five minutes to two hours for completion in the case of the leaflets of *Acacia lophantha* and *Trifolium pratense*, and of the terminal leaflets of *Desmodium gyrans*, whereas the leaves of *Impatiens noli-me-tangere* sink considerably but do not attain the full nyctitropic position under these circumstances. The leaves of

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[1] Cf. Ewart, l. c., pp. 448–59, 480.

[2] Pfeffer, l. c., p. 60.

[3] Oltmanns, Bot. Ztg., 1895, p. 51.

[4] Pfeffer, Period. Bewegungen d. Blattorgane, 1875, p. 34 seq.

Sigesbeckia orientalis do not droop through an angle of more than 10° to 30°, whereas when the normal daily movements are performed the leaves droop vertically downwards at night, moving therefore through an angle of 90°[1].

Plants exposed to the normal daily changes of illumination also afford a measure of the photonastic irritability and response, for darkening during the daytime produces a slight photonastic curvature in *Sigesbeckia*, but a pronounced one in *Acacia* and the other plants named above. In general the photonastic reactions produced by variation movements are more rapid and pronounced than those due to nutation. The pulvini of *Portulaca sativa* only react feebly, however, whereas the nutating leaves of *Impatiens noli-me-tangere* and of *I. parviflora* are strongly photonastic[2]. In the Tropics motile leaflets usually begin to assume the sleep position at about 5 p.m., and have completed the movement commonly by 5.30, that is half an hour before the fall of night. Naturally, however, the times fluctuate somewhat in different plants, and they are also affected by the clearness of the sky and by the humidity of the soil and of the air[3].

When the periodicity has been removed by continuous illumination, a photonastic reaction does not merely cause a single to and fro movement, but also produces an after-effect which is naturally but slight when the reaction is feeble as in *Sigesbeckia.* In this case the gradual return to the full amplitude of movement can readily be traced as the result of the co-operation of new rhythmically repeated photonastic reactions with the after-effects of previous ones. Thus a plant of *Sigesbeckia orientalis*, after five days' continuous illumination had removed the daily periodicity, was placed in darkness daily from 8 a.m. to 4 p.m. The first darkening produced curvatures in the leaves of 10° to 30°, the second curvatures of 15° to 45°, which had increased to ones of 40° to 80° on the fourth day, and of 70° to 100° on the fifth day. Five periodic repetitions were therefore required to reproduce approximately the normal amplitude of movement in this plant.

This induction and summation cannot of course be followed when the first darkening produces the full or nearly the full nyctinastic movement, as in the case of the leaflets of *Acacia lophantha* which fold together when first darkened after prolonged previous constant illumination. Even in this case, however, only two periodic movements are shown as the after-effect

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[1] Pfeffer, l. c., p. 39. The plant termed *Sigesbeckia flexuosa* proves to be a form of *Sigesbeckia orientalis* L.

[2] Pfeffer, l. c., pp. 15, 39.

[3] Ewart, Annals of Botany, 1897, Vol. XI, p. 453 seq. [The midday sleep-movements of *Mimosa pudica* and of similar plants do not appear to induce any distinct secondary periodicity, although they might do so when regular and prolonged.]

of a single reaction, whereas when the daily periodicity is fully induced four or five periodic movements may be shown under constant illumination.

It is evident, therefore, that the nyctinastic periodicity is induced by the rhythmically-repeated photonastic reactions and their after-effects. The daily periodicity of growth is produced in a similar way, and a photonastic periodicity must always result from the rhythmic and regular repetition of changes of illumination whenever these affect either growth or the energy of expansion of motile tissues[1]. The after-effects of photonastic stimulation enable a phototonic plant to perform movements of considerable amplitude, although the primary movement directly due to the photonastic stimulation may be comparatively feeble, and in addition a plant with a pronounced periodicity of this kind will tend to be more regular in its daily movements than if nearly the full movement was produced in response to a single change of illumination.

An analogy is afforded by a pendulum whose amplitude of oscillation is gradually increased up to a maximum by a series of rhythmically-repeated impulses, and which then continues to oscillate with gradually decreasing amplitude but without any appreciable change of period[2]. In the living plant, although the cumulative after-effects of the previous rhythmic stimulation may be phenomena of complex origin, we can nevertheless deal with them as with other empirically established facts. Not all movements or stimulatory reactions are able to exercise appreciable after-effects, and since when they result from a particular reaction they may vary in character according to the nature of the plant and its power of reaction, it is to be expected that specific peculiarities should be shown in regard to the after-effects of photonastic stimulation. In fact they may persist for a long time in some plants but only for a day in others, even when they had been performing pronounced sleep-movements every night during the whole of their adult existence. In addition, no periodic after-affects appear to be produced in photonastic flowers by the alternation of night and day, and little or no after-effect appears to be exercised by the pronounced thermonastic opening and closing movements of the flowers of *Crocus* and *Tulipa*[3].

The periodic after-affects when present follow approximately the same rhythm as the nyctinastic movements which give rise to them, and hence the one aids the other. The times of oscillation of a simple pendulum swinging in still air vary somewhat according to their amplitude, and the successive after-effects of periodic stimulation are still less isochronous than

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[1] On the feeble periodicity induced by rhythmically-repeated geotropic or heliotropic stimuli, cf. Darwin and Pertz, Annals of Botany, 1903, Vol. XVII, p. 93.

[2] Pfeffer, l. c. It is difficult to understand how Schwendener (1897, Gesammelte bot. Mittheil., Bd. II, p. 241) can be in any doubt as to the propriety of using this analogy with a pendulum as an illustration of the nature of periodicity and of periodic phenomena.

[3] Pfeffer, l. c., p. 133; Jost, Jahrb. f. wiss. Bot., 1898, Bd. XXXI, p. 349.

the swings of a pendulum. The rhythm of a simple pendulum is constant so long as its length and the force of gravity are unaltered. On the other hand, the photonastic rhythm of a living organ can be made to follow periods of more or of less than twenty-four hours by corresponding alterations of the periods of illumination and darkness[1].

It is worthy of note that the nyctinastic periodicity vanishes comparatively rapidly and hence never becomes hereditary, although it may have been regularly repeated through countless generations. Only in very few cases, in fact, is a hereditary transmission of a long induced periodicity possible. This actually applies to the resting and flowering periods of certain plants, for when transferred to other climates, a new hereditary rhythm may be gradually induced which is appropriate to the altered seasons.

The spontaneous movements of the leaflets of *Oxalis*, *Trifolium*, and of the terminal leaflet of *Desmodium gyrans* retain the same rhythm of forty-five minutes to four hours under continuous illumination, whereas the periodic nyctinastic movements gradually cease. Hence the latter cannot be derived by the regulation of the spontaneous movements[2], although in other cases a particular rhythm may result from the regulation of an inherent periodicity, as is in part the case with the yearly periodicity.

The power of photonastic response is not necessarily coupled with a pronounced thermonastic irritability, and most photonastic organs are irresponsive to mechanical stimuli such as produce pronounced movements in the leaflets of *Mimosa* and *Oxalis*[3]. Pronounced spontaneous movements are shown by certain leaves, but are absent from most organs capable of sleep-movements such as the leaves of *Acacia lophantha*, *Impatiens*, and *Sigesbeckia*, while the lateral leaflets of *Desmodium gyrans* which show rapid spontaneous movements perform no sleep-movements[4].

Historical. The sleep-movements of certain plants were first noted by Pliny, and by Albertus Magnus, but Linnaeus was the first to call attention to the common occurrence of nyctinastic movements among leaves and flowers[5]. The subsequent researches, which were mainly concerned with the mechanics and causes of the phenomenon, left it uncertain whether the daily rhythm was due to the periodic

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[1] Cf. Pfeffer, l. c., pp. 39, 43, 53. The time of reaction naturally sets a limit to the possible shortening of the rhythmic period.

[2] Pfeffer, l. c., pp. 35, 52.

[3] Conversely mechanically irritable organs such as the stamens of Cynareae, various stigmas and tendrils, perform no sleep-movements, and the same applies to the leaves of *Dionaea* (Munk, Die elektrischen u. Bewegungserscheinungen von Dionaea, 1876, p. 101), and of *Drosera rotundifolia* (Kabsch, Bot. Ztg., 1860, p. 247).

[4] Darwin, The Power of Movement in Plants.

[5] For details on the historical development of this subject see Pfeffer, Periodische Bewegungen, 1875, pp. 30, 163.

changes of illumination or of temperature, or whether it was the result of the regulation of a hereditary periodicity. De Candolle at first inclined to the former view, but later appears to have assumed that the periodicity was hereditary[1]. Dutrochet[2], Sachs[3], and Hofmeister[4] all adopted the same view, and apparently considered that the periodic illumination regulated the rhythm, but did not induce it, while the continuance of the movements in darkness was ascribed either to a hereditary periodicity or to the incomplete absence of light. Pfeffer then showed, in 1876, the induced character of the periodicity, and pointed out that the daily movements might be produced by thermonastic responses as well as by photonastic ones, or by a combination of the two. Royer[5] went, however, too far in ascribing all sleep-movements of flowers to changes of temperature, while it is evident that all daily movements are not the result of circumnutation as Darwin supposed, nor is the daily periodicity capable of hereditary transmission.

Methods. Pfeffer employed the light from a couple of Argand burners, which was passed through cold water to diminish the heating effect[6]. Nowadays, incandescent burners, arc lights, or Nernst lamps might be used in preference. The incandescent electric light is less suitable for the reinduction of the photonastic periodicity, since it contains relatively fewer of the blue rays, which exercise the greatest photonastic action[7]. It has been observed that certain plants cease to perform sleep-movements during the continuous summer day of high northern latitudes, as in the north of Norway[8]. By the aid of artificial illumination, the periodicity may be reversed, so that the sleep-movements take place in the daytime, or it may be lengthened or shortened[9]. Experiments in darkness are only decisive when the absence of light does not appreciably affect the power of reaction.

SECTION 24. **Thermonastic Curvatures.**

Apart from the general influence of temperature on growth, a special power of thermonastic response has been developed by various flowers, in which low temperatures produce closing movements and high temperatures opening ones. The flowers of *Crocus vernus* and *Crocus luteus* are especially responsive, as are also those of *Tulipa Gesneriana*, for these flowers perceptibly respond to a change of temperature of half a degree centigrade,

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[1] A. P. de Candolle, Physiologie des Plantes, a German translation by Röper, 1835, Bd. II, p. 640.

[2] Dutrochet, Mémoires p. serv. à l'histoire etc., Bruxelles, 1837, p. 287.

[3] Sachs, Flora, 1863, p. 469.

[4] Hofmeister, Pflanzenzelle, 1867, p. 331.

[5] Royer, Ann. de sci. nat., 1868, v^e sér., T. IX, p. 355. Cf. Pfeffer, l. c., p. 170.

[6] Pfeffer, l. c., p. 31. The experiments of other authors are discussed here.

[7] Cf. Pfeffer, l. c., p. 67.

[8] Cf. Schübler, Die Pflanzenwelt Norwegens, 1873, p. 88; Bot. Jahresb., 1880, p. 262.

[9] Pfeffer, l. c., pp. 40, 55. On the registration of the movement see Baranetzsky, Ber. d. bot. Ges., 1899, p. 190.

and which pass from the closed to the fully expanded condition in a few minutes when the temperature rises from 12° to 22° C. (Fig. 32). The flowers of *Adonis vernalis*, *Ornithogalum umbellatum*, and *Colchicum autumnale* react more slowly and less strongly, while those of *Ranunculus Ficaria*, *Anemone nemorosa*, and *Malope trifida* are still less sensitive, although they respond to changes of temperature of 5° to 10° C. by a distinct movement. On the other hand, such changes of temperature induce only a slight thermonastic movement in the flowers of *Oxalis rosea*, *Nymphaea alba*, *Leontodon*, and *Taraxacum*[1], and flowers which open once only show no distinct thermonastic responses, although their opening is hastened by moderately high temperatures and retarded by low ones.

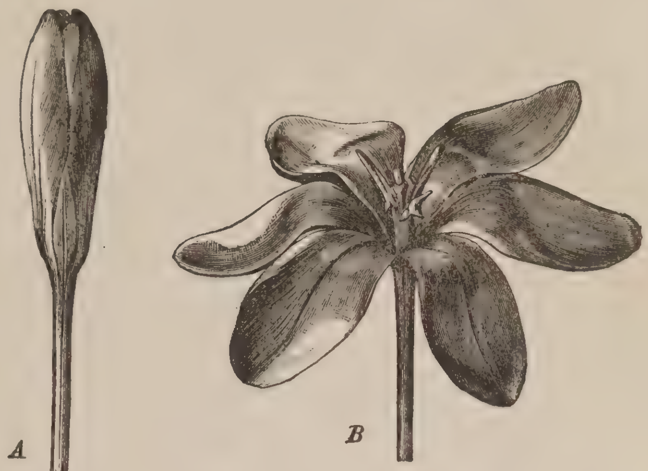

FIG. 32. Flower of *Crocus luteus*. *A* closed, *B* expanded owing to a rise of temperature.

Foliage-leaves usually react but feebly to changes of temperature, although these induce perceptible thermonastic responses in the pulvini of the leaflets of *Oxalis acetosella*, *Desmodium gyrans*, *Averrhoa Bilimbi*, and *Mimosa pudica*[2]. In addition, the bilobed leaf of *Aldrovanda* only opens when the temperature is raised sufficiently, while either a rise or a pronounced fall of temperature may produce a thermonastic curvature in dorsiventral tendrils and this is similar in character to the thigmotropic curvature[3].

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[1] Pfeffer, Physiol. Unters., 1873, p. 194; Periodische Bewegungen, 1875, p. 122. *Crocus* and *Tulipa* react so rapidly that the movement may be demonstrated to a large audience by means of a projection lantern. Cf. Pfeffer, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 731. The simple observation that warming hastened the opening of the flowers of an anemone was made by Cornutus (quoted by Ray, Historia plantarum, 1686, Vol. I, p. 2). Hofmeister (Flora, 1862, p. 516) found that variations of temperature produced opening and closing movements in the flower of the garden tulip; and Royer (Ann. sci. nat., 1868, v^{e} sér., T. IX, p. 355) regarded changes of humidity and temperature as being responsible for the opening and closing of flowers. The true relationships were then established by Pfeffer. Additional instances of thermonastic flowers are given by Hansgirg, Physiolog. u. Phycophytolog. Unters., 1893, pp. 27, 64. According to Mikosch (Bot. Jahrb., 1878, p. 219), changes of temperature induce the opening and closing of the anthers of *Bulbocodium vernum* and of certain species of *Alchemilla*, but it is not certain whether the reaction is a true thermonastic one.

[2] Pfeffer, Physiol. Unters., 1873, pp. 65, 78; Periodische Bewegungen, 1875, p. 135; Darwin, The Power of Movement in Plants; Jost, Jahrb. f. wiss. Bot., 1898, Bd. XXXI, p. 376; Bot. Ztg., 1897, p. 35.

[3] Correns, Bot. Ztg., 1896, p. 2; Macdougal, Bot. Centralbl., 1896, Bd. LXVI, p. 145; Fitting, Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 562.

According to Vöchting[1], sufficient cooling causes certain shoots of *Mimulus Tilingii* and the flower-stalks of *Anemone stellata* to assume a drooping position; and, according to Lidforss[2], the same applies to the shoots of such plants as *Lamium purpureum*, *Veronica chamaedrys*, and *Chrysanthemum leucanthemum*. In addition, the evening drooping of certain flowers and inflorescences appears in part to be the result of a thermonastic reaction, such as may also be responsible for the drooping of the shoot and leaves of many plants under natural conditions when the temperature falls nearly to the freezing-point. It has, however, yet to be determined whether these latter effects are actually due to a thermonastic reaction, or are merely the result of the tissues being flaccid. The phenomenon may indeed be as complex in origin as is the downward curvature and plagiotropic position shown by the shoots of various plants in autumn and winter[3]. It is worthy of note that the changed orientation takes place slowly, and that the daily changes of illumination induce no marked movement in these cases.

Rapidly reacting thermonastic organs usually pass at first beyond the position which they ultimately assume when the changed temperature is maintained for some time. This is especially well shown by the flowers of *Crocus luteus*, for the perianth-segments become temporarily partially reflexed when the temperature is suddenly raised (Fig. 32, p. 113), whereas when the temperature is raised slowly they hardly pass beyond the position maintained by them so long as the new temperature remains constant.

After the removal of all the perianth-segments but one, exactly similar reactions to sudden and to gradual falls of temperatures can be traced for the closing movement as for that of opening. As the result of its thermonastic properties the intact flower of *Crocus* may pass through its entire period of development without ever opening if the temperature is kept below 8° or even 12° C.[4] The inflorescences of *Leontodon hastilis*, *Hieracium vulgatum* and the flowers of *Oxalis rosea* remain closed at 1° to 3° C. even in diffuse daylight, partially open at 8° to 10° C., but do not fully

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[1] Vöchting, Ber. d. bot. Ges., 1898, p. 42; Jahrb. f. wiss. Bot., 1890, Bd. XXI, p. 285.

[2] Lidforss, Bot. Centralbl., 1901, Bd. LXXXVI, p. 169; Jahrb. f. wiss. Bot., 1902, Bd. XXXVIII, p. 343. According to Vöchting (Bot. Ztg., 1902, pp. 90, 107), a fall of temperature also causes young potato-shoots to droop. We are here only dealing with the results of a change of temperature under otherwise constant conditions, and leave it an open question as to how far the results observed are due to induced changes of geotropic irritability.

[3] Cf. Vöchting, Ber. d. bot. Ges., 1898, p. 50; Warming, Oekologische Pflanzengeographie, a German translation by Knoblauch, 1896, p. 26; Krašan, Engler's bot. Jahrb., 1882, p. 185; Lidforss, l. c.

[4] Pfeffer, Physiol. Unters., 1873, p. 189; Period. Bewegungen, 1875, p. 131; Jost, Jahrb. f. wiss. Bot., 1898, Bd. XXXI, p. 352.

expand until the temperature is still more favourable[1]. In addition, the flowers of *Spergula salina*, as well as those of *Hordeum distichum*, and of a few other grasses, remain closed at low temperatures, while there are presumably numerous plants whose flowers perform no pronounced opening and closing movements but remain closed at low temperatures[2].

Many organs are capable of both thermonastic and photonastic movement, although usually those organs which are highly thermonastic are only feebly photonastic, and the converse is also true[3]. Thus the daily opening and closing of the feebly photonastic flowers of *Crocus* and *Tulipa* are mainly determined by the changes of temperature; and the rapid opening usually produced by insolation is mainly the result of the heating effect of the sun's rays. Even a small fall of temperature is sufficient to produce the closure of the flower in spite of the feeble opposed photonastic action produced by exposure to diffuse daylight.

The daily temperature-curve, and hence also that of the resulting thermonastic movements, are much more irregular than the periodicity dependent upon the changes of illumination. Hence the absence or feebleness of any induced periodicity in the flowers of *Crocus* and *Tulipa*, and in other thermonastic organs, enables them to assume positions directly corresponding to the prevailing temperatures. In this way spring flowers, among which most strongly thermonastic flowers are included, are able to remain closed on cold days—a fact of considerable biological importance.

When an organ is capable of both thermonastic and photonastic response, increases of temperature and of illumination usually produce similarly directed movements, and the same applies to decreases. In general, therefore, the changes of illumination and of temperature co-operate in producing the sleep-movements. Curvature can be induced in dorsiventral organs in various ways even when the general rate of growth is accelerated by a moderate rise of temperature but slightly retarded by a concomitant increase of illumination. In addition, a transitory acceleration of growth may result from the shock due to a sudden change of temperature or of illumination. Nor is it surprising that in certain cases the thermonastic and photonastic responses should be dissimilar in character. Thus Vöchting[4] found that a decrease of illumination produced an upward curvature in certain shoots of *Mimulus Tilingii*, and, according to Jost[5], decreases of temperature and of illumination produce opposed movements in the case of the leaflets of *Mimosa pudica*. It is, however, not certain whether in all cases a rise of temperature above the optimum might produce a reversal

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[1] Pfeffer, 1873, l. c., p. 189.

[2] For facts see Hansgirg, Physiolog. u. Phycophytologische Unters., 1893, pp. 30, 46, 64; Fritsch, Bot. Ztg., 1852, p. 897. Further critical investigation of these facts is, however, requisite.

[3] Pfeffer, Period. Bewegungen, 1875, p. 122.

[4] Ber. d. bot. Ges., 1898, pp. 39, 45.

[5] Bot. Ztg., 1897, p. 35.

of the thermonastic response such as is shown by photonastic organs exposed to increasing illumination. A reversal of this kind does actually appear to occur in the flowers of *Crocus*[1], and possibly also in the leaves of *Oxalis* when the temperature rises above the optimum. It is, in fact, not impossible that thermonastic reactions of this kind may play a more or less prominent part in the assumption of the midday sleep-positions of the leaves of so many tropical plants.

SECTION 25. **Hydronastic Movements.**

As is well known, changes in the percentage of water in plants commonly cause disturbances of equilibrium leading to movement. Thus the diminished rigidity due to a decrease of turgidity leads to the flaccid drooping of shoots and leaves, and in the case of dorsiventral organs changes of turgidity which affect the antagonistic tissues unequally may cause curvature. In general, the percentage and supply of water form physiological conditions whose modification affects the activity of growth and the power of response in much the same way that changes of temperature do. Granted an appropriate structure, changes in the hydric relationships may even induce hydronastic curvatures, as physiological stimulatory reactions which are widely distinct in character from the purely physical movements mentioned above. It is of course always possible that the same loss of turgidity which primarily produces a drooping movement may also act as a stimulus to a physiological curvature of like or of unlike kind. Furthermore, this curvature may either result from a modification of growth or may be a variation movement due to appropriate changes of turgor induced in response to stimulation.

The use of the term hydronasty to denote curvatures produced by changes in the hydric relationships says nothing as to the nature of this form of irritability or as to the mode of perception of stimuli. The hydric relationships may, however, exercise various stimulatory actions on growth, so that hydronastic responses may be of varied origin. Hitherto the researches have mainly been confined to determining the existence of such reactions, and frequently no proper discrimination has been made between the physical and physiological responses. Hence only a general account of the phenomena observed and their distribution is possible at present. Indeed, it will always be difficult to determine whether, in a given case, the actual excitation is due to a fall of turgor, to a movement of water with or without transpiration, to changes of consistency, or to other factors[2].

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[1] Cf. Pfeffer, Physiol. Unters., 1873, p. 190; Jost, Jahrb. f. wiss. Bot., 1898, Bd. XXXI, pp. 351, 358.

[2] Since these movements are not solely produced in response to changes of turgor, the general

It is possibly owing to a hydronastic response that the position of many foliage and floral leaves alters when the plant is freely watered or is brought from dry air into a moist chamber. The changed position is maintained under the new conditions, and ultimately becomes permanent when the adult leaf ceases to grow. Evidently we are dealing with a physiological growth-reaction, and not with a movement due to a temporary change of turgor. Similarly, the changes in the position of the foliage and floral leaves observed by Kraus, Wiesner, and Hansgirg[1], as the result of alterations of turgidity, appear largely to be hydronastic in character. Unfortunately, the other external conditions were frequently not kept constant during these observations, and, in addition, insufficient attention has been paid to the physical movements resulting from the changes of turgor and to the influence of the latter upon the power of physiological response. Hence the observations are not altogether satisfactory, and fail to indicate the extent to which hydronastic reactions are responsible for the result observed. From Kraus's researches it does, however, appear as though the hydronastic equilibrium of the foliage-leaves of a variety of plants was considerably disturbed by pronounced rises or falls of turgidity, and the experiments of Wiesner and Hansgirg seem to indicate the same for floral leaves. Thus the flowers of *Anagallis coerulea* and *Gentiana amarella* close or remain closed in air saturated with moisture, according to Wiesner, even when exposed to optimal illumination; and the same applies to the flowers of *Stellaria media* and *Holosteum medium*, according to Hansgirg, when submerged under water[2].

Since a variety of factors come into play under natural conditions, it is not possible to say in what degree hydronastic actions may be responsible for the assumption of different fixed positions by leaves on dry and moist habitats[3]. Hydronastic responses take little or no part in the daily movements of leaves and of periodic flowers, for these are primarily induced by

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term 'hydronasty' for this phenomenon seems preferable to that of turgonasty employed by Hansgirg (Physiol. und Phycophytol. Unters., 1893, p. 11). [No additional terms are likely to become essential even when the subject is further studied, and there seems to be no valid reason for retaining the term turgonasty to represent those instances in which changes of turgor act as the stimulus. In any case the terminations '-nasty' and '-tropism' must be restricted to physiological responses, and no special terms are needed for physical movements induced by turgor, by hygroscopicity, or by imbibition and swelling. To invent unnecessary special terms is merely to strew the path of knowledge with useless lumber which tends to acquire a fictitious value in the eyes of those forced subsequently to struggle over these obstacles.]

[1] C. Kraus, Flora, 1879, p. 11; Wiesner, Sitzungsb. d. Wiener Akad., 1882, Bd. LXXXVI, Abth. I, p. 212; Hansgirg, Physiol. u. Phycophytol. Unters., 1893, pp. 32, 42, 48.

[2] According to the authors named (cf. also Planchon, Bull. de la Soc. bot. de France, 1896, T. XLIII) there are also flowers which close when their turgidity decreases, and it appears that certain flowers which are expanded when the turgidity is normal perform a hydronastic closing movement when the turgidity either rises or falls.

[3] Cf. Stenström, Flora, 1895, p. 132.

changes of illumination and of temperature, and may still continue under water, or in air saturated with moisture, in which the turgidity of the tissues is maintained at the highest possible limit. The fact that such flowers and leaves often perform sleep-movements when the sky becomes cloudy or before the fall of rain is due to the induction of a photonastic or thermonastic response, which is accelerated by the rise of turgor due to the diminution of transpiration[1]. It has, however, yet to be shown that any plants exist in which pronounced daily hydronastic sleep-movements are produced by the normal daily changes of turgidity.

Kraus, Wiesner, and Hansgirg have all shown that in many cases a moderate change of turgidity produces a pronounced physical curvature, resulting in the sinking of leaves or the closure of flowers, quite apart from the usual drooping due to a pronounced fall of turgor. These movements often have considerable biological importance by reducing the exposure, and in the same way the rolling-up or folding of certain leaves by reducing the surface exposed aids in rendering them resistant to desiccation[2]. The daily changes of turgor due to transpiration may naturally cause the periodic repetition of the associated physical movements. Naturally also, oscillations are bound to occur when the changes of turgor due to the sudden withdrawal or absorption of water are produced with unequal rapidity in the tissues on opposite sides of an organ[3].

Physical movements of this kind are possible, not only in growing organs, but also in adult pulvini, although in most cases little or no effect is produced by a moderate loss of water. A readier response is, however, given by a certain form of *Porliera hygrometrica*, in which a deficiency of water causes a more or less complete folding of the leaflets[4]. The contradictory observations upon the influence of moisture upon the leaf movements of *Porliera* are partly due to the fact that all forms are not equally sensitive, and that the removal of water was less pronounced in some cases than in others. Paoletti and Pantanelli[5] have recently shown that the daily sleep-movements of this plant are produced in the usual way by changes of illumination.

The continuance of the daily movements under water shows that they are not of hydronastic origin, although in time the movement and power of reaction disappear from the submerged plant. This is, in part, due to the injurious action exercised by the insufficient supply of oxygen, owing to the diminution or almost complete cessation of the gaseous exchanges, and by the cessation of transpiration.

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[1] Cf. Pfeffer, Physiol. Unters., 1873, p. 188; Period. Bewegungen, 1875, p. 137, and the literature quoted in these works. Kraus, l. c., p. 35; F. W. Oliver, Bot. Centralbl., 1891, Bd. XLV, p. 52; Hansgirg, l. c., pp. 40, 122.

[2] See Ludwig, Biologie d. Pflanzen, 1895, p. 194; Tschirch, Jahrb. f. wiss. Bot., 1882, Bd. XIII, p. 544.

[3] Cf. Pfeffer, Period. Bewegungen, 1875, p. 137.

[4] Darwin, The Power of Movement in Plants.

[5] Paoletti, Nuovo giornale botanico italiano, 1892, T. XXIV, p. 65; Pantanelli, Studi d'anat. e fisiolog. sui pulvini motori, 1901, p. 258.

The former action alone is sufficient to explain the decrease in or cessation of the power of reaction as the result of injecting the intercellular spaces with water [1]. The growth and development of many plants are strongly affected by submersion in water, and hence it is not surprising that, according to Hansgirg, certain flowers which remain closed under water open when placed in air saturated with moisture, although the turgidity remains at its maximal limit. In addition, the leaves of *Callitriche* assume different positions in moist air to what they do in water [2].

SECTION 26. **Conjoint Effects.**

Changes of temperature and of turgor always influence to a greater or less extent the progress and amplitude of the photonastic daily movements, either owing to their influence upon the power of response, or to their awakening special thermonastic or hydronastic reactions. In addition, the induced after-effects may cause a periodic repetition of the movements, and this tendency acts in the same way as that to a movement of autonomic origin. The simplest series of combinations is given when only the illumination varies, the other conditions remaining constant, so that the daily movements are due to the co-operation of the photonastic responses to changes of illumination with the periodic after-effects which, under normal conditions, follow approximately the same rhythm.

The degree to which the directly induced closing or opening movements exceed that due to the after-effect of previous stimulation will depend upon the readiness of the plant's photonastic response, and upon the intensity of the after-effect. Naturally, however, the full possible movement may not be shown when the different responding organs press against one another. Both the after-effect and the original photonastic response involve oscillations about the ultimate position of equilibrium, and hence action excites reaction. It depends upon the time period of the after-effect of the photonastic reaction whether the maximum movement is attained immediately after sunrise or sunfall, or later on in the day or night, and also whether the opening and closing of flowers is rapidly or slowly induced.

On cloudy days the photonastic reactions are feebler than usual at morning and evening, so that the amplitude of the daily movements is considerably reduced when the after-effects are less active than the direct photonastic reactions. Naturally also, a plant placed in darkness from morning onwards will perform less pronounced sleep-movements, or will take longer to produce them, than one illuminated during the day and hence strongly stimulated by the failure of the light in the evening. These and similar consequences follow naturally from the facts put forward by

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[1] Pfeffer, Physiol. Unters., 1873, pp. 75, 98, 188.

[2] Frank, Cohn's Beiträge zur Biologie, 1872, Bd. I, Heft 2, p. 80.

Pfeffer[1], but sufficient attention has not always been paid to this by Oltmanns[2] in his interpretation of the opening and closing movements of flowers.

Since the power of reaction is always present, numerous and often pronounced oscillations may occur as the result of variations of illumination during the day, especially in the case of organs exhibiting strong photonastic irritability. Darkening at midday produces, however, more effect than in the morning, since in the first case the photonastic response is aided by the incipient periodic after-effect. Hence the appearance of thunder-clouds at midday may cause the leaves and flowers of many plants to perform sleep-movements, whereas the same darkening during the early morning may only induce a feeble closing movement[3]. If, however, the periodic after-effect is strong, but the direct photonastic reaction feeble, darkening in the morning may cause an only temporary retardation or reversal of the opening movement, which is ultimately resumed and completed[4].

Illumination during the evening closure acts in the same manner, and in strongly photonastic plants such as *Mimosa* and *Acacia* the leaves may be brought back into the expanded position by illumination applied at the close of a cloudy day[5]. If a plant is illuminated during the night and darkened during the day, a rhythm corresponding to the altered conditions will be more or less rapidly induced after a few irregularities, and the new rhythm may be capable of persisting for more or for less than a day.

Since some time is required for the accommodation to the new conditions, a previously darkened plant must be exposed to light for some time before renewed darkening is able to produce a perceptible response. The leaves of *Acacia lophantha*, and of *Impatiens noli-me-tangere*, are able to show a feeble photonastic response to darkening after five to ten minutes' illumination, and after thirty minutes to an hour's exposure they are capable of exhibiting a maximal photonastic response, which undergoes no further increase, even after prolonged constant illumination[6]. [The photonastic response to intense illumination is much more rapidly produced, and in this way its utility as a protection against temporary intense exposure is considerably enhanced. Thus, in highly turgid plants of *Mimosa pudica*, the leaflets begin to fold together a second or two after strong sunlight falls upon them, and in thirty seconds to a minute become completely folded. The re-expansion in weak diffuse daylight takes from one to three minutes after short exposure, but a longer time is required when the exposure has been more prolonged. After midday the responses are usually less rapid, but this appears to be due merely to the lessened turgidity. Owing to the existence of a latent period, and an after-effect, the stimuli due to short periods of exposure may be summated so as to produce a response, and for the same

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[1] Period. Bewegungen, 1875.

[2] Bot. Ztg., 1895, p. 44.

[3] Pfeffer, Physiol. Unters., 1873, p. 201.

[4] L. c., 1875, p. 71.

[5] This opposed action was utilized by Pfeffer to produce a more rapid elimination of the daily periodicity under continuous illumination (l. c., 1875, pp. 35, 71).

[6] Pfeffer, l. c., 1875, p. 57.

reason leaflets folded in sunlight re-expand at first in darkness before they show a nyctinastic response. The leaves of *Acacia*, *Dalbergia*, and *Robinia* require at least two to three minutes to fold together in sunlight, and may fully expand after being shaded for five to eight minutes. The leaves of *Bauhinia*, *Albizzia*, *Calliandra*, and *Cassia* respond still more slowly, the closure requiring five minutes to half an hour, and the re-expansion ten minutes to two hours[1].]

A thermonastic response is also only possible when the change of temperature persists for some time and, since in all cases we are dealing with phenomena of irritability, the extent of the reaction always depends upon the power of perception. It is clear, however, that the time required to produce the maximal movement of a pulvinus will depend upon the rapidity with which a change of turgor follows a change of illumination. Furthermore, in cases where the movement is due to growth, rapidly repeated intense stimulation may produce a certain fatigue effect, such as appears to be shown by the flowers of *Crocus* after several responses to thermonastic stimulation[2].

It is, however, not certain whether the power of photonastic reaction is affected by the movement subsequently induced, for other extraneous demands often influence the power of response. Nevertheless, the increased action of darkening after midday appears to be due merely to the co-operation of the photonastic reaction with the induced periodicity. In any case, however, the summation of dissimilar stimuli involves more complex reactions than that due to the frequent repetition of the same stimulus.

The latent period of stimulation is shorter in the case of parahelionastic responses than of nyctinastic ones. The minimal difference of illumination required to produce a perceptible response varies in different cases, the leaflets of *Mimosa pudica* being especially sensitive. Increasing stimulation produces increasing responses within certain limits, but the stimulation needs to increase in geometric proportion to produce equal additional increments of response, quite apart from the reversal of the reaction which ensues under intense illumination.

Further investigation is needed to determine whether increases of illumination or temperature always produce the same amount of response as decreases, and whether the response is equally rapid in both cases. As regards parahelionastic responses, the closure of the leaflets is always more rapidly produced than the expansion under diminished illumination[3]. The influence of increases and decreases of temperature and of illumination on growth are not equally pronounced, and exposure to light produces a smaller rise of the leaves of *Impatiens noli-me-tangere* than the subsequent fall on darkening. It is, however, always possible that in such cases the leaf had an inherent tendency to curve to one side, which would minimize the induced curvature in the opposite direction. Especially in the case of transitory stimulation, increases of illumination or temperature may exercise effects which differ quantitatively and qualitatively from those produced by similar decreases. Correns[4] found, in fact,

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[1] Ewart, Annals of Botany, Vol. XI, 1897, p. 447 seq.

[2] Pfeffer, Physiol. Unters., 1873, p. 182.

[3] Cf. Ewart, Annals of Botany, Vol. XI, 1897, p. 447.

[4] Bot. Ztg., 1896, p. 13.

an increase of temperature produced a greater curvature in tendrils than a corresponding decrease. In the case of thermonastic flowers, however, if the same peculiarity were always shown, it should be possible, by repeated equal and slight rises and falls of temperature, to make the flower become fully expanded at comparatively low temperatures.

The sensation we experience on passing from darkness into intense light is not the same as is produced by the reverse procedure, and the same may apply to plants. Indeed, certain micro-organisms show a different response to increases of illumination to that produced by decreases. In addition, many organisms are able to withstand sudden increases in the concentration of the surrounding medium, whereas corresponding decreases may cause them to burst. Finally, very many chemical changes which are induced by rises of temperature or of illumination are not reversible.

An analogy is afforded by two metal thermometers of which one responds more rapidly than the other, and which are so arranged that, when warmed, contact is made, and an electric bell-circuit completed when a certain temperature is reached, whereas a fall to the same temperature produces no contact or electrical excitation. In addition, a clock strikes when the hands are moved round in the normal way, but not when they are turned in the opposite direction.

In the case of the mainly thermonastic flowers of *Crocus* and *Tulipa* a slight rise of temperature is sufficient to overcome the tendency to closure induced by darkness, whereas a pronounced fall of temperature is unable to reverse the daily opening movement of the mainly photonastic flowers of *Nymphaea alba*, *Oxalis rosea*, *Leontodon hastilis* and *Taraxacum officinale*[1]. Similarly, many photonastic flowers do not open at low temperatures such as 1° C. to 3° C., or only experience a slight temporary or permanent opening movement when illuminated under these conditions. Further, many flowers which open early and only close in the evening may remain open only for a short period of the day under special conditions[2]. The heads of *Leontodon hastilis* and of *Taraxacum officinale* may open little or not at all during the day if kept during the day and previous night at a temperature of 3° to 4° C., and may open in the evening in darkness as the result of the inductive action of the previous illumination when the temperature is raised to about 20° C.[3]

In addition to these factors the influence of the turgor upon the power of reaction may cause the daily rhythm of the sleep-movements to experience certain modifications which may in some cases become extremely pronounced, while the times of opening and closing of flowers may

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[1] Pfeffer, Physiol. Unters., 1873, pp. 195, 206; Period. Bewegungen, 1875, p. 133.

[2] Cf. Oltmanns, Bot. Ztg., 1895, pp. 31, 50. Oltmanns puts forward, however, a one-sided interpretation of the origin of the early-closing movement.

[3] Pfeffer, Physiol. Unters., 1873, p. 197

fluctuate for similar reasons, and also in accordance with the length of the day[1].

SECTION 27. **Conjoint Effects** (*continued*).

The simplest response involves such factors as the mechanical resistance of the curving organ, as well as the stimulatory effects due to the mere progress of the curvature and to the altered geotropic induction due to the changes of position. The statical moment of a leaf alters when it passes from the horizontally expanded position into a vertical one, and this is bound to exercise a certain influence upon the progress of the curvature, as does also the fact that more work is done when a leaf is raised than when it sinks downwards.

The energy of movement is, however, usually so great that the mechanical factors due to the weight of the leaf are of minor importance or may be negligible[2]. In the case of *Mimosa pudica*, however, the secondary petioles move forwards at evening[3], and the increased statical moment of the leaf causes a pronounced sinking of the primary petiole, which only rises above the position during the progress of the night, although darkening during the day always causes it to perform an upward photonastic movement[3]. That this evening fall of the primary petiole results from a photonastic reaction coupled with the increased moment exercised when the secondary petioles come more into line with the main one is shown by the fact that it gradually ceases when the change of position of the secondary petioles is mechanically prevented. The evening movement of the primary petiole then corresponds from the commencement with that produced by darkening, as it does in other plants. When the secondary petioles are released, a certain sinking of the main petiole ensues on the following evening, and increases gradually until, after five or ten days, it has reached its original amplitude. The evening fall is, therefore, due to the co-operation of the evening photonastic action with the after-effects of previous response and the mechanical actions resulting from the movement of the secondary petioles. As the result of the induced after-effects, the evening fall of the primary petiole only ceases a week or a fortnight after the secondary petioles have been fixed.

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[1] On the opening and closing times of flowers and on floral clocks cf. Kerner, Pflanzenleben, 1891, Bd. II, p. 211 (Natural History of Plants, 1895, Vol. II, p. 212); Burgerstein, Ueber die nyctitropischen Bewegungen der Perianthien, 1887, p. 39; Oesterreich. Bot. Ztg., 1901, Nr. 1.

[2] Cf. Pfeffer, Period. Bewegungen, 1875, p. 144. The mechanically stimulated leaf shown in Fig. 19, p. 61, will serve also to show the evening position.

[3] Pfeffer, Period. Bewegungen, 1875, p. 73. The normal progress of the daily movements was described in detail by Millardet, Nouv. Recherches sur la périodicité de la tension, 1869 (reprinted from Mém. de la Soc. d. sci. nat. de Strasbourg, T. VI).

Although the dependence of the sinking of the primary petiole upon the movement of the secondary petioles has been empirically determined, it does not follow that the fall is directly due to their increased statical moment, which may sometimes increase by as much as one-half. A suddenly increased load does actually cause a perceptible fall of the primary petiole, but there can be no doubt that we are here dealing with a complex physiological reaction. Indeed, in their normal habitat, the primary pulvini of *Mimosa* are capable of response to mechanical excitation, even when the petiole has reached its lowest nyctinastic position, and when the plant is highly turgid the pulvinus may curve to such an extent as to temporarily bend the leaf back across the stem in a partially inverted position, so that the mechanical moment is considerably increased[1]. Pfeffer inclines to regard the gradual increase of the mechanical moment as being the stimulus responsible for the fall of the primary petiole, but it might also occur in indirect correlation with the other movements without being directly due to them. In addition, this fall does not always appear to occur[2], while Schilling has shown that, during the daytime, a load causing an enforced curvature of the main pulvinus of *Mimosa* excites a reaction tending to the restoration of the original position of equilibrium[3].

If leaves capable of sleep-movements are exposed during the day to light coming from one side only, so that the plane of the leaf remains oblique during the day, next morning they may again assume a similar position, even when in darkness[4]. This after-effect may, however, be different in character to those resulting from realized sleep-movements, which, even when mechanically prevented, may lead to after-effects if the plant strives to produce them.

Photonastic and thermonastic curvatures are not only possible when the required physiological dorsiventrality is of internal origin, but also when it is due to the stable or labile induction of external factors. In the last case, the power of aitionastic curvature is naturally only retained as long as the induction persists, and the reaction is, therefore, rapidly modified when an alteration in the external condition modifies the tone of the organ. Certain negatively geotropic pulvini afford good instances of the modification of the photonastic reaction by labile geotropic in-

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[1] Ewart, Annals of Botany, Vol. XI, 1898, p. 453. [The mechanical moment is less in the fully drooping position than in any other. In addition, the mechanical moment may increase during the assumption of the parahelionastic position by as much as it does at the commencement of the nyctinastic movement without producing any distinct fall of the primary petiole.]

[2] Cunningham, Annals of the Royal Botanical Garden of Calcutta, 1895, Vol. VI, p. 135. [In some cases the fall may take place without any movement of the secondary petioles, and the temperature appears to have some effect. Plants of *Mimosa pudica* appear rarely to be capable of the same rapidity of response in European hothouses as in their natural habitat, and in addition readily fall into an irresponsive condition although the leaflets may remain green, normal, and capable of photosynthesis.] The mechanical considerations put forward by Schwendener (Ges. bot. Mittheil., 1897, Bd. II, p. 238) do not alter the facts in the least.

[3] Schilling, Der Einfluss der Bewegungshemmungen auf die Arbeitsleistungen d. Blattgelenke von *Mimosa pudica*, 1895.

[4] Darwin and Pertz, Proc. of the Phil. Soc., Cambridge, 1900, Vol. X, p. 259; Annals of Botany, 1903, Vol. XVII, p. 93.

duction[1]. When such plants are inverted or rotated on a klinostat the absence of the geotropic stimulus or its reversal causes the position of the leaves to alter. This takes place with such rapidity in the case of *Phaseolus multiflorus* and *P. vulgaris* that when the plant is inverted, a leaf in the day position passes in the course of a few hours into a position resembling that assumed during night (Fig. 33, *a* and *b*). The pulvini still perform photonastic curvatures, but these now take place in the opposite direction in regard to the plant.

Similar changes are shown by *Desmodium gyrans*, although in the inverted position the terminal leaflet does not quite reach the same angle as under normal conditions. In most pulvini, however, the dorsiventrality is fixed to such an extent that after inversion the sleep-movements retain the same direction in regard to the plant as before. Fischer[2] has shown that the same is the case when the geotropic action of gravity is eliminated by rotation on a klinostat. Under these conditions the sleep-movements of *Phaseolus vulgaris*, *P. multiflorus*, and *Lupinus albus* cease mainly or entirely, so that the pulvini of these plants are physiologically radial to photonastic stimuli in the absence of any geotropic induction. On the other hand, in most plants such as *Acacia lophantha*, *Trifolium pratense*, *Amicia*, and *Biophytum sensitivum* the photonastic reaction is mainly the result of an inherent physiological dorsiventrality, since the sleep-movements continue on a klinostat with considerable amplitude and in the same direction as before.

FIG. 33. Inverted plant of *Phaseolus multiflorus*. The petioles of the first pair of foliage-leaves are fixed by the wire *d*, so that only the pulvinus at the base of the lamina is able to curve. The leaf *a* is in the day position, while *b* is shown in the night position. The leaflets of the trifoliate leaf *c* are brought into the normal light position by the curvature of the basal pulvinus, and hence carry out the normal sleep-movements.

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[1] Pfeffer, Period. Bewegungen, 1875, p. 138.

[2] Fischer, Bot. Ztg., 1890, p. 672.

The amplitude of the daily movements of *Cassia marylandica* decreases on the klinostat, while the geotropic induction seems to overcome the inherent physiological dorsiventrality of *Desmodium gyrans*, since Fischer found the sleep-movements of this plant continue in the usual direction on a klinostat, and Pfeffer found that in the inverted position they were reversed. It is, in fact, only natural that intermediate conditions should exist between strictly autonyctinastic and strictly geonyctinastic plants[1].

Owing to the induced periodicity the daily movements do not at once cease on a klinostat, but continue for some days with decreasing amplitude, and under normal conditions slowly regain their original value. When a plant of *Phaseolus* is inverted, however, the dominating influence of the geotropic induction causes the sleep-movements to be reversed on the very first day. Since the curvature of the pulvinus influences not only the geotropic induction but also the photonastic tone, the progress of the movement exerts a certain modifying influence upon its continuance, quite apart from any geotropic or heliotropic action. Stahl[2], in discussing the subject solely from a biological standpoint, has unfortunately not properly distinguished the tropic orienting movements from the aitionastic ones. Indeed, the movements of the leaves on vertical branches may differ slightly from those on more horizontal ones for a variety of reasons[3]. Hitherto experiments have been performed only upon the variation movements of pulvini, but it seems probable that similar relationships will be found to hold good for the daily movements due to growth[4].

Dorsiventrality, whether morphological or physiological, usually involves a more or less pronounced power of aitionastic reaction, and many cases in which a labile or stable dorsiventrality is induced by unilateral stimulation afford at the same time instances of the induction of photonasty, thermonasty, and the like. Probably no tropic action leaves the power of aitionastic reaction entirely unaffected, and *Phaseolus* affords a good instance of the reversal or induction of the power of photonastic response by geotropic action. Although in this case the induction is coupled with a geotropic curvature, nevertheless in other cases pronounced structural induction may take place without any special motile response. The structure, however, affords no indication of the existence of a power of aitionastic, tropic, or other irritability, and hence the photonastic irritability of the pulvinus of *Phaseolus* may be induced or reversed without the dorsiventral structure of the pulvinus experiencing any perceptible alteration.

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[1] A. Fischer, l. c., p. 711. The term autonyctinastic is employed here in preference to that of autonyctitropic. According to Fischer (l. c., p. 709), *Mimosa pudica* is also autonyctinastic, but it is not stated whether the evening fall of the primary petiole continues on the klinostat.

[2] Stahl, Bot. Ztg., 1897, p. 86.

[3] Darwin, The Power of Movement in Plants, 1880, p. 263.

[4] Cf. Pfeffer, l. c., p. 143.

All aitionastic reactions dependent upon physiological reactions need not, however, result in rapid or pronounced movement, for slow movements may be of the utmost value in ensuring appropriate positions of the subaerial organs more especially in regard to light. The rhizomes of *Adoxa moschatellina*, of *Circaea*, and of a few other plants show no power of photonastic reaction when rotated on a klinostat, but do so when exposed to the inductive action of gravity. When the rhizome has assumed a transversely geotropic position in darkness, exposure to diffuse light excites a downward curvature which increases to a certain maximum as the illumination increases. Renewed darkening results in the assumption of the original diageotropic position. The subaerial runners of certain plants behave in the same way, for they become erect in darkness, and curve to a horizontal position when exposed to sufficiently strong diffuse illumination. Geotropic induction may indeed take place in several photonastic responses, especially when the organ possesses a strong geotropic irritability. According to Lidforss, the thermonastic reaction of the shoots of *Holosteum umbellatum*, *Lamium purpureum*, *Veronica chamaedrys*, and *Mimulus Tilingii* depends upon geotropic induction, but not that of the peduncles of *Anemone nemorosa*[1].

These curvatures are to be classed as photonastic, since under this head we include all reactions due to changes in the intensity of the diffuse illumination without specifying the detailed mode of perception and response. The same would still be the case when the illumination merely modified the geotropic irritability, and hence produced varying geotropic curvatures according to its intensity. Indeed, if primary importance is attached to the geotropic irritability, the illumination and temperature may be regarded as modifying the geotropic tone, for, apart from all considerations as to the internal physiological reactions, it remains the fact that the same tropic action of gravity may produce varying degrees of curvature according to whether the plant is strongly or feebly illuminated, that is according to its phototonic condition.

The knowledge that a particular curvature is due to the co-operation of light and gravity, the former altering while the latter remains constant, does not reveal all that is to be learnt about the phenomenon. The geotropic irritability might alter according to the intensity of the illumination ; or, the former remaining unaltered, the dorsiventrality induced by the constant stimulus of gravity might co-operate with the variable photonastic response. Other factors might also come into play, but it is clear that in all cases the geotropic stimulus is as directive in character as when the photonastic irritability is based upon an inherent dorsiventrality, and

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[1] Lidforss, Bot. Centralbl., 1901, Bd. LXXXVIII, p. 169; Jahrb. f. wiss. Bot., 1902, Bd. XXXVIII, p. 343.

the position of equilibrium results from the co-operation of photonastic and geotropic reactions. It is also evident that a physiologically radial organ will no longer respond on a klinostat to changes of illumination, independently of whether the action of gravity renders possible a photonastic response by inducing a labile physiological dorsiventrality, or whether the geotropic irritability alters according to the illumination.

No safe argument can be drawn by analogy, since the same result and purpose may be obtained in various ways. Even if in a particular case a labile induction, responsible for a photonastic reaction, persisted for a time after the removal of the inducing external agent, its detection would not show that the conjoint action of tropic and diffuse stimuli always takes place in this way. It is, in fact, well known that both the geotropic and phototropic irritabilities are capable not only of autonomic modification, but may also be affected by various external factors.

The production of a power of photonastic response in the pulvini of *Phaseolus* appears to be due to geotropic induction, for the photonastic irritability is acquired or modified in conjunction with the performance of a pronounced geotropic curvature, and for this reaction illumination is not essential. Noll's[1] view, according to which we are here dealing with a modification of the geotropic irritability of illumination, is the result of a biased and incomplete comprehension of the problem. In any case, however, it is still necessary to determine whether the changed reaction is due to a modification of the photonastic irritability or to an altered power of movement in the antagonistic halves of the pulvinus. That the latter is possible is shown by the fact that the geotropic curvature considerably modifies the expansive energy of the opposed halves, that in the lower side after reversal increasing, and that in the side now facing upwards decreasing. Since in general the existent mechanical considerations influence the progress and in some cases the activity of the response, it is not inconceivable that on darkening the increased expansion which produces the photonastic curvature should always take place more rapidly in the less expanded half of the pulvinus than in the more expanded one.

SECTION 28. **The Mechanics of Nutation Movements.**

We must confine ourselves to photonastic and thermonastic movements, since no researches have as yet been performed upon the mechanics of hydronastic curvature. It is evident that whenever a rise or fall of temperature or illumination affects the growth of the two sides of an organ unequally a curvature will result, which will continue until a position of equilibrium

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[1] Noll, Die heterogene Induction, 1892, p. 12.

is reached. This depends upon the growth tendencies of the different tissues, coupled with the mechanical and physiological reactions due to the realized curvature.

It depends upon the properties of the organ, and upon the rapidity of the change of temperature or illumination, whether the new position is assumed directly, or after a number of oscillations. These may arise either owing to the fact that the different tissues assume rates of growth proportionate to the new conditions with unequal rapidity, or they may be due to the fact that the shock-stimulus produces a transitory and unequal acceleration or retardation of growth. These transitory oscillations must be reduced and finally eliminated when the change of temperature or other condition is brought about sufficiently slowly. Their production has, however, no influence upon the ultimate position, which when once attained is maintained so long as no internal or external change occurs. An organ may, however, react in such a way that the change produces pronounced oscillation, but no permanent alteration of the original position.

It is impossible, therefore, to say whether any shock-effect comes into play. The new rapidity of growth corresponding to changed conditions of temperature or illumination is, however, usually assumed without any perceptible transitory disturbances being shown, and hence more especially the slower photonastic and thermonastic curvatures, and possibly also certain typical sleep-movements, may be produced without any transitory acceleration or retardation of growth due to the effect of shock. A shock-stimulation is, however, exercised in many cases[1] in which a fall or rise of temperature or illumination produces a certain transitory acceleration of growth. As in the case of tendrils this renders the reaction more rapid, and enables a flower of *Crocus* to close rapidly when subjected to a fall of temperature at which growth ultimately almost ceases.

This acceleration of growth is as pronounced in highly photonastic or thermonastic plants as in the case of tendrils. Thus the growth of the middle lamella of the petiole of *Impatiens noli-me-tangere* may temporarily attain about twenty times its previous rapidity when an energetic photonastic reaction is produced by sudden darkening[2]. In one experiment the marks on the petiole covered 183·5 of the micrometer divisions after four hours instead of the original 182, which indicated a growth in length of 0·21 per cent. per hour. After darkening the leaf curved strongly downwards in half an hour, and since the marks extended on the upper side from 184 to 192 micrometer divisions the growth in length was 8·68 per cent.

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[1] Pfeffer, Period. Bewegungen, 1875, pp. 13, 122, 171. The text is based mainly on these researches and upon those of Jost.

[2] Pfeffer, l. c., p. 21.

per hour. The simultaneous measurement of the under side gave a shortening of 0·53 per cent., so that the growth of the middle lamella was 4·07 per cent., or half the algebraic sum of the growth on the two sides. Similarly in the flower of *Crocus* a sudden fall of temperature from 17° to 7° C. may cause the average growth of the middle lamella of the active zone of the perianth to increase transitorily from seven to ten times in rapidity, although ultimately growth is strongly retarded at 7° C. Observations on *Tulipa* also showed an increase of growth to eighteen times its previous rapidity when the temperature was suddenly raised from 11° to 18° C. and, even allowing for the permanent increase at the higher temperature, the transitory rise is eight times greater.

As in the case of the curvature of tendrils, during these photonastic or thermonastic responses the concave side retains the same length or experiences a very slight shortening during curvature. During the return movement by which the leaf of *Impatiens* nearly regains the day position after being darkened, the previously accelerated side grows but little or not at all. The recent researches of Wiedersheim carried out at Leipzig under Pfeffer's direction show that the return movement is accompanied by a secondary feebler acceleration of the growth of the middle lamella, as in the case of tendrils. This secondary acceleration is shown by the flowers of *Crocus* and *Tulipa*, but is comparatively feeble, since the return movement only takes place to an extent sufficient to remove the excess of curvature.

As in the case of tendrils, a transitory change only produces a temporary curvature, the organ returning to its original position when the previous conditions of temperature or illumination are restored. In such cases the secondary acceleration of growth during the return movement naturally becomes more pronounced. Although the curvature of tendrils results from a tropic stimulus, and those of thermonastic and photonastic organs from diffuse stimulation, the growth-mechanisms involved are the same in both cases. The entire active zone on both sides of the organ experiences an acceleration of growth, which begins at a later time on the side which becomes concave, but which, whenever the organ straightens again, ultimately produces the same total growth in spite of its originally slower rate on the concave side. It follows, therefore, that the production of a permanent curvature involves either a partial inhibition of the slower but more prolonged growth response on the concave side or the prolongation of the growth period on the convex side.

Among the factors responsible for these reactions the stimulating effects of shock and of the realized movement are to be included. It is not, however, certain whether the latter is directly responsible for the return movement by which the original position may be partially or entirely restored. Wiedersheim has, however, found that when a fixed leaf of *Impatiens parviflora* is darkened two opposed successive accelerations of growth ensue just as in the case of stimulated tendrils. That a secondary acceleration of growth actually occurs on the concave side is shown by the tendency to a return curvature in a fixed leaf, as well as by direct measurement. Fixed perianth-segments of *Crocus* and *Tulipa* show a feebler secondary acceleration of growth, owing to the fact that a permanent change of temperature alters the position of equilibrium in such manner as to lessen the return movement. It is, however, possible that the return movement, although excited in the absence of any realized curvature, may result from the altered tensions in the tissues. However this may be, there can be no doubt that, in the case of variation movements, correlative influences, as apart from mechanical ones, do travel between the closely related halves of motile pulvini.

A direct or indirect regulation of the growth in the different parts is essential to produce a definite reaction. The fact that the concave side may retain approximately its original length during the curvature of tendrils as well as of photonastic and thermonastic organs simply shows that the growth acceleration lessens towards the concave side, for in the middle lamella of this side the growth will be ten times accelerated when the growth of the middle lamella of the entire organ is accelerated twenty times. The slight shortening sometimes shown on the concave side is probably the result of compression, and would be greater during curvature were it not for the simultaneous awakening of an increased tendency to growth[1].

Jost[2] erroneously supposed that the thermonastic or photonastic stimulation directly accelerated the growth on one side and retarded it on the other, and does not sufficiently distinguish between the transitory and stationary reactions and their results. It is not, however, impossible that in isolated cases some such antagonistic action may be exercised, or that as the result of shock-stimulation particular cells may experience a temporary retardation of growth followed by the usual acceleration. The new constant conditions of temperature or illumination always, however, produce the same qualitative effect on growth although not always the same quantitative effect, and special peculiarities may be shown when the temperature or the illumination rises above the optimal values. Apart from this the formal effect of a rise of temperature or decrease of illumination is an acceleration of growth, while a permanent fall of temperature or increase of illumination produces a retardation of growth. As the result of shock, however, a sudden rise or fall of temperature or illumination may produce either a transitory acceleration or retardation of growth according to the nature of the plant. True[3] observed that a sudden rise or fall of temperature produced a transitory retardation of growth in the radicle, but it is

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[1] Pfeffer, Period. Bewegungen, 1875, p. 17.

[2] Jost, Jahrb. f. wiss. Bot., 1898, Bd. XXXI, p. 368.

[3] True, Annals of Botany, 1895, Vol. IX, p. 365.

also possible, though hardly probable, that a decrease of temperature or illumination might transitorily affect growth but not an increase. It is also possible that in thermonastic flowers a temporary retardation of growth may precede its acceleration, but may be too transient to be capable of detection, or may merely antagonize the first tendency to increased growth, thus increasing the latent period of response.

In any case when we remember the influence of the specific properties and its variable tone upon its power of response, it is not surprising to find that the results obtained do not in all cases precisely agree. Thus Pfeffer[1] found that a fall of temperature produced a very pronounced acceleration of growth in the perianth-segments of *Crocus*, but that a sudden rise produced no perceptible acceleration in the growth of the middle lamella, whereas Jost[2] observed in both cases a strong acceleration of growth in the perianth of the *Tulip*.

It is uncertain to what extent sudden changes of illumination may exercise shock-effects upon photonastic organs. During the daily movements of the flowers of *Leontodon hastilis*[3] and of *Taraxacum officinale*[4] the average growth is accelerated, but here the effect of the direct stimulation is coupled with the induced periodicity. Since this periodicity and also the daily periodicity of growth in length are induced by periodic changes of illumination, we may assume that every photonastic reaction is coupled with a temporary acceleration of growth. Even when the opening and closing movements assume a more rapid rhythm in constant darkness, each periodic reaction involves a temporary acceleration of the average growth.

A very pronounced movement and acceleration of growth is produced by darkening the leaves of *Impatiens noli-me-tangere* and *I. parviflora*. Illumination only produces a feeble movement, but it is not certain whether the acceleration of the average growth is also feebler than when the leaf is suddenly placed in darkness.

A transitory acceleration of growth may enable more rapid curvature, but it is not essential, and probably is either absent or feeble in many thermonastic and photonastic movements. In the latter case it is easily overlooked, since the activity of growth is always liable to spontaneous fluctuations, and since it assumes a different stationary value in response to the new conditions. Pfeffer[5] was, however, overcautious in refusing to accept the general acceleration of growth shown by his measurements as being the result of the shock-stimulus.

Special instances. The following results have been obtained by micrometric

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[1] Pfeffer, Period. Bewegungen, 1875, p. 122.

[2] Jost, Jahrb. f. wiss. Bot., 1898, Bd. XXXI, p. 346.

[3] Cf. Table 4, p. 134, and Pfeffer, l. c., p. 26.

[4] Jost, l. c., p. 354.

[5] Pfeffer, l. c.

measurements of the distances between exactly opposite pairs of marks on the two sides of the active zone of the perianth. From these hourly measurements percentage values have been calculated for the opposed sides. The half of the algebraic sum of the two values gives the percentage growth of the actual or ideal middle lamella (Tables 3 and 4). In Tables 1 and 2 only this average growth is given, but since in these estimations with the flower of the *Crocus* the concave side remained of the same length or shortened very slightly, twice the average growth gives that of the convex side.

The values in Tables 1 and 2 [1] are the averages of six separate estimations, those of Table 3 [2] of three, and those of Table 4 are obtained from three separate flowers [3].

The measurements were made on a single remaining perianth-segment of *Crocus* and *Tulipa*, and on a single remaining floret of *Leontodon*. Table 1 shows that the cooling of the flower of *Crocus* [4] produced a pronounced acceleration of growth in fifteen minutes, which rapidly lessened and had almost ceased after half an hour. A feeble transitory acceleration of growth also appears in Table 2, but is less evident (1·51 as compared with 1·03). A pronounced transient acceleration is, however, shown in Table 3, and after two hours a return curvature is shown, which is accompanied by an acceleration of growth on the outer side of the perianth, and a retardation on the inner side.

TABLE 1. *Crocus* sp. Percentage Growth of the Middle Lamella per hour.

Temperature 17–18° C. Time of observation.		Then at 7–7½° C. and measured		
16½–16¾ hours.	3 hours.	after 15–20 minutes.	25–30 minutes later.	3 hours to 3 hours 20 minutes later.
0·75	0·54	5·24	2·44	0·29

TABLE 2. *Crocus* sp. Percentage Growth of the Middle Lamella per hour.

Temperature 8–9° C.	Then at 20–21° C. and measured		
Time of Observation. 3–6 hours.	after 20–45 minutes.	40 minutes to 2 hours 20 minutes later.	45 minutes to 2 hours later.
0·24	1·51	1·26	1·03

TABLE 3. *Tulipa Gesneriana* (Duc van Toll). Percentage Growth per hour.

	Temperature 11° C.		Then at 18° C.			
	5.30–9 a.m.	9–12 a.m.	12.40 a.m. to 1.40 p.m.	1.40 p.m. to 2.40 p.m.	2.40 p.m. to 3.40 p.m.	3.40 p.m. to 5.40 p.m.
Outer side . . .	0·16	0·20	1·1	5·79	1·46	0·78
Middle lamella .	0·22	0·17	3·76	2·98	1·75	0·48
Inner side . . .	0·29	0·15	6·43	0·18	2·05	0·19

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[1] Pfeffer, Period. Bewegungen, p. 125, Tables XI *b*, and p. 127, Table XIII *b*.

[2] Jost, l. c., p. 354.

[3] Pfeffer, l. c., p. 27, Tables VII *b* and VII *c*.

[4] A large white-flowered garden variety was used.

TABLE 4. *Leontodon hastilis.* Percentage Growth per hour.

		Daylight.	Darkness.	Daylight.	
		11.30 a.m. to 10.30 p.m.	10.30 p.m. to 6 a.m.	6 a.m. to 8.45 a.m.	8.45 a.m. to 4 p.m.
Experiment 1	Outer side	1·47	0·17	0·46	2·37
	Middle lamella . .	0·45	0·82	2·03	1·67
	Inner side	0·43	1·47	3·60	0·97
Experiment 2	Outer side	0·47	0	0·15	2·17
	Middle lamella . .	0·3	0·66	2·23	1·47
	Inner side	0·13	1·33	4·32	0·77
Experiment 3	Outer side	?	0	0	1·54
	Middle lamella . .		0·82	1·92	0·83
	Inner side	0	1·65	3·84	0·13

Table 4 shows that after a day's illumination, mainly the outer side of the corolla grew in length during the evening curvature. During the night the flower returned halfway to the day position, owing to the growth of the inner side, and this growth was accelerated by the light at 6 a.m., leading to the assumption of the full day position by 8 a.m. At 4 p.m. the closing movement begins again, while between 6 and 8.45 a.m. the growth of the middle lamella was accelerated.

SECTION 29. **The Mechanics of Variation Movements.**

Most variation movements are photonastic in character, and show a general resemblance to nutation movement except that the curvature is produced by the unequal expansive energy of the turgid tissues instead of by unequal growth. A decrease of illumination produces an increase of the expansive energy in the antagonistic tissues, but this takes place more actively in one-half of the pulvinus than in the other, the tissues of the latter being therefore compressed. Owing to the continued increase of the expansive energy in the compressed half of the pulvinus a partial return to the original position occurs, the fall of illumination exciting a movement in excess of the permanent position adapted to the new constant conditions of illumination. In darkness or in diminished illumination growth in general is accelerated, while the expansive energy of the motile tissues is increased, and to the same extent in both halves of the pulvinus when the leaf returns to its original position. On returning to the previous strong illumination the expansive energy assumes its original value, and possibly a sudden rise of illumination may act as a transitory stimulus and produce an excess of movement. The latter may, however, not be as pronounced as when a fall of illumination occurs, and indeed it may be imperceptible in most cases.

In constant darkness or illumination the periodic movements are produced by opposed changes of the expansive force of the halves of the pulvinus without any general rise being shown, which indeed is no more essential for curvature than is a general acceleration of growth for a nutation movement. The automatic variation movements are produced in the same way by an increase of the expansive energy in one-half of the pulvinus and a decrease in the other, for in both cases the rigidity of the pulvinus is unaltered during the movement, whereas a fall or rise of rigidity would inevitably ensue if the movement was due to an increase or decrease of the expansive energy on one side only of the pulvinus.

These conclusions are mainly attained from estimations of the rigidity of the intact pulvinus under different circumstances, for although no simple relationship exists between the tissue-strains and the weight supported, nevertheless a decreased rigidity indicates a fall, and an increased rigidity a rise of the expansive energy of the active tissues. The original determinations were made by Brücke, who noted the angular displacement in the normal and inverted positions with or without the addition of loads. Since the divergences may be from one and a half to two and a half times greater in light than in darkness, it follows that darkness produces a permanent rise of the expansive energy on both sides of the pulvinus [1].

In the pulvini of *Phaseolus*, *Trifolium*, and *Desmodium* the maximal rigidity is attained at or before the completion of the curvature induced by the withdrawal of light, and since the rigidity is unaltered during the return movement, the latter can only be due to a decrease in the energy of expansion in the contracting half of the pulvinus. If this were not the case, and if, for instance, the partial or complete elimination of the primary curvature were due to a rise in the expansive energy of the compressed half of the pulvinus, then an increase of rigidity would accompany the return movement as well as the original curvature. If, however, the return movement were due solely to a fall of the enhanced expansive energy in the active half of the pulvinus, it would be accompanied by a perceptible decrease of rigidity. Hence there can be no doubt that the expansive energy of the active half of the pulvinus undergoes a transitory increase beyond the stationary value [2], and the same probably applies even to slowly reacting pulvini. The permanent rise of rigidity after the curvature produced by darkness has been eliminated shows that a permanent rise of expansive energy is produced in the half of the pulvinus which is at first compressed.

These facts do not, however, enable us to say whether the darkening does not also produce a certain transitory decrease of expansive energy in the compressed half of the pulvinus, for perceptible changes of rigidity are only produced by pronounced alterations in the expansive energy of the pulvinar

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[1] Pfeffer, Period. Bewegungen, 1875, p. 88 seq.

[2] [So that the excess curvature cannot be due to the momentum of the moving leaf. The mechanics of the whole subject require further elucidation and investigation.]

tissues, and a decreased expansive energy in the less responsive half of the pulvinus might be masked as regards changes of rigidity by a corresponding increase in the more rapidly reacting half. The behaviour of pulvini, from which one-half has been removed, as well as the analogy with nutation reactions, point against the occurrence of any such transitory decrease of expansive energy [1].

The effective energy of expansion is considerable in the case of the primordial leaves of *Phaseolus vulgaris*, for the pressure required to prevent movement, as measured by a dynamometer or spring-balance, is such as to show that the upper half of the pulvinus generates an energy of expansion equalling two to five atmospheres. This is, however, merely the excess pressure over that in the lower half of the pulvinus, so that the pressure in the upper half must be at least from five to seven atmospheres [2]. A pronounced energy of movement is also developed in a mechanically-stimulated leaf of *Mimosa pudica*, but in this case a pronounced fall of rigidity takes place.

The tension exerted on the dynamometer shows that the progress of an attempted curvature resembles that of a realized one, while the same increase of expansion in darkness is ultimately shown in the more slowly reacting half of the pulvinus of a fixed leaf, as when a curvature can take place. It remains, however, possible that the realized curvature may act as a retarding stimulus to the expansion of the compressed half of the pulvinus. At the same time the structure of the pulvinus is such that when an attempted curvature is prevented the increased energy of expansion exerts no tension on the opposed half of the pulvinus. This does occur, however, in growing organs, and indeed it is largely by tensions of this kind that growth is regulated and the development of pronounced strains avoided. Hence during nutation curvatures no pronounced rise of rigidity is shown, nor can any pronounced pressure be exercised against a resistance which prevents the attempted movement [3].

The behaviour of pulvini from which one of the antagonistic halves has been removed supports the above conclusions [4]. Under these circumstances the remaining half, whether the upper or under one, shows an increased tendency to expansion when the illumination decreases, and a decrease when it increases, so that in both cases a curvature is produced. The inherent periodicity is shown by the changes in the separate halves of the pulvinus being opposite in character. Hence the leaves of *Phaseolus* fall at evening, whichever half of the pulvinus is present. If only the under

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[1] [The varying mechanical moment of the leaf in its different positions is a factor of the utmost importance in this connexion.]

[2] Pfeffer, Period. Bewegungen, 1875, p. 97 seq.; Meischke, Jahrb. f. wiss. Bot., 1899, Bd. XXXIII, p. 347.

[3] Pfeffer, l. c., pp. 92, 111.

[4] Pfeffer, l. c., pp. 7, 84.

half is present sudden darkening during the evening produces a reaction opposed to the normal periodic one, whereas in the intact pulvinus the photonastic and periodic reactions would coincide.

The general agreement of the facts observed points to the conclusion that each half of the pulvinus when freed from its counterpart reacts in the same way as it did in the intact pulvinus. The behaviour of pulvini which have been operated upon does not, however, indicate with certainty what goes out in the pulvinus as a whole, for it is well known that mechanical or other injurious agencies often very strongly modify the power of reaction. Hence, although after operation the remaining under half of the pulvinus of *Phaseolus* shows a rapid increase of expansive energy, it does not follow that this half of the pulvinus reacts equally rapidly in the intact pulvinus.

Similar observations indicate that darkening also causes an expansion in the halves of the pulvinus, but since it takes the same progress on both sides no curvature results under normal conditions[1]. The same applies to the upper and under halves when the plant is rotated on a klinostat. The primary similarity can be removed by exposure to the action of gravity, and it depends upon the normal or inverted position of the plant whether the dorsal or ventral half of the pulvinus is compressed when a curvature follows darkening. This fact points to the conclusion that the photonastic curvature of this plant involves a quantitatively but not a qualitatively dissimilar reaction in the antagonistic halves of the pulvinus.

Historical. Dassen[2] distinguished between curvatures with and without pulvini, but did not recognize that in the one case the movement is one of variation, and in the other is due to growth. Pfeffer[3] showed that the opening and closing movements of flowers were due to growth; and the same was observed by Batalin[4] in a few foliage-leaves, but this author erroneously supposed that the movements of pulvini were also due to unequal growth. The true condition of affairs was revealed by Pfeffer's investigations on periodic movement[5]. Burgerstein's[6] statement that the opening of flowers is not due to growth, but to stretching by turgor, is either based on error or on an incorrect grasp of the facts. It is difficult to see how this author in his later work is able to deny that growth is responsible for the movements of the perianth-segments of *Crocus* and *Tulipa*, for growth always occurs when a permanent elongation takes place. How the growth is produced is naturally another matter.

A fact of great importance was that observed by Brücke[7], who found the rigidity

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[1] Pfeffer, Physiol. Unters., 1873, p. 11.

[2] Dassen, Wiegmann's Archiv f. Naturgeschichte, 1838, IV. Jahrg., Bd. 1, p. 214; IV. 2, p. 159. For additional literature see Pfeffer, Period. Bewegungen, 1875, p. 163.

[3] Pfeffer, l. c., p. 161.

[4] Batalin, Flora, 1873, p. 450.

[5] Pfeffer, Period. Bewegungen, 1875.

[6] Burgerstein, Oesterreich. Bot. Zeitschrift, 1901, Nr. 6; Ueber die Bewegungserscheinungen der Perigonblätter von *Tulipa* und *Crocus*, 1902.

[7] Brücke, Müller's Archiv f. Anatomie u. Physiologie, 1848, p. 440.

of the pulvinus of *Mimosa pudica* increased in the evening, so that the sleep-movements are not produced by one-half of the pulvinus becoming flaccid, as are those following mechanical excitation. A natural result of this fact is that in the drooping evening position the main pulvinus is still capable of a pronounced curvature in response to mechanical excitation [1]. Long before Brücke's time Dutrochet [2] had concluded, mainly from observations upon operated pulvini, that the sleep-movements were due to opposite changes of the energy of expansion in the antagonistic halves of the pulvinus. Dassen, Brücke, and Sachs [3] came into more or less accordance with this view, whereas Millardet [4] and Bert [5] concluded that the changes of expansion were alike in character in both halves, but differed quantitatively, and also in their progress in time. The subject was then fully explained as in the text by Pfeffer's researches. Previously to these researches the effects of the periodicity and of the direct stimulation were not properly distinguished, with the result that the observations upon operated pulvini led to contradictory conclusions. The completeness of the operation is also of great importance, for if the parenchyma is removed from the upper half of a pulvinus of *Phaseolus* down to the upper surface of the vascular cylinder only, a fall is produced by darkening just as in the intact pulvinus, owing to the fact that the expansive energy of the remaining portion of the pulvinus is still greater than that of the lower half. If, however, the parenchyma is removed down to a plane passing through the middle of the vascular cylinder, the leaf rises in darkness, showing that the expansive energy of the lower half of the pulvinus has increased [6]. It was probably owing to the incomplete removal of the upper half of the pulvinar tissue that Schwendener and Jost [7] obtained contrary results with *Phaseolus*, while Schwendener observed in a few other cases a shortening of the remaining half of the pulvinus on darkening, if this is the half which is compressed when intact. Pantanelli [8] has found recently that both halves of the operated pulvini of *Robinia pseudacacia* and *Porliera hygrometrica* react similarly to darkening. Schwendener [9] also observed that after operation the main pulvinus of *Mimosa pudica* carried out the same daily movements as before, provided that the periodicity was not disturbed by any excessive and abnormal photonastic reaction. This result confirms that obtained by Pfeffer.

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[1] Ewart, Annals of Botany, Vol. XI, 1898, p. 453.

[2] Dutrochet, Rech. anatom. et physiol. s. la structure intime d. animaux et d. végétaux, 1824, p. 134. For the detailed literature see Pfeffer, Period. Bewegungen, 1875, pp. 6, 163; Physiol. Unters., 1873, p. 3. Cf. also Schwendener (1896), Gesammelte Botanische Mittheilungen, Bd. II, p. 219.

[3] Sachs, Bot. Ztg., 1857, No. 46 a, 47.

[4] Millardet, Nouvelles recherches sur la périodicité de la tension, 1869, pp. 31, 48.

[5] Bert, Mém. de la Soc. d. scienc. physiques et naturelles de Bordeaux, 1870, p. 51 of the reprint. Cf. Pfeffer, l. c., 1875, p. 7.

[6] Giessler and Wiedersheim have repeatedly found that the completion of the removal of the upper half of the pulvinus always results in the shortening of the lower half on darkening being converted into a lengthening. These results therefore confirm the original ones by Pfeffer (l. c.).

[7] Schwendener (1898), Gesammelte Bot. Mittheilungen, Bd. II, p. 246; Jost, Jahrb. f. wiss. Bot., 1898, Bd. XXXI, p. 370.

[8] Pantanelli, Studii d' anatomia e fisiologia sui pulvini motori, 1901, pp. 225, 230.

[9] Schwendener, 1897, l. c., p. 229.

Since transition stimuli may exercise various shock-effects, it is not impossible that in certain plants darkening may excite opposed reactions in the two halves of the pulvinus, or transitory changes may occur without producing any pronounced movement or altered rigidity. A slight increase of rigidity appears to be shown by many plants in darkness, but the results which Schwendener[1] obtained with chloroformed plants are not altogether satisfactory, since the treatment with chloroform slightly increases the rigidity and may exercise other effects as well[2]. The changes of rigidity in *Mimosa pudica* may be readily followed by working at low temperatures, when the sleep-movements are still performed, but the seismonic irritability is largely suspended.

The acceleration of growth in darkness is naturally not always alike in all plants or in all parts of these, and the increased activity of growth produced by the withdrawal of light in the convex side of an organ which performs a pronounced nutation curvature in darkness is not of necessity permanent in character, but is in fact usually transitory. As the effect of the stimulus due to the change passes away, the growth assumes the same somewhat enhanced rate in all parts so long as no autonomic modifications ensue.

Internal factors. It is certain that the modifications of growth produced by light and temperature are not the direct result of changes of turgor, and until the exact way in which these agencies influence growth is known it is impossible to gain any insight into the mode of production of photonastic and thermonastic nutation curvatures. Even in the case of variation movements the increased expansive energy might result from a change in the elasticity of the cell-wall as well as from a rise of turgor. Hilburg[3] was unable to detect any change of turgor in the active pulvinar tissues by plasmolytic methods during photonastic and thermonastic curvature, but this might simply be because the changes of turgor are rapidly produced, or are affected by the mode of preparation necessarily adopted. The turgor of the active parenchyma cells sinks after prolonged immersal in water, but not after lying in a solution of potassium nitrate and of a few other salts. Whether this is a question of diffusion, selective absorption, or of some stimulatory action is, however, uncertain, and no light is thrown upon the mechanism of curvature. The geotropic and heliotropic curvatures of pulvini are, however, accompanied by changes of turgor equivalent to about 1 per cent. solutions of potassium nitrate, according to the same author, so that there appears to be some difference in the mode of production of the variation movement according to the character of the stimulus applied. Even when different mechanisms are in play variation and nutation may co-operate in producing the curvature of a pulvinus, just as geotropism and photonasty may co-operate in certain stems.

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[1] Schwendener, Ges. Bot. Mittheil., p. 236.

[2] Cf. Pfeffer, Physiol. Unters., 1873, p. 65.

[3] Hilburg, Unters. a. d. bot. Inst. zu Tübingen, 1881, Bd. 1, p. 23.

It is evident from the above that the movements of pulvini are not produced in such a simple manner as Bert[1] supposed. This author concluded that they were the direct result of the changes of turgor due to the accumulation of the glucose produced by photosynthesis during the daytime, and its gradual removal at night. The mere facts that the daily movements continue in air deprived of carbon dioxide, and that the periodic movements are repeated several times in continued darkness, are sufficient to disprove this supposition.

PART V

THE INFLUENCE OF THE EXTERNAL CONDITIONS UPON AITIONASTIC CURVATURE

SECTION 30. **Special and General Actions.**

Since modifications of growth and of the tissue-strains are more obvious when they find expression in curvature, reactions of this kind serve especially well to demonstrate the influence of the external conditions. It is easy to see, for instance, that the movements of *Mimosa pudica* and of the stamens of Cynareae take place most rapidly and actively at a certain optimum temperature, and cease at high and low temperatures, owing to the onset of cold or heat rigor. Provided that the unfavourable temperature is not too severe or too prolonged in duration, the power of reaction is more or less rapidly regained at a favourable temperature as the inhibitory after-effect of the previous exposure disappears. Similar results are produced by the partial or complete withdrawal of oxygen, by the excessive loss of water, and by the action of ether or chloroform. It is, however, worthy of note that the excitation of the pronounced seismonic movements of *Mimosa pudica* is not essential to its growth and normal development, while the tone of this plant and of plants in general is not only affected by the temperature but also by substances such as chloroform and ether, which the plant never encounters under natural conditions.

It is in some cases possible by special treatment to inhibit certain partial functions, and in this way to obtain some insight into the relationship between the sensory and motory processes. Thus the repeated shaking of *Mimosa pudica* causes the suspension of the seismonic irritability alone, as also do low temperatures and anaesthetization, whereas the autonomic

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[1] Bert, Compt. rendus, 1878, T. LXXXVII, p. 421; also in Mém. de la Soc. d. sci. phys. et nat. de Bordeaux, 1870, T. VIII, p. 53. Cf. also the reference in Bot. Ztg., 1879, p. 187. The speculations of G. Kraus (Flora, 1877, p. 73) are of no importance.

and daily movements continue. The latter cease, however, before the power of response to mechanical stimuli is lost, when the air surrounding the plant is rarefied.

So long as the power of growth is retained, or in general, whenever the motor mechanism remains capable of action, a cessation of the power of response under particular conditions can only be due to their influence upon the power of perception or upon the processes of induction. For instance, when the air is gradually rarefied, first the heliotropic and later the geotropic irritabilities disappear, whereas growth only ceases when a still lower partial pressure of oxygen is reached. The fact that the leaf of *Mimosa pudica* returns to its original position when the recovery of the seismonic irritability is prevented by chloroform, cold, or shaking, shows that the return movement is not dependent upon the restoration of seismonic irritability. Since the re-expansion of the active tissues takes place in the chloroformed pulvinus, it is evident the anaesthetization affects some stage of sensation.

Temperature. The minimum temperature for the photonastic movements of the flowers of *Crocus*, and for those of the flowers and leaves of various indigenous plants, lies between 0° C. and 4° C. The stamens of *Berberis* also react to strong mechanical stimuli at comparatively low temperatures, whereas no response is produced in the leaves of *Mimosa pudica* when the temperature falls below 15° C.[1], although weakened sleep-movements and autonomic movements continue. Sachs[2] found that transitory heat-rigor was produced by exposure to 40° C. for an hour, at 45° C. in half an hour and at 49° C. to 50° C. in a very short time. In some cases plants which were still irritable at 40° C. became transitorily rigid when brought to a normal temperature, either as the after-effect of the previous exposure, or owing to the shock-effect of the sudden change.

Light. Organs which are able to develop more or less normally in darkness are also able to curve in response to stimuli in the absence of light. Thus flowers of *Crocus* and *Tulipa* which have grown in darkness react strongly to changes of temperature, while tendrils as well as the stamens of flowers of *Cynara scolymus* which have expanded in darkness[3] are sensitive to mechanical stimuli. Indeed even the leaves of *Mimosa pudica* acquire their seismonic and photonastic irritabilities when brought by special treatment to develop strongly in darkness.

Exposure to light is essential for the continuance of the variation movements of adult *phototonic* leaves. In darkness the pulvini gradually fall into

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[1] Sachs, Flora, 1863, p. 451. The older researches of Dutrochet are quoted by Sachs. A few details on the dependence of various aitionastic movements upon the external conditions are given in the previously quoted works of Kabsch and Morren. Cf. also Hansgirg, Physiol. u. phycophytol. Unters., 1893, p. 62.

[2] Sachs, l. c., p. 453.

[3] Pfeffer, Period. Bewegungen, 1875, p. 64.

an immotile condition[1]. This occurs in *Mimosa pudica* after three to six days' darkness, and the pulvini of other plants behave similarly. Very feeble illumination induces rigor in the leaves of *Mimosa pudica*, but suffices to keep the pulvini of the shade-loving *Oxalis acetosella* in a phototonic condition. According to Jost, the seismonic irritability disappears first in some cases, but usually the photonastic irritability is lost first, while the rigor is usually, but not always, more rapidly induced at high temperatures[2]. The rigor of the pulvini of foliage-leaves is apparently the result of a pathological condition induced by continued darkness, and ultimately leading to death[3]. Since the leaves are also injured when exposed to light in air deprived of carbon dioxide in which photosynthesis is reduced to a very low ebb[4], the pathological condition induced by darkness is probably the result of the leaf being unable to perform its normal function. The rigor does not appear to be due to any deficiency of food or to the lack of any autoassimilatory products, for it is produced without any fall of turgor[5], and in some cases when the leaves are abundantly provided with food[6], as also are accompanying pathological changes, such as the alteration in colour of the chloroplastids and the temporary or permanent loss of the power of photosynthesis[7]. It is not surprising that a leaf developed in light may be unable to accommodate itself to darkness, whereas under special circumstances a leaf may develop to a considerable size and acquire irritability in continuous darkness.

The experiments with coloured light lack critical precision, but, as far as they go, seem to indicate that phototonus is maintained by the more refrangible as well as by the less refrangible halves of the spectrum[8]. Although the blue and violet rays exercise a stronger photonastic action, nevertheless the red and yellow rays are able to induce the sleep-movements of leaves. The movements, however, begin earlier, and take place more rapidly in blue light than in red, just as when the effects of strong and of feeble illumination are compared. Similar differences are shown by the nutation movements of chlorophyllous and non-chlorophyllous organs, while flowers open less in red light or under feeble white light than when exposed to the blue rays[9].

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[1] Sachs, Flora, 1863, p. 499, and the literature there given; Jost, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 457.

[2] Jost, l. c., pp. 465, 469.

[3] Pfeffer, Period. Bewegungen, 1875, p. 64; Jost, l. c., p. 457.

[4] Ewart, Journ. Linn. Soc., Vol. XXXI, 1897, p. 569.

[5] Pfeffer, l. c., p. 68.

[6] Pfeffer, l. c., p. 64.

[7] Ewart, l. c., pp. 568, 570.

[8] Daubeny, Phil. Trans., 1836, I, p. 519; Bert, Mém. de l'Acad. de Bordeaux, 1871, p. 28 of reprint; W. P. Wilson, Contrib. from the Bot. Lab. of Pennsylvania, 1892, Vol. I, p. 71; Macfarlane, Bot. Centralbl., 1895, Bd. LXI, p. 136.

[9] Hansgirg, Physiol. u. phycophytol. Unters., 1893, p. 60.

Oxygen. All aerobic organisms rapidly lose the power of movement and curvature in the absence of oxygen[1], but the rigor is not immediately produced in the tentacles of *Drosera*, for Correns found that they remain for a time responsive to mechanical and chemical stimuli, just as a muscle does in the temporary absence of oxygen. Similarly the leaves of *Mimosa pudica* may show a feeble power of seismonic movement immediately after the oxygen pressure has been reduced almost to nil[2]. In any case, the seismonic irritability of *Mimosa pudica* is lost at a lower partial pressure of oxygen than the photonastic irritability which, in *Mimosa* as well as in other plants examined by Correns, disappears in air at a pressure of 15 to 35 millimetres of mercury[3]. Tendrils cease to react to contact in air at a pressure of 15 to 30 mm. of mercury, but their growth appears to be still possible, for an induced movement continues to a slight extent at still lower pressures in which the power of perception is lost. Correns was, however, unable to observe any such after-effect when seedling-stems were brought after geotropic or heliotropic induction into air sufficiently rarefied to suppress the power of perception of these stimuli. The seedling-stem of *Helianthus annuus*, however, continues to grow for a time in the absence of air[4], and is able to perform a geotropic curvature in an almost complete vacuum, whereas no heliotropic response is possible when the air-pressure falls below 75 mm. of mercury. It has, however, not been determined whether the power of aitionastic curvature in general is lost sooner than the power of growth, or whether shock-stimuli become ineffective at a higher pressure of oxygen than continuous stimuli.

The seedling-stem of *Sinapis alba* is capable of a geotropic curvature at an air-pressure of 30 to 37·5 mm. of mercury, but is unable to perform a heliotropic reaction below an air-pressure of 45 mm. Hence below this air-pressure the stem is capable of a geotropic but not of a heliotropic response. After exposure to geotropic or heliotropic induction in air too rarefied to permit of any response, no after-effect is shown on the return to ordinary air. Heliotropic induction, and to a less extent geotropic induction, are therefore suppressed by a fall of the air-pressure to limits which permit of growth and geotropic curvature, whereas no heliotropic curvature follows previous stimulatory induction in ordinary air. It follows, therefore, that in rarefied air not only is the power of perception of heliotropic stimuli lost, but also the process of induction is suppressed.

The action of geotropic and heliotropic stimuli is little or not at all

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[1] Correns, Flora, 1892, p. 87; Sachs, Flora, 1863, p. 501; Kabsch, Bot. Ztg., 1862, p. 341; Dutrochet, Mémoires d. végétaux et d. animaux, Bruxelles, 1837, pp. 186, 259.

[2] Correns, l. c., pp. 96, 144.

[3] Correns, l. c., p. 117.

[4] Cf. Nabokich, Beiheft z. Bot. Centralbl., 1902, Bd. XIII, p. 272.

affected by the transference of the plant to pure oxygen at atmospheric pressure[1]. The injurious action of oxygen observed by Kabsch, in a few cases, is apparently due to the presence of poisonous impurities, oxygen made from potassium chlorate usually containing traces of chlorine unless carefully purified. Kabsch also found that the irritability was retained in nitrous oxide, but Correns[2] has shown that this is not the case with the stamens of *Berberis*, while Borzi[3] found that *Mimosa* soon becomes rigid in this gas. Borzi states that *Mimosa* regains its irritability and power of movement after being for some time in an atmosphere of nitrous oxide, but this is probably due to the presence of free oxygen in the nitrous oxide, coupled with the gradual accommodation of the plant to a low partial pressure of oxygen. Pure carbon dioxide is highly injurious and produces a rapid suspension of irritability[4].

Ether and Chloroform. All poisonous substances affect the power of movement when sufficiently concentrated, but the action of anaesthetics is of especial interest, since by them the reactions may be analysed and their character revealed to a greater or less extent[5].

It has long been known that ether and chloroform suspend the irritability of the pulvini of *Mimosa pudica* and of the stamens of *Berberis*. The same applies to the leaves of *Dionaea*[6], the stigmas of *Bignonia* and *Catalpa*[7], and the stamens of *Cynareae*. Moderate doses of chloroform suspend the seismonic irritability of *Mimosa*, but not the daily and autonomic movements of the leaves. It is not certain whether these latter movements can in all plants be temporarily suspended by anaesthetization without causing permanent injury. In fact a complete suspension of the irritability of tendrils, of thermonastic and photonastic movement, and of growth[8] in general seems only to be produced by anaesthetization which seriously injures the plant when slightly more prolonged. Slight etherization produces a temporary acceleration of growth, but it is not certain whether such treatment also accelerates induced curvatures.

Darwin[9] observed no suppression of irritability in etherized tendrils,

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[1] Correns, Flora, 1892, pp. 109, 120, 150.

[2] Correns, l. c., pp. 108, 150.

[3] Borzi, Rivista di Scienze Biologiche, 1899, Fasc. IV; Bot. Centralbl., 1899, Bd. LXXX, p. 351.

[4] Correns, l. c., pp. 109, 121, 130.

[5] On the influence of different substances see Göppert, De acidi hydrocyanici vi in plantas commentatio, 1827; Marcet, Biblioth. universelle de Genève, Archiv, 1848, Bd. LX, p. 204; Bert, Mém. de l'Acad. de Bordeaux, 1866, p. 30; Bernard, Leçons s. l. phénomènes de la vie, 1885, 2e éd., T. I, p. 258; Tassi, Nuovo giornale botanico italiano, 1887, T. IX, p. 30; Krutickij, Bot. Centralbl., 1889, Bd. XXXIX, p. 379; Borzi, L'apparato di moto delle Sensitive, 1899; Paoletti, Nuovo giornale botanico italiano, 1892, T. XXIV, p. 65.

[6] Darwin, Insectivorous Plants.

[7] Heckel, Compt. rend., 1874, T. LXXIX, p. 702.

[8] Detmer, Landw. Jahrb., 1882, Bd. XI, p. 227; Townsend, Annals of Botany, 1897, Vol. XI, p. 522.

[9] Darwin, Climbing Plants.

but possibly more intense and prolonged etherization might have this effect. The anaesthetized tentacles of *Drosera* become in some cases inexcitable, but not always[1]. It is, however, not certain whether ether and chloroform suppress the excitability of tendrils and of the tentacles of *Drosera* before the power of growth is lost. Czapek[2] finds that the power of geotropic curvature is sooner and more readily inhibited by anaesthetics than the power of geotropic sensation. Hence by applying appropriate concentrations of chloroform to the radicles of *Vicia Faba* and *Lupinus albus* it is possible to subject them to geotropic induction, which only finds visible expression when the chloroform is removed. Similar results may be obtained by the use of carbon dioxide, caffein, and a few other substances, as well as by low temperatures, not only with the radicles but also with the sporangiophore of *Phycomyces*[3]. In the case of the pulvini of *Mimosa pudica*, however, the loss of the power of response is due to the interference of the anaesthetics with the process of sensation.

Electricity. From the available but incomplete researches on the general action of electricity on growth it may be concluded that the varying kinds of curvature are not appreciably affected by weak constant currents, and that stronger currents retard curvature and ultimately act injuriously or fatally. It is, however, uncertain whether a particular intensity of current may act as an excitation and awaken curvature.

Electrical discharges and induction-shocks act like mechanical excitations. Hence the full amplitude of movement is produced in the pulvinus of *Mimosa pudica* and in the stamens of *Centaurea* and *Berberis* by a single make- or break-shock, whereas repeated induction-shocks are required to produce a similar effect in the pulvini of leaflets of *Oxalis acetosella* and other species of this genus[4]. Continued induction-shocks act in the same way as repeated blows upon the leaves of *Mimosa pudica*, which in both cases become inexcitable and, accommodating themselves to the continued stimulation, re-expand and return to their original position[5]. Sensitive tendrils are stimulated to curvature by weak induction-shocks[6], although Hofmeister[7] was only able to obtain this result by using strong induction-shocks. Nitschke[8] obtained negative results with the

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[1] Darwin, Insectivorous Plants. Cf. also Heckel, Compt. rend., 1876, T. LXXXII, p. 525.

[2] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 199.

[3] Steyer, Reizkrümmungen bei *Phycomyces*, 1901, pp. 7, 25. Cf. also Correns, Flora, 1892, p. 134.

[4] The older literature is given in the works already quoted of Treviranus, de Candolle, &c. Cf. also Kabsch, Bot. Ztg., 1861, p. 358; Cohn, Abhandlg. d. schles. Ges. für vaterl. Cultur, 1861, Heft 1, p. 21 (Stamens of Cynareae); Blondeau, Compt. rend., 1867, T. LXV, p. 304; Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. I, pp. 505, 521.

[5] Cf. Pfeffer, l. c., p. 521.

[6] See Pfeffer, l. c., p. 505.

[7] Hofmeister, Pflanzenzelle, 1867, p. 313.

[8] Bot. Ztg., 1860, p. 229.

tentacles of *Drosera*, but probably positive results could be gained by properly graduated and applied induction-shocks.

According to Mohl[1], constant electrical currents are without effect upon tendrils, but it is not certain whether the tone, and hence the power of response to various stimuli, may be modified by a continuous current, or by the continued application of induction-shocks. According to Kabsch[2], the lateral leaflets of *Desmodium gyrans*, which have become motionless at 22° C., are caused to move by weak induction-shocks, but further investigation of this phenomenon is required. It is not, however, surprising that induction-shocks should act like a blow and excite the rapid movement of the gynostemium of *Stylidium*, or the sudden dehiscence of the fruit of *Impatiens*[3].

PART VI

DEHISCENCE AND DISPERSAL MOVEMENTS

SECTION 31. **Special and General.**

The modes of dehiscence of fruits, anthers, sporangia, the splitting of the integuments of seeds and of the membranes of spores, as well as the mechanisms of dispersal of seeds, spores and other reproductive bodies are all of great biological importance[4]. In most cases, however, the phenomena are physical in origin, but even here the development of the requisite physical conditions is a physiological problem.

The hygroscopic movements of dry fruits, of the carpellary beaks of *Erodium*, and of certain hairs are the result of unequal imbibition and swelling, whereas in other cases the fall of turgor consequent upon the death of certain cells may result in purposeful movements or may aid in the rupture of tissues. Even without actual death, movements may result from the liberation of strains set up by attempted growth. It is in this way that the rapid movements of the stamens of *Parietaria* and the sudden dehiscence of the fruit of *Impatiens* are brought about. In these cases the active tissues remain living, whereas the sudden escape of the contents of the dehiscing spore-sacs of certain Ascomycetes is connected with the death of the sac. In neither case, however, can the process be repeated, since even where the active tissues remain living they are no longer capable of reproducing the requisite tissue-strains. This does, however, occur during the autonomic movement of the gynostemium of *Stylidium*, which is able to perform repeated sudden movements.

In all such movements not only the strains but also the conditions for

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[1] Mohl, Ranken- und Schlingpflanzen, 1827, p. 70.

[2] Kabsch, Bot. Ztg., 1861, p. 361.

[3] Kabsch, l. c., p. 358.

[4] See the accounts given by Ludwig, Biologie d. Pflanzen, 1895, pp. 296, 326; Kerner, Pflanzenleben, 1891, Bd. 1, u. 2 (Natural History of Plants, 1895, Vol. II, pp. 91, 140, 429, 833).

their release are prepared by the activity of the organism, either by so raising the strains, loosening the tissues or weakening the cell-walls, that the existent strain, or a slight mechanical excitation, serves to produce the sudden dehiscence. The plant prepares in the same way for the abscission of leaves, flowers, and fruits either by the provision of special abscission layers, in which the cells readily separate, or by the death of intervening tracts of tissue.

As soon as the required instability has been produced, mechanical agencies of external or of internal origin may release the dehiscing mechanism. Changes of turgor or of the tissue-strains may act in this way, whether produced by transpiration or by some indirect stimulatory reaction of light, heat, or of chemical substances. In some cases a localized stimulus may act at a distance. Thus Darwin[1] has shown that a touch upon the antenna-like prolongation of the rostellum of the orchid *Catasetum* causes the pollinia to be shot forth by the release of pre-existent strains. Direct contact with the pollinia is ineffective, so that presumably the antenna receives a contact or seismonic stimulus and transmits an excitation to the pollinium, causing the hindrance to movement to be removed.

Apart from the above movements which take place in plants fully supplied with water, movements and change of shape may be produced by a fall or loss of turgor due to excessive transpiration or plasmolysis. Phenomena of this kind, though physical in origin, are nevertheless of considerable biological importance, as, for instance, when the drooping of flaccid insolated leaves aids in shielding them from an excessive loss of water. From a mechanical standpoint it is naturally immaterial whether the loss of turgor is due to death, transpiration, or plasmolysis. Delicate tissues shrivel when very much water is removed from them, but it is only when all the free water has been displaced that further drying removes the water of imbibition and produces changes of shape in the cell-walls which may lead to hygroscopic movements and curvatures. Movements of this kind take place in dead as well as in living tissues, although turgor can only be restored in cells which have not been killed by drying.

Movements due to turgor or to the tissue-strains dependent on turgor. An instance of sudden movement without any tearing of the tissues is afforded by the stamens of *Parietaria*, *Urtica*, *Pilea*, *Spinacia*, *Atriplex* and a few other plants. The stamens of *Urtica* are inwardly curved and fixed between the perianth and the ovary, or when the latter is absent they are pressed against one another. As development progresses strains arise which mainly find expression in the compression of the inner under side of the filament. When this is sufficient to overcome the mechanical

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[1] Darwin, The various contrivances by which Orchids are fertilized; Haberlandt, Sinnesorgane im Pflanzenreich, 1901, p. 62.

resistance, the filament suddenly straightens like a spring and scatters the pollen from the dehiscing anthers. The movement takes place spontaneously, but may be accelerated by the action of pressure or contact on the perianth or stamens. If the stamens are not quite ripe the removal of the external resistance is not immediately followed by the straightening of the filaments. Askenasy[1] has shown that this sudden dehiscence is due to the filaments being pressed into the grooves between the anther-lobes, and clinging to these with a certain energy.

The sudden protrusion of the sexual organs in the flowers of *Sarothamnus* and *Genista tinctoria* is due to resistance being overcome or removed[2], and the same applies to the sudden opening of the flower of *Stanhopea oculata*[3], which produces a perceptible sound, and to the repeated rapid movements of the gynostemium of *Stylidium adnatum*.

In other cases the vital activity gradually provides for the rupture of the tissues at definite points, and for the sudden release of the strains produced by growth. It is in this way that spontaneously, or as the result of a slight touch, the fruits of *Impatiens noli-me-tangere* and *I. balsaminea*, of *Cardamine hirsuta* and *Cyclanthera* suddenly dehisce, the valves of the fruit rolling up with considerable force and the seeds being shot to a greater or less distance away[4]. The separation of the elongated cells of *Zygnema* and *Mougeotia* is effected in a similar fashion by the splitting of the common wall. The sudden splitting of the cuticle, coupled with the outward bulging of the end walls previously flattened by mutual pressure, causes the cells to shoot apart, and the spores of Basidiomycetes appear to be thrown off by the basidia in this way. Any agencies such as induction-shocks, chloroform, or iodine, which aid in the rupture of the cuticle, induce the sudden separation of the cells if applied when the segmentation is completed[5].

In the case of *Momordica* (*Ecballium*) *elaterium* the fruit-stalk forms a plug at the base of the fruit, and becomes loosened when the latter is ripe, so that the seeds together with a slimy liquid spurt out from the interior. Dutrochet[6] recognized that the required energy was derived from the elastic distension of the walls of the fruit by the compressed

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[1] Askenasy, Verhandl. d. naturhist.-med. Vereins zu Heidelberg, 1879, N. F., Bd. II, p. 274.

[2] Cf. Ludwig, Biologie der Pflanzen, 1895, p. 472.

[3] Pfitzer, Beobachtungen über Bau und Entwickelung d. Orchideen, 1877, p. 12. Reprint from Verhandl. d. natur.-med. Vereins zu Heidelberg, Bd. II.

[4] Dutrochet, Mémoires d. végétaux et d. animaux, Bruxelles, 1837, p. 229; Hildebrand, Jahrb. f. wiss. Bot., 1873–4, Bd. IX, p. 238; Eichholz, ibid., 1886, Bd. XVII, p. 543; Ludwig, l. c., p. 332. Other mechanisms, including that by which the seeds of *Oxalis* are dispersed, are discussed in these works. On the mechanism of *Sphaerobolus stellatus* see Zopf, l. c., pp. 84, 374.

[5] See Benecke, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 453. On the fragmentation of the frond of *Rhodomela* see Tobler, Ber. d. bot. Ges., 1902, p. 361.

[6] Dutrochet, l. c., p. 229; Hildebrand, l. c., p. 238; Roze, Journal de Botanique, 1894, T. VIII, p. 308.

contents. When the latter have escaped the wall of the fruit contracts considerably, and the escape is prepared for by the loosening of the tissue round the top of the fruit-stalk. A similar spurting mechanism is responsible for the escape of the spores from the spore-sacs of many Discomycetes, Pyrenomycetes and Lichens, for the spores, together with a portion of the unused contents of the sporangium, may be thrown out sometimes to a distance of several centimetres[1]. After dehiscence the wall of the ascus distended by turgor may contract to three-quarters or two-thirds of its previous length, as when a short rubber-tube distended with water is pricked and the contents allowed to escape. A similar contraction is naturally also shown by the ascus when its contents are plasmolysed.

In certain Pyrenomycetes, previously to the dehiscence of the ascus, its outer cuticular wall ruptures and the distensible inner wall elongates to as much as twice its original length, so that the apex of the ascus reaches to or protrudes beyond the narrow mouth of the fructification[2]. (Fig. 34.) In some cases the spores all collect at the apex and are thrown out simultaneously, but in other cases they follow one another. Each blocks the apex for a while until the turgor has risen sufficiently to throw it out, when another blocks the narrow opening and, after a pause, is thrown out in its turn, when the turgor is once more restored. The fact that the dehiscence takes place at a definite point shows either that the membrane has remained weaker here than elsewhere or else that the protoplasm has produced a diminution of the cohesion of the wall at this point previously to dehiscence. In the former case a rise of turgor would be required to produce dehiscence, but not necessarily in the latter. It is, however, not surprising that shaking or changes in the moistness of the air may excite or accelerate the dehiscence.

In many cases a pronounced swelling of the wall takes place, which may aid in producing dehiscence and in narrowing the cavity of the ascus. Prior to dehiscence the swelling is possibly prevented by the pressure exerted by the contents on the wall. The rupture of cuticular membranes is by no means uncommon and occurs normally whenever the inner walls continue to grow, or when cuticularized gland-cells are actively excreting. The threads which escape from the grandular hairs of *Dipsacus* under water are probably extended through cracks in the cuticle. They appear to be products of the metamorphosis of the cell-wall, and their peculiar movements are probably similar in character to those shown during the formation of myelin threads[3].

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[1] De Bary, Morphologie u. Biologie d. Pilze, 1884, p. 90 (Fungi, Mycetozoa and Bacteria); Zopf, Die Pilze, 1890, p. 87; Ludwig, Biologie der Pflanzen, 1895, p. 328.

[2] Pringsheim, Jahrb. f. wiss. Bot., 1858, Bd. I, p. 190.

[3] Cohn, Bot. Ztg., 1878, p. 122; F. Darwin, Journal of Microscopical Science, 1877, Vol. XVII, p. 245, and 1878, Vol. XVIII, p. 73.

A still more striking instance of the same mechanism is afforded by the ripe sporangium of *Pilobolus crystallinus*, which, according to Coemans, may be thrown to a height of 105 centimetres. [Relatively to size, this is higher than a man can throw a cricket-ball, even neglecting the air-resistance which, relatively to the masses, is several hundred times greater in the case of the sporangium. This energetic movement is produced by the gradual swelling of the basal membranous wall, which loosens the union between the sporangium and the swollen apex of the sporangiophore. The latter then ruptures at the apex and the jet of escaping liquid throws the sporangium away [1]. The beginnings of this special mechanism are seen in *Mucor*, where the apex of the sporangiophore (columella) bulges into the sporangium and causes the rupture of the brittle sporangial wall. The spores of *Empusa muscae* and of various Basidiomycetes are jerked away in a similar fashion by pressures created by turgidity. Spermatozoa and zoospores when not ejected by the dehiscence of the antheridium or zoosporangium make their own way out through the point of rupture, and the large zoospores of *Vaucheria* may be nipped in two during their exit from the narrow opening of the zoosporangium [2].]

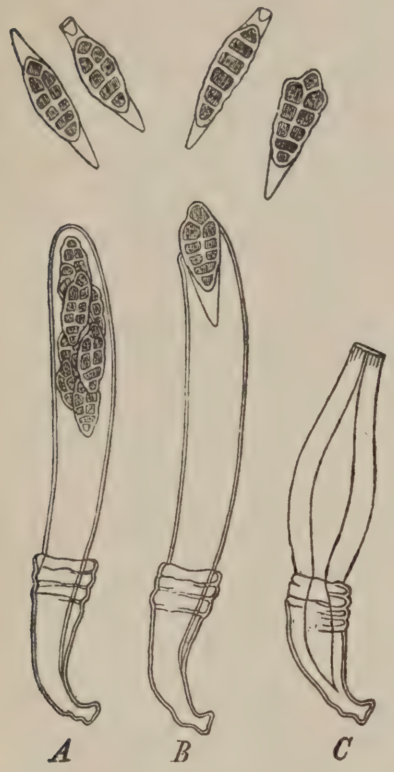

FIG. 34. *Sphaeria Scirpi* (*Pleospora scirpicola*) (after Pringsheim). *A*, unopened ascus after the splitting of the cuticular membrane. *B*, the same with the spores all escaped except one momentarily blocking the apical opening. *C*, the same after all the spores have escaped.

The hygroscopic movements of dead organs are often of great use [3]. Thus the fact that many dry fruits and anthers open in dry air but close when moistened ensures that the seeds or pollen-grains shall not be dispersed during wet weather. Similarly the peristomes of many mosses close the mouth of the capsule when moist but expand and allow

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[1] Cf. de Bary, Morphologie u. Biologie der Pilze, 1884, pp. 77, 90; Zopf, Die Pilze, 1890, p. 81.

[2] On the escape of zoospores see de Bary, l. c., p. 87; Falkenberg, in Schenck's Handbuch der Botanik, 1882, Bd. II, p. 195; Strasburger, Wirkung des Lichtes und der Wärme auf Schwärmsporen, 1878, p. 14; Walz, Bot. Ztg., 1874, p. 689; Rothert, in Cohn's Beiträge z. Biologie, 1892, Bd. V, p. 344; Klebs, Bot. Ztg., 1891, p. 859; Goebel, Ann. du Jard. bot. de Buitenzorg, 1898, Suppl. II, p. 65.

[3] Ludwig, Biologie d. Pflanzen, 1895, pp. 327, 344; Kerner, Pflanzenleben, 1891, Bd. II, p. 421 (Natural History of Plants, 1895, Vol. II, p. 447); Haberlandt, Physiolog. Pflanzenanatomie, 1896, 2. Aufl., pp. 469, 488; Hildebrand, Jahrb. f. wiss. Bot., 1873–4, Bd. IX, p. 245; Steinbrinck, Unters. üb. d. anat. Ursachen des Aufspringens d. Früchte, 1873, Bot. Ztg., 1878, p. 561; Geovanozzi, Nuovo giornale botanico italiano, 1901, T. VIII, p. 207.

the spores to escape when the air is dry. During moist weather the dead involucral leaves of *Carlina* and *Helichrysum* bend inwards and prevent the dispersal of the seeds, whereas when dry they bend backwards and remove the hindrance to dispersal [1]. In addition the pappus of Compositae expands during dry weather when dispersal is possible, and closes when the air is moist, so that any soaring fruits overtaken by rain are soon washed to the ground. The well-known Rose of Jericho (*Anastatica hierochuntica*) affords a striking instance of drought causing the branches to curl up into a ball enclosing the fruits. When the rains begin they re-expand, the fruits dehisce and the seeds take root in the soil [2]. Many dry capsules are also capable of hygroscopic expansion and contraction.

Hygroscopic torsions are performed by the setas of *Funaria* and other mosses [3], as well as by the conidiophores of *Peronospora* and a few other fungi [4]. This is especially marked in the beaks of the carpels of *Erodium gruinum*, which is often used as a hygrometer; and these movements, like those of *Stipa* and *Avena*, help the fruit to bore into the soil [5].

Changes of shape produced by the loss of water are only the result of the removal of the imbibed water of the cell-wall when the cell contains no free water. The collapse and wrinkling of the cell-walls of a dead tissue when a portion of the water filling the cells is removed results, according to Kamerling, Steinbrinck, and Schrodt [6] from the cohesion and high breaking-stress of the diminishing volume of water, while its adhesion to the cell-wall causes the latter to be drawn inwards and crumpled. The aid of the external atmospheric pressure does not appear to be necessary, since, according to Steinbrinck, the same phenomenon is shown in a vacuum. When the water in the cells ruptures, air rapidly penetrates the cell, according to Steinbrinck [7], so that the air-pressure is rapidly equalized within the cell.

When dry organs are placed in moist air, no water appears in the cavities of the cells so long as the formation of dew is avoided. Hence

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[1] Dutrochet, Mémoires, &c., Bruxelles, 1837, p. 236; Detmer, Journal für Landw., 1879, Bd. XXVII, p. 111.

[2] Ascherson, Ber. d. bot. Ges., 1892, p. 94.

[3] Wichura, Jahrb. f. wiss. Bot., 1860, Bd. II, p. 198; Goebel, Flora, 1895, p. 483.

[4] Cf. Zopf, Pilze, 1890, p. 86.

[5] Hanstein, Bot. Ztg., 1869, p. 526; F. Darwin, Trans. of the Linnean Society, 1873, 2nd ser., Vol. I, p. 149; Steinbrinck, Bot. Ztg., 1878, p. 580.

[6] Kamerling, Bot. Centralbl., 1897, Bd. LXXII, p. 53; ibid., 1898, Bd. LXXIII, p. 472; Flora, 1898, p. 152. See also the summary in Bot. Ztg., 1898, p. 330; Steinbrinck, Festschrift für Schwendener, 1899, p. 165; Ber. d. bot. Ges., 1899, pp. 99, 325; ibid., 1900, pp. 48, 217, 275, 286. Steinbrinck (l.c., 1900, p. 219) suggests the term 'Schrumpfeln' for crumpling caused by the cohesion-mechanism, but a special term is quite unnecessary.

[7] Schrodt, Ber. d. bot. Ges., 1897, p. 100; Steinbrinck, l.c., 1900, pp. 275, 286. Cf. also Claussen, Flora, 1901, p. 422.

any movements performed can only be due to the imbibition and swelling of the cell-walls. This applies to the hygroscopic movements of many dry fruits as well as of the awns of Grasses and of *Erodium*, although when the parts are still turgid the cohesion-mechanism may produce the first movements. It is possible that both mechanisms may produce the same kind of movement, so that Steinbrinck and Schwendener[1] may each be partly right, although the former ascribes the opening and closing of the anthers to the water-cohesion-mechanism, and the latter to imbibition and swelling.

The movement naturally in all cases depends upon the properties of the organ, upon the power of swelling of the walls, and upon their rigidity and the arrangement of the cells and tissues[2]. The power of imbibition varies in the different layers of the cell-wall, so that the swelling may not be equal in all directions. Since imbibition takes place with great energy, movements due to the swelling of the cell-walls can overcome more resistance than those due to the water-cohesion-mechanism, which is usually unable to produce any distinct changes of shape in thick-walled cells. Both the cohesion-mechanism and the decreased swelling of the cell-walls may be responsible for the dehiscence of different fruits, and may produce in many cases strains which when released cause sudden movement. In the annulus of the sporangia of Polypodiaceae, as the water evaporates from the cells they are more and more contracted and deformed, the thin outer walls being drawn inwards. When the strain reaches a certain limit the walls of the sporangium rupture at the loosened lip-cells. Immersal in glycerine excites dehiscence by removing the water rapidly from the annulus-cells, and after the water in the annulus-cells has ruptured the recurved annulus straightens more or less.

Historical. The existence of movements due to death, or to changes in the moistness of dead organs, was recognized by de Candolle[3], and these were distinguished from movements due to vital activity by Dutrochet[4], who also gave explanations of the movements of dehiscence and dispersal which were in the main correct.

The influence of the external conditions can be predicted in the case of dead objects from purely physical considerations, although the external conditions may also affect the course of the preparation for dehiscence and dispersal. Changes in the percentage of water may, for instance, act both physiologically and physically,

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[1] Schwendener, Sitzungsb. d. Berl. Akad., 1899, p. 101; Steinbrinck, Ber. d. bot. Ges., 1901, p. 552; 1902, p. 117; 1903, p. 217; Schrodt, Ber. d. bot. Ges., 1901, p. 483; Schwendener, Sitzungsb. d. Berl. Akad., 1902, p. 1056; Ursprung, Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 635.

[2] Cf. Haberlandt, Physiol. Pflanzenanat., 2. Aufl., 1896, p. 465, and the works quoted by Haberlandt on p. 488.

[3] A. P. de Candolle, Physiologie des Plantes, a German translation by Röper, 1833, Bd. I, p. 13.

[4] Dutrochet, Mémoires pour servir à l'histoire d. végétaux et d. animaux, Bruxelles, 1837, pp. 225, 235.

while a deficiency of oxygen may render proper ripening difficult or impossible, so that if all free oxygen is removed while the sporangia or zoospores are unripe no dispersal or dehiscence takes place[1].

Apart from the physical action of temperature upon imbibition and the like, a physiological action is also exercised upon the development preparatory to dehiscence and dispersal. Plants adapted to low temperatures are able to throw off organs and to discharge their swarm-spores or other reproductive bodies at temperatures approaching the freezing-point of water or even slightly below it, especially in the case of Arctic marine Algae[2]. Certain observations of Thuret seem to indicate that the escape of the zoospores is delayed at temperatures above the optimum, while in some cases changes of temperature appear to accelerate the escape. Thus, Dodel observed a premature birth of the zoospores of *Ulothrix* when frozen filaments of this Alga were rapidly thawed.

Light appears to exercise little or no direct physical influence upon these movements, for when it accelerates transpiration or induces the development of reacting organs, or of a reacting condition, its action is as indirect as when illumination causes movement by modifying the growth or turgor of responsive cells[3].

The dehiscence and dispersal movements of ripe organs may take place in temporary darkness even when the organs are unable to develop or do not develop normally in continued darkness. Illumination or changes of illumination do, however, appear in certain cases to favour these movements. Thus the illumination of previously darkened plants hastens the throwing off of the sporangia of *Pilobolus crystallinus*[4] and the ejaculation of the spores of *Ascobalus furfuraceus*[5]. In addition, light appears to favour the escape of the swarm-spores of many Algae, and in darkness the zoosporangia may not be as completely emptied, or their contents as well dispersed, as when illuminated[6].

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[1] Cf. Rothert, Cohn's Beiträge z. Biologie, 1892, Bd. v, p. 344, and the literature quoted by him.

[2] For instances see Kjellmann, Bot. Ztg., 1875, p. 774; G. Kraus, ibid., 1875, p. 774; Dodel, ibid., 1876, p. 178; Strasburger, Wirkung des Lichts und der Wärme auf Schwärmsporen, 1878, p. 44; Klebs, Die Bedingungen der Fortpflanzung einiger Algen und Pilze, 1896.

[3] [The implied suggestion that the physical action of light is always a direct one, and its physiological action indirect, is somewhat misleading. Possibly the only direct physical action of light is the mechanical pressure exercised upon an illuminated surface by the impinging light-rays. The chemical, heating, and fluorescent effects of light are as much indirect actions as when illumination affects turgor or transpiration, and in each case the percentage of the light energy utilized depends upon the properties of the material affected.]

[4] According to Coemans and to Hofmeister, Pflanzenzelle, 1867, p. 290. G. Kraus (Bot. Ztg., 1876, p. 507) states that the blue and violet rays are most effective.

[5] Coemans, quoted by de Bary, Morphologie und Biologie der Pilze, 1884, p. 99.

[6] For the literature see Braun, Verjüngung, 1851, p. 237; Thuret, Ann. sci. nat., 1850, 3e sér., T. XIV, p. 247; Strasburger, l. c., p. 15; Walz, Bot. Ztg., 1868, p. 497; Dodel-Port, ibid., 1876, p. 177; Rostafinski u. Woronin, ibid., 1877, p. 667; Klebs, l. c.

CHAPTER III

TROPIC[1] MOVEMENTS

PART I

INTRODUCTORY

SECTION 32. **General.**

IN order that the plant and its organs may attain situations adapted for the performance of their different functions they must possess special tropic[1] irritabilities. These determine the primary orientation of the main axis, upon which the lateral organs have definite positions assured to them when they merely follow their inherent autotropic tendencies. This applies to hairs and to the finer rootlets, whereas runners, leaves, and lateral roots of the first order assume positions mainly determined by external tropic stimuli. The latter induce movements which result in the organ placing itself at a definite angle to the direction of the exciting stimulus, and naturally such responses are best studied when the other external conditions are kept constant and are diffusely applied.

The terms geotropism[1], heliotropism (phototropism), thermotropism, chemotropism, osmotropism, hydrotropism, rheotropism, thigmotropism (haptotropism), galvanotropism and autotropism, merely indicate the exciting agency and say nothing as to the physiological response involved. It was in this sense that the term heliotropism was used by de Candolle and other early authors, so that Wiesner is neither historically correct nor practically justified in restricting it to curvatures produced by growth[2]. The curvatures may, in fact, either be produced by heterauxesis or by variation movements, and the locomotory and orienting movements of free-swimming organisms are produced in a variety of ways. In the latter case it is permissible to use the terms phototaxis, chemotaxis, and the like, although frequently no sharp line of demarcation can be drawn between tropic and tactic movements[3]. An organism which passes through motile and fixed stages may show at one time tropic and at another tactic responses, while the movements of the chloroplastids of plant-cells, though usually more tactic in character, simulate tropic movements in the case of

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[1] Pronounced, trōpic, trōpism.

[2] Die heliotropischen Erscheinungen, 1880, Bd. II, p. 22.

[3] Pfeffer, Druck- und Arbeitsleistungen, 1893, p. 414, footnote.

Mesocarpus. In such cases the character of the responding mechanism determines the dissimilar modes of response, and hence the latter afford no evidence as to whether the sensory processes are alike or dissimilar in tactic and tropic organisms.

When the organism or reacting organ places its main axis parallel to the direction of the exciting stimulus we may speak of parallelotropism, in preference to the term orthotropism or to the longitudinal tropism of Frank. Plagiotropism may be used in a general sense, when the main axis is inclined to the direction of the exciting agency. Diatropism was used by Darwin to indicate a tendency to place the main axis at right angles to the orienting stimulus, and is preferable to the 'transversal tropism' of Frank or the 'homolotropism' of Noll. The word klinotropism may be employed when the angle between the main axis and the direction of the exciting agency is less than a right angle but greater than zero. The term heliotropism was first used by de Candolle[1], while that of geotropism was invented by Frank[2]. The terms negative and positive heliotropism were introduced by Hofmeister[3], while various special terms were employed by Darwin, Rothert, and Massart[4]. Curvatures towards the exciting agency may be denoted as positive instead of using the word 'protropic' suggested by Rothert, or 'anatropic' as employed by Massart. The reverse curvature will naturally be negative, so that the 'apotropism' of Darwin, and the 'katatropism' of Massart are unnecessary. In the same way we may speak of positive and negative klinotropism in preference to 'anaklinotropism' and 'kataklinotropism,' and in certain circumstances the use of the following signs may prevent misconception: ↑ positive parallelotropism, ↓ negative parallelotropism; |→ diatropism; |↗ positive klinotropism, |↘ negative klinotropism.

A displaced parallelotropic organ returns to its original position either by a positive curvature only (stem) or by a negative curvature only (root), whereas a displaced plagiotropic organ may assume its normal orientation either by a negative or positive curvature according to the direction of displacement. Flattened organs like leaves may assume profile positions, a phenomenon to which the term of paraheliotropism was given by Darwin[5]; and if the movement involves torsion Czapek speaks of 'strophism' (geostrophism, photostrophism), and Schwendener of 'tortism'[6].

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[1] A. P. de Candolle, Physiologie des Plantes, a German translation by Röper, 1835, Bd. II, p. 609.

[2] Frank, Die natürliche wagerechte Richtung, 1870.

[3] Hofmeister, Jahrb. f. wiss. Bot., 1863, Bd. III, p. 86.

[4] Darwin, The Power of Movement in Plants, 1881, p. 4; Rothert, Cohn's Beiträge z. Biologie, 1896, Bd. VII, p. 5; Massart, Biol. Centralbl., 1902, Bd. XXII, p. 70.

[5] L. c., p. 357.

[6] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 273; Schwendener and Krabbe, 1892, Gesammelte Mittheil., Bd. II, p. 302. [Since the torsion is the result of growth it is difficult to see

Sachs[1] used the terms parallelotropic (orthotropic) and plagiotropic more to distinguish between perpendicular and horizontal organs, but they may be used in a general sense to indicate the mode of orientation to any directive agency, and if necessary the latter can be indicated by the usual prefixes as in the terms geoparallelotropic, photoplagiotropic, aitiotropic and autotropic. The words orthotropic and campylotropic or skoliotropic have been used to indicate whether an organ is straight or curved[2], and hence Sachs' use of the term orthotropic seems inadvisable.

The natural positions of the different organs are not solely due to tropic stimuli, and in fact many organs have no tropic irritability, while in all cases the autotropic tendencies of the organs come more or less into play. Tropic irritability is naturally most strongly developed in the organs where it is of greatest importance, and may be mainly or solely responsible for the orientation of various parts. Since the different tropic irritabilities may occur singly as well as in combination, it is evident that each involves a definite form of sense-perception. Hence one positively geotropic organ may be also positively heliotropic, but another may show negative or plagio-heliotropism, while yet another may be devoid of one form of irritability, or may have it modified without affecting its other senses[3].

Even in non-cellular plants the different organs develop varying irritabilities, and the strong heliotropic irritability of the sporangiophore of *Phycomyces* is absent from the hyphae. Changes of tone of internal or external origin may also modify the result obtained by stimulating reacting organs, as when the absence of light causes a dia-geotropic organ to assume a klinotropic or parallelotropic position. In addition a rise in the intensity of the stimulus may alter the orientation, as when a sufficient increase of illumination causes the positively parallelotropic position of the filaments of *Vaucheria*, the sporangiophore of *Phycomyces*, and the young shoot of various flowering plants to be replaced by a plagio-heliotropic one. All plants do not show such pronounced reactions, but nevertheless in all cases the existent and pre-existent conditions have a considerable influence upon the irritable tone.

Many radial organs may react plagiotropically, for the filaments of *Vaucheria* and *Phycomyces*, lateral roots of the first order, as well as the rhizomes of *Heleocharis*, *Sparganium*, *Scirpus*, and *Agropyrum*, and the runners of *Lysimachia nummularia*, *Glechoma* and *Vinca* are not only

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any need for a special term in preference to the general one of 'tropism.' In the case of an organ which partly twists and partly curves towards the light it might become necessary to say that it possessed a positively paralleloheliotropocampylostrophismic (tortismic) irritability.]

[1] Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 227.

[2] Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 312.

[3] A few instances in regard to geotropism and heliotropism are given by Frank, Beiträge zur Pflanzenphysiologie, 1868, p. 89.

morphologically but also physiologically radial. The latter is shown by the fact that the same tropic position is assumed whichever side is turned undermost, whereas in responsive dorsiventral organs a stable position is only gained when it twists or curves until a particular side occupies a definite position in regard to the orienting stimulus.

The plagiotropic position suits most dorsiventral organs best, and hence the majority of such organs have developed a plagiotropic irritability, although in some cases they are parallelotropic. The strongly dorsiventral thallus of *Marchantia* is, for instance, photo-plagiotropic, but in darkness is parallelo-geotropic, while certain leaves assume a photo-parallelotropic position in intense sunlight[1]. In addition, *Bodo saltans* and the zoospores of certain Phaeophyceae, although dorsiventral in structure, show a parallelotactic orientation to photic stimuli. Plagiotropic irritability does not indeed involve either morphological or physiological dorsiventralities, though favoured by their presence. Sachs was therefore in error in supposing that all dorsiventral organs were plagiotropic.

Other tendencies may influence the position assumed in response to a tropic reaction. Thus the mere weight of the organ may cause a pronounced curvature, although in other cases such action is feeble or imperceptible. In addition, the realization of any curvature awakens a physiological and mechanical counteraction, and tropic stimulation may excite other forms of curvature. Thus a negatively or even a positively klinotropic position may result from the antagonism of epinasty and negative geotropism. Photonastic, thermonastic, and hydronastic responses may also often co-operate with tropic reactions when the organ possesses these forms of irritability, for an increase in the intensity of the direct lateral illumination, for instance, also involves an increase in the general diffuse illumination.

SECTION 33 (*continued*).

Phototropic and geotropic reactions may result from a variety of stimulatory actions exercised by the exciting agency, and in certain cases the same agency may awaken two tropic actions simultaneously as, for instance, when a solution exerts an osmotactic and a chemotactic action upon the same organism. Since the osmotactic action is a function of osmotic concentration, whereas the chemotactic action depends upon chemical quality and is not exercised by all substances, it is easily possible to study the two actions apart from one another as well as together. Light also exercises two dissimilar stimulatory actions upon organs possessing both

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[1] A few additional instances are given by Noll, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 478; and by Goebel, Organography, 1900, p. 234.

[2] Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 227.

phototropic and thermotropic irritabilities. In addition, the blue and red rays may awaken two different tropic reactions, which co-operate in producing the position assumed in mixed light.

An orienting stimulus exerts a double action when it induces dorsiventrality in a radial tropic organ, and this induced dorsiventrality may result ultimately in the assumption of a permanently plagiotropic position, as in the thallus of *Marchantia.* The same thing applies to the prothallus of the Fern, although here the unilateral illumination only induces a labile dorsiventrality. Labile or stable hyponastic or epinastic tendencies may also be induced in connexion with the labile or stable dorsiventrality, and the appearance of the latter may awaken or modify special tropic or nastic powers of response.

Even when no dorsiventrality is induced, a single agency may exert two dissimilar tropic reactions, as, for instance, in the case of the radial plagiotropic branches of trees, in which the action of gravity appears to excite an epitropic tendency to curvature on the upper side, and a hypotropic one on the under side. Both responses may be regarded as geotropic curvatures, whether they are indirectly or directed excited, or whether the epitropic response follows as a counter-action to the induced tendency to hypotropic curvature. Differences in the times of reaction and induction merely show that dissimilar stimulatory actions are involved, and afford no argument against both being geotropic responses. Every tropic reaction may indeed involve epinasty or hyponasty, unless we elect to restrict these terms to curvatures produced by diffuse stimuli. The hypotropic reaction of the branch does, in fact, appear and disappear more rapidly than the epitropic one on the upper side, so that the existence of the two dissimilar tendencies is readily detected, whereas this would be impossible if the times of induction and the duration of the after-effect were alike in both cases.

Naturally no curvature results if the antagonistic stimulatory actions balance, and the same applies when the direction of the stimulus alters, provided that the opposing reactions increase or decrease in the same proportion. This must actually be the case in such branches as continue to grow in a new direction forcibly impressed upon them ; for if their altered position in regard to the perpendicular caused unequal geotropic responses to be given by the upper and under sides, the natural result would be to produce a curvature of the branch to its original line of growth where the geotropic actions balanced. Dissimilar tropic agencies or reactions may also antagonize each other, and in the case of an organism which is positively chemotactic and negatively osmotactic to a particular substance, a position of equilibrium is reached at a definite point in the zones of diffusion, owing to the fact that the negative osmotactic action increases more rapidly than the positively chemotactic action with increasing concentration. Similar relationships may often be responsible for the changed reaction produced by increasing intensity of stimulation.

There is no reason, however, for assuming that all tropic or more especially all plagiotropic reactions involve the antagonism of two or more dissimilar stimulatory actions and responses. A single action may induce or modify movement in organisms as well as in machines. Thus the continued turning of a steam-cock (increasing stimulation) may induce first a forward and then a backward movement of a locomotive. The admission of steam into the cylinders can, however, produce no movement if the wheels are fixed; and in the same way an organ may be non-geotropic or non-heliotropic either because the motor mechanism or the perceptive mechanism is undeveloped or out of gear, or because the connecting links between the two are incomplete.

Even in simple cases it is often difficult to determine whether a particular plagiotropic position results from a tropic action alone or involves other co-operating factors, and many instances of such conjoint action are known. The parallelo-heliotropism or the parallelo-geotropism of an organ are easily determined separately, and hence it is possible to show that the plagiotropic position assumed by certain organs under horizontal illumination is the result of the co-operation of negative parallelo-geotropism, and positive parallelo-heliotropism. In other cases the plagiotropism of a shoot may be due to the interaction of its negative geotropism and autogenic epinasty, the latter permanently preventing the assumption of a parallelotropic position. When the stimulus of gravity is eliminated on a klinostat, the epinastic curvature continues until the autogenic campylotropism is fully satisfied. If gravity is once more allowed to act the campylotropic curvature is decreased by the negatively geotropic reaction, but is increased when the stem is inverted until the plagiotropic position is once more assumed. Similar results may be obtained when a growing branch is split longitudinally for a portion of its length, for each of the outwardly curving halves shows an autogenic epinasty. If an organ is placed so that the epinastic curvature takes place horizontally, the geotropic reaction takes place at right angles to the curvature, so that an obliquely ascending curve is performed.

A plagiotropic position can equally well result from the co-operation of autogenic epinasty with plagio-geotropism, as is actually the case in many foliage-leaves. The pronounced backward curvature which these often show on a klinostat demonstrates their autogenic campylotropism, and also shows the part played by gravity in their plagiotropic orientation; for when the stimulus of gravity again acts the leaves raise themselves into a horizontal position. If the leaf is pointed vertically upward it descends into the plagiotropic position, which results from klino-geotropism and epinasty, not from negative parallelo-geotropism and epinasty.

A plagiotropic position may, however, also be attained without the aid of any epinasty, as when a leaf, owing to the position of the stem, has to curve beyond the epinastic position of equilibrium. In such cases the epinasty is no longer essential, and may modify the position assumed little or not at all if the leaf orients itself definitely in regard to gravity, whether it has to overcome epinasty, photonasty, and the like, or not. The fact that the angle the leaf makes with the stem may vary indefinitely suffices to show that the orienting action of the stem is either absent or is so weak as to be ineffective.

De Vries considered that tropic stimuli always produced a parallelotropic reaction, so that a plagiotropic position could only result from the combination of a tropic action with some other attempted curvature. This view is, however, not supported by the facts, nor is it easy to see any reason why a responding organ should not be able to directly set itself at right angles to an orienting agency.

When the expansive tissues are symmetrically arranged, an autogenic epinastic curvature may be prevented, but may take place when the organ is split longitudinally, and may then cause the parallelo-geotropic halves to assume plagiotropic positions. In the same way two leaves bound together with their upper surfaces together form a symmetric arrangement, and may in certain circumstances react parallelo-geotropically because the opposed plagiotropic tendencies only equilibrate in a vertical plane.

Dorsiventral organs are much more liable to nastic curvatures than radial ones, and any dissimilarity in the sensitivity or power of reaction of the upper and under surfaces is bound to affect the tropic responses. Thus the physiological dorsiventrality of certain tendrils results in the fact that a curvature is only produced when contact is applied to the sensitive concave side. In addition, a stem cannot place itself parallel to the incident rays of light when one side has a feebler heliotropic irritability than the other, or when one side is smeared with indian ink. Hence a plagio-phototropic orientation is to be expected when the structure is such that light penetrates more readily on one side than on the other. Under such circumstances a photonastic curvature might result in diffuse daylight, although this is actually due to unequal phototropic stimulation. Care is needed in the interpretation of such phenomena, as is well shown in the case of dorsiventral tendrils; for although contact on the convex side does not excite a curvature, it is able to suppress one when the concave side is also stimulated, so that both sides are irritable, though in unlike degree.

It is difficult to determine from the tropic reactions in what degree the irritabilities of the upper and under sides differ in intensity or in quality. By altering the incidence of the light a plagio-phototropic leaf may be caused to assume its proper position of equilibrium either by a positively or negatively directed movement, whereas illumination of the under side always produces a positive curvature towards the light. This is, however, the natural result of the altered orienting action, and fails to reveal the distribution of irritability in the leaf, for the movement continues only until the appropriate plagio-phototropic position is again assumed.

Historical. Numerous facts concerning orienting movements were noted by Bonnet[1], while Knight and de Candolle investigated the geotropic and heliotropic responses more intimately. Dutrochet[2] then pointed out that light and gravity acted as inducing stimuli, and showed that natural orientation is the result of the varied co-operation of geotropism, heliotropism, autotropism, weight, and so forth. Our special knowledge of the different modes of orientation is due mainly to the labours of Hofmeister, Frank, Sachs, de Vries, Darwin and F. Darwin, Pfeffer, Wiesner, Krabbe, and Vochting. Subsequent authors are quoted in the text concerned with their special studies.

Frank[3] followed Dutrochet in his attempt to give a full account of the various factors concerned in the orientation of the plant and its organs. Apart from a few errors and certain hypotheses based on insufficient proof, such as the supposed polarity of the cell-wall, Frank's work corresponds in its general outlines to our modern views. This applies also to Frank's transverse heliotropism and geotropism, although de Vries[4] erroneously concluded that the unilateral action of gravity and light was only capable of inducing parallelotropic orientation, and hence considered that all plagiotropic positions were due to the antagonism of parallelotropism with other tendencies to curvature. The actual existence of a diaheliotropic irritability has been shown by Darwin and F. Darwin, while Pfeffer on more general grounds came to the same conclusion[5]. A variety of instances of plagiotropic orientation due to the isolated action of a single tropic agency were then brought forward[6]. Several authors have, however, unfortunately failed to distinguish clearly between nastic and tropic curvatures.

Sachs adopted de Vries's view, and applied it to dorsiventral organs, incidentally discovering several important facts, and more especially showing that the same agency might simultaneously excite more than one tendency to curvature. Sachs[7] supposed that the thallus of *Marchantia* might be considered to consist of cylindrical elements arranged at right angles to the surface, and showing parallelotropic orientation; but the facts that unicellular organs may show various modes of orientation,

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[1] Bonnet, Unters. über den Nutzen der Blätter, 1762.

[2] Dutrochet, Recherches anatomiques et physiologiques, 1824, p. 92.

[3] A. B. Frank, Die natürl. wagerechte Richtung von Pflanzentheilen, 1870; Bot. Ztg., 1873, p. 17.

[4] De Vries, Arb. d. bot. Inst. in Würzburg, 1872, Bd. I, p. 223. The supposition of Wiesner (Die heliotropischen Erscheinungen, 1880, II, p. 50), that the fixed light-position of leaves is due to the antagonism of their negative geotropism and negative heliotropism comes under the same category.

[5] Darwin, The Power of Movement in Plants, 1881, p. 374; F. Darwin, Linnean Society Journal, 1881, Vol. XVIII, p. 420; Pfeffer, Pflanzenphysiologie, 1. Aufl., 1881, Bd. II, p. 291.

[6] Vöchting, Bot. Ztg., 1888, p. 200; Krabbe, Jahrb. f. wiss. Bot., 1889, Bd. XX, p. 211; Schwendener und Krabbe, 1892, Gesammelte Abhandlg., Bd. II, pp. 255 u. s. w.; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 271.

[7] Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, pp. 226, 254.

and that an increase in the intensity of the stimulus may convert the parallelotropic position into a plagiotropic one, suffice to show the useless character of this hypothesis. It is of course always possible that a dorsiventral thallus might be produced in this way, but it is incorrect to suppose that the plagio-geotropic position of the lateral roots merely results from their feeble parallelo-geotropism.

Sachs also incorrectly supposed that all tropically reacting dorsiventral organs showed a plagiotropic orientation, and that the union of such objects to form a radial or bilateral structure must result in the acquirement of a parallelotropic power of reaction. This is, however, not the case, for a diatropic rhizome yields when split two klinotropic halves which form a plagiotropic organ when bound together again. Naturally no curvature is possible when opposed sides have the same tendency to curvature, and two plagio-geotropic leaves bound together may assume a parallelo-geotropic position. The same result is to be expected when the plagiotropic thallus of *Marchantia* or *Peltigera* is rolled into a cylinder. To what degree radial organs are formed in this way is uncertain, for the same result might be obtained by a change in the power of reaction. Noll[1] concludes that this actually occurs when the apothecium of *Peltigera* is formed and assumes a parallelotropic position, for the edges of the apothecium begin to rise upwards before the cylindrical shape has been assumed. According to Noll, all leaves do not react parallelo-tropically when cylindrically coiled in the bud, and they still perform a plagiotropic orienting movement when they are prevented from unrolling by means of a thread.

PART II

THE VARIOUS FORMS OF TROPIC CURVATURE

SECTION 34. **Geotropism.**

The constantly perpendicular direction of the force of gravity and its universal action render it of more importance as an orienting agent to rooted plants than any other, since in response to it the different parts of the plant are caused to place themselves in such positions as will best enable them to carry on their different functional activities. Other orienting actions also go on to a greater or less degree, and in the case of the organs which grow above the soil that of light becomes of special importance. Indeed it is often sufficiently powerful to determine the proper position of the subaerial organs even when it has to act against their geotropic irritability. In other cases, again, the stimulus of light is used to produce movements which are not directed towards the better utilization of the stimulating agent. This is the case in those attaching roots and tendrils whose negative heliotropism aids them in fixing themselves to a support, and also in the strongly heliotropic sporangiophores of many

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[1] Noll, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 478.

Fungi, which are aided by this means to develop their spores in air where dispersal is possible but which do not primarily need illumination.

The lateral roots of the third or fourth order, thorns, hairs, and the stems of the Mistletoe, are nearly or entirely devoid of geotropic and heliotropic irritability, and hence grow in all directions independently of the direction of gravity and of the illumination. The presence of a geotropic irritability in a fungus mycelium might even become injurious by causing it to pass from a suitable medium to comparatively innutritive soil.

The fact that the perpendicularity of the main axis is determined by gravity is at once shown when a seedling is laid horizontally, for the growing zone of the root curves downwards, and of the stem upwards (Fig. 35). The lateral parts of the first order possess a definite diageotropism, since they assume much the same angle with the perpendicular whether the main root is laid horizontally or is even placed upside down[1]. The same fact shows that they are radial organs, and that directive influences radiating from the main root exercise little or no effect upon them. In all experiments of this kind it is naturally essential that the conditions should be kept as constant as possible, and in this case the geotropic response of the lateral roots is dependent not only upon the intensity of the stimulus but also upon the external conditions and the tone of the root. The lateral roots arising from the hypocotyl and base of the main root often grow more or less horizontally as the result of their diageotropism, whereas later roots arising at the base may form angles of 80° to 60° or even of 45° with the perpendicular. In order that the root-system may spread thoroughly through the soil it is necessary that the geotropic irritability of side roots of the second and third order should diminish; and in fact, according to Sachs, the roots of the second order of *Zea Mays* have only a feeble, and those of *Cucurbita Pepo* no geotropic irritability. It does not, however, follow that lateral axes are always less irritable geotropically or heliotropically than the main axis, for we are dealing here with special phenomena of accommodation.

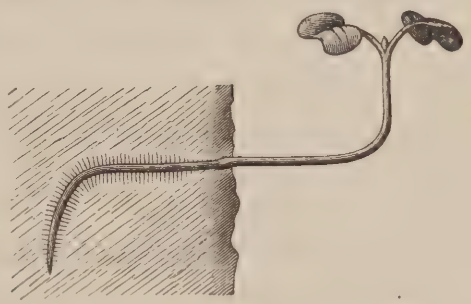

FIG. 35. Seedling of *Brassica nigra* in which root and stem have curved into a vertical position after being laid horizontally.

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[1] Dutrochet (Rech. s. la structure d. animaux et d. végétaux, 1824, p. 102) supposed the direction of the lateral roots to be determined as the resultant of their geotropism and their tendency to set themselves at right angles to the main root. The matter was more fully explained by Sachs, Arb. d. bot. Inst. in Würzburg, 1874, Bd. I, p. 602. Cf. also Czapek, Sitzungsb. d. Wiener Akad., 1895, Bd. CIV, Abth. I, p. 1197; Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 328; 1898, Bd. XXXII, p. 247; Schober, Bot. Ztg., 1898, p. 1; Guillon, Compt. rend., 1901, T. CXXXII, p. 589.

In accordance with their special function, the attaching roots of the Ivy, of Aroids, and of Orchids show usually little or no geotropism, but are commonly provided with a distinct heliotropic irritability. The erect growth of the breathing-roots (pneumatophores) of certain Mangrove-trees, on the other hand, appears to be due to their negative geotropism[1]. The roots of many plants such as Palms, Sugar-canes and others appear, however, above the soil when the latter is kept wet[2], and it requires to be determined whether this is due to aerotropism, to negative geotropism induced by the peculiar conditions, or to other causes.

Most horizontally-growing rhizomes maintain their position by the aid of their strong diageotropism, and the growing zones curve back to the normal position when the rhizome is disturbed. This applies not only to dorsiventral rhizomes but also to physiologically radial and more erect ones, including the root-stocks of *Heliocharis palustris*, *Sparganium ramosum*, and *Scirpus maritimus*[3]. The subterranean runners of *Adoxa moschatellina*, *Trientalis europaea*, and *Circaea lutetiana* are physiologically radial, but nevertheless assume a more or less horizontal position in darkness or in the soil. Exposure to diffuse light, however, induces such an alteration in their geotropic irritability as to cause them to assume a positively klinotropic, or even under special circumstances a positively parallelotropic direction of growth[4].

The downwardly-growing rhizomes of *Yucca* and *Cordyline* seem to possess positive geotropism[5], which appears also to be responsible for the downward curvature of the peduncle of *Papaver*, which later becomes negatively geotropic and straightens as the flower expands[6]. An alteration of irritability is sometimes, but not always, employed to produce the upward growth of the foliage-bearing portion of a sympodial rhizome, and to induce changes in the position of flower-buds, flowers, fruits, and even of

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[1] Karsten, Bibl. bot., 1891, Heft 22, pp. 49, 55; Schimper, Bot. Mitth. a. d. Tropen, 1891, Heft 3, p. 37; Went, Ann. d. Jard. bot. de Buitenzorg, 1894, Vol. XII, p. 26; Goebel, Organography, Part II. On the radicle of *Trapa* cf. Kerner, Pflanzenleben, 1887, Bd. I, p. 83. On negatively geotropic aerial roots cf. Wiesner, Die heliotropischen Erscheinungen, 1880, II, p. 77.

[2] Kerner, Natural History of Plants, 1895, Vol. I, p. 88. See also Sachs, Flora, 1893, p. 4. According to Eriksson, Bot. Centralbl., 1895, Bd. LXI, p. 273, *Carex arenaria* and other sand-plants possess upwardly-growing roots.

[3] Elfving, Arb. d. bot. Inst. in Würzburg, 1880, Bd. II, p. 489; Czapek, Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, Abth. I, p. 1218. According to Barth (Die geotrop. Wachsthumskrümmung d. Knoten, 1894, p. 35), the subterranean runners of *Triticum repens* show no perceptible geotropic irritability.

[4] Stahl, Ber. d. bot. Ges., 1884, p. 385; Goebel, Bot. Ztg., 1880, p. 790; Czapek, l. c., p. 1230; Rimbach, Fünfstück's Beitr. z. wiss. Bot., 1899, Bd. III, p. 201.

[5] See the literature given in Vol. II, p. 194.

[6] The literature will be given later, and it will be shown that we are dealing with a true geotropic curvature, and not with a mere mechanical drooping produced by the weight of the flower-bud. Wiesner (Sitzungsb. d. Wien. Akad., 1902, Bd. CXI, Abth. I, p. 747) does not, however, now consider the downward curvature of the peduncle of a Poppy to be geotropic in character.

the floral organs although the latter are in most cases nearly or entirely devoid of geotropic irritability[1].

Geotropism is in some cases of great importance in determining the positions of plagiotropic main and side shoots, but in other cases takes little or no part in the orientation. The shoots of *Lysimachia nummularia*, *Atriplex latifolia*, and of *Polygonum aviculare* react plagio-geotropically in strong light, but almost or entirely parallelo-geotropically in darkness, and high and low temperatures may exert a similar effect.

Foliage-leaves are very commonly plagio-geotropic, although in many cases a special power of geotropic reaction is developed for particular purposes. Thus in seedlings of *Phoenix*, *Allium*, and *Yucca* the positive geotropism of a portion of the cotyledon carries the radicle and axis of the stem downwards into the ground[2]. According to Copeland[3], the hypocotyls of seedlings of *Lupinus albus*, *Robinia pseud-acacia*, *Helianthus annuus* and *Cucurbita Pepo* act in the same way, owing to the fact that their original positive geotropism soon becomes negative.

The sporangiophores of *Phycomyces nitens* and *Mucor mucedo* are strongly negatively geotropic[4], whereas the mycelial hyphae of these fungi[5], as well as the stolons of *Mucor stolonifer*[6] show no perceptible geotropism. The rhizoids of *Bryopsis muscosa* and of *Caulerpa prolifera* are positively, the shoots negatively geotropic[7]. The same applies to *Chara* and *Nitella*[8] whose shoots show a fairly strong negatively geotropic reaction, as also do the stalks of the perithecia of *Xylaria carpophila*, of *Claviceps purpurea*, and the stalks of the sporophores of various of the larger Agaricineae[9]. The lamellae, tubes, or lobes of the hymenium are, however, positively geotropic[10]. Among Thallophyta in general, however, geotropism is less used for

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[1] See the literature already given, and Wiesner, Sitzungsb. d. Wien. Akad., 1902, Bd. CXI, Abth. I, p. 760. The downward bending of the fertilized flowers of *Trifolium subterraneum* and of *Arachis hypogaea*, which causes the ripening fruits to be pushed into the soil, appears to be the result of a change in the geotropic irritability. See Darwin, The Power of Movement in Plants; Ross, Malpighia, 1892, Fasc. VII–IX; Huth, Ueber pericarpe, amphicarpe und heterocarpe Pflanzen, 1890.

[2] Sachs, Bot. Ztg., 1863, p. 59; 1862, p. 241; Copeland, Botanical Gazette, 1901, Vol. XXXI, p. 410; Neubert, Jahrb. f. wiss. Bot., 1902, Bd. XXXVIII, p. 119 (*Allium*).

[3] Copeland, l. c. The stimulus appears in this case to be perceived by the root-tip.

[4] Hofmeister, Pflanzenzelle, 1867, p. 286; Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 222; Wortmann, Bot. Ztg., 1881, p. 368; Dietz, Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. II, p. 482; Steyer, Reizkrümmungen bei *Phycomyces nitens*, Leipzig. Diss., 1901, p. 6.

[5] Kny, Sitzungsb. d. bot. Vereins f. Brandenburg, 12. Juni, 1881; Steyer, l. c., p. 28. Kny (l. c.) and Stammeroff (Flora, 1897, p. 148) found that pollen-tubes possess no geotropism. [They appear also to be devoid of any heliotropic irritability.]

[6] Wortmann, l. c., p. 384.

[7] Noll, Arb. d. Würzburger Inst., 1888, Bd. III, p. 467; Klemm, Flora, 1893, p. 472.

[8] Hofmeister, l. c., p. 286; Richter, Flora, 1894, p. 408.

[9] J. Schmitz, Linnaea, 1843, Bd. XVII, p. 474; Zopf, Die Pilze, 1890, p. 208.

[10] Sachs, Experimentalphysiologie, 1865, p. 93; Jahrb. f. wiss. Bot., 1863, Bd. III, p. 93. [The stipes of *Lentinus lepideus* only become geotropic when the formation of a pileus has been induced by exposure to light. Buller, Ann. of Bot., 1905, Vol. XIX, p. 427.]

purposes of orientation[1] than in most terrestrial flowering plants, while the Bryophyta and certain flowering aquatics occupy an intermediate position in this respect[2].

SECTION 35. **Methods of Investigating Geotropism.**

The orienting action of gravity only began to be properly understood when Knight showed[3] that centrifugal force exercised a similar orienting action upon seedlings. On a rapidly rotating vertical wheel, for instance, Knight found that the radicle grew outwards, the plumule inwards, both organs curving so as to place themselves parallel to the direction of the orienting force. In this case the disturbing action of gravity is eliminated by the vertical rotation of the wheel, but if the wheel is rotated horizontally the forces of gravity and of centrifugal force act at right angles to one another upon the seedlings, and the ultimate position of the axis is along a resultant line which bisects the angles between the forces if they are equal, but is nearer to the more powerful one when they are unequal. When the wheel is rotated very rapidly the axes of the seedlings grow almost horizontally[4].

If a seedling is slowly and steadily rotated in a horizontal or vertical position on a klinostat so that a revolution is performed in three to forty minutes, the position of the plant is continually altered before any inductive stimulating action of gravity can be made manifest[5]. For most plants two to three revolutions per hour are sufficient, for at this rate practically no centrifugal action is exercised, while at the same time neither the shoot nor root has time to make a curvature before its position is reversed. If each rotation takes several hours the slight, continually changing curvature results in the production of a kind of circumnutation[6].

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[1] Cf. Berthold, Jahrb. f. wiss. Bot., 1882, Bd. XII, p. 572.

[2] The unicellular rhizoids of *Marchantia* are geotropic, but the thallus less so. Mirbel, Mém. de l'Acad. royale de Paris, 1835, T. XIII, p. 354; Pfeffer, Arb. d. bot. Inst. in Würzburg, 1871, Bd. I, p. 89. A few facts concerning the Jungermanniaceae are given by Hofmeister, Pflanzenzelle, 1867, p. 294; Frank, Die natürliche wagerechte Richtung von Pflanzenth., 1870, p. 66. On the Muscineae cf. Bastit, Rev. gén. de Bot., 1891, T. III, p. 380; Jönsson, Bot. Ztg., 1899, Referate, p. 132.

[3] Knight, Phil. Trans., 1806, I, p. 99. Knight used a water-wheel, and carried out experiments on rotation in both vertical and horizontal planes. The older and newer literature has been collected by Cisielski, Unters. über d. Abwärtskrümmung d. Wurzel, Dissertation, 1870. The same work without the review of the literature is given in Cohn's Beiträgen z. Biologie, 1871, Bd. I, Heft 2. Cf. also Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 209.

[4] Cf. Wigand, Bot. Unters., 1854, p. 149; Hofmeister, Jahrb. f. wiss. Bot., 1863, Bd. III, p. 141.

[5] This term was given by Sachs (Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 217), who was the first to use this method to any great extent for the elimination of gravity, although Hunter had used it long ago to a limited extent, and also Dutrochet and Wigand. Hunter, Trans. Soc. Imp. med., 1800, Vol. II. See A. P. de Candolle, Pflanzenphysiol., 1835, Bd. II, p. 556. Cf. also F. Darwin, Linnean Soc. Journal, 1881, XVIII, p. 425.

[6] Darwin and Pertz. Annals of Botany, 1892, Vol. VII, p. 245; 1903, Vol. XVII, p. 93.

The heliotropic curvature produced by unilateral illumination may also be prevented by rotation on a klinostat, so that both the heliotropic and geotropic action may be eliminated if the plant is rotated about a horizontal axis at right angles to the direction of the illumination. A slight phototropic action may, however, be produced if the shadow of the axis of the klinostat—or of the slice of bread commonly used to grow mould fungi—falls upon the plant for a sufficient length of time at each rotation. If the axis of rotation is horizontal but parallel to the incidental rays of light, the action of gravity is eliminated, but not that of light; and the same applies whether the plant is fixed so that its own axis is parallel or at right angles to that of the klinostat.

Dorsiventral organs often perform aitionastic movements under the influence of changes in the diffuse external conditions. A photonastic curvature may in fact be produced when a dorsiventral organ is rotated on a klinostat so that it is equally illuminated on all sides. The same applies to other agencies, including gravity, although under natural conditions the latter never acts equally on all sides, as diffuse light may do without causing any tropic curvature.

Tropic stimulatory reactions appear to be suppressed on a klinostat in the same way as when the exciting agent is equally distributed on all sides, but it must be remembered that specific irritabilities and the power of response to a particular excitation may be excited or modified by tropic stimulation[1]. On the other hand, opposed stimuli acting on different flanks in rapid succession may antagonize each other without producing any responsive curvature either way. Under simultaneous stimulation of this kind a dorsiventral tendril does not perform any curvature, and the same effect follows when the tendril is revolved on a klinostat so that the point of contact passes rapidly round and round an excitable zone. If, however, the intervals between the successive stimuli are sufficiently long, a tropic curvature will be produced which the stimulatory actions on the opposed sides may be unable to eliminate. Finally, if both sides are equally responsive, successive stimulations may be expected to produce the same result as continuous diffuse excitation.

These and other considerations show that the tropic reactions of a dorsiventral organ are not always entirely eliminated on a klinostat, although when the rotation is sufficiently rapid, the action of a unilateral agency will usually be the same as when it is diffusely applied. Nevertheless something depends upon the point of application of the stimulus, as is shown by the fact that the stimulus of gravity reawakens the growth

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[1] In this way Wiesner (Die heliotropischen Erscheinungen, 1878, I, p. 55; 1880, II, p. 76) and also H. Müller (Flora, 1876, p. 76) were able to obtain heliotropic reactions on feebly sensitive plants, which show none so long as they are exposed to geotropic induction.

of the nodes of grasses when the haulm is rotated horizontally so that gravity acts at right angles to the stem and equally on all sides, but does not exercise this action to any appreciable extent when the haulm is rotated in a vertical plane so that it is horizontally inclined only for short periods of time. Similarly when an organ is equally illuminated on all sides, the direction of the light rays is by no means immaterial, since more penetrate when they fall perpendicularly to the surface than when they fall obliquely. Swarm-spores react phototactically in spite of their rapid revolution around their longitudinal axes, and this fact is an indication that a special distribution of irritability may be able to prevent a tropic action being eliminated by revolution on a klinostat.

Neither Czapek nor Noll[1] has paid full attention to these considerations, for the former concludes that all geotropic action can be eliminated by sufficiently rapid revolution on a klinostat, while both authors often do not sufficiently distinguish between tropic and nastic stimuli and reactions, and ignore the possibility of changes of tone being produced by the transition from diffuse to unilateral stimulation[2].

Seedlings should be kept in moist air when used for experiments, and the older adult portions of the root may be covered with wet filter-paper with one end of the strip in water. In order to observe roots or rhizomes in earth or sawdust, they should be grown in wood or zinc troughs with sloping glass sides, and pierced with holes beneath[3]. Cut branches and peduncles may be placed in moist sand heaped up beneath a covered zinc or glass cylinder.

Any apparatus may be used as a klinostat which is capable of performing regular rotation, but the form prepared by Albrecht of Tübingen under Pfeffer's instructions is extremely exact and serviceable[4]. (Fig. 36.)

The movement is produced by a strong spring regulated by a fan, the mechanism being attached to the lid (*b*) of the heavy box (*h*). One of the three axes on the upper surface of the lid is joined by the gimbal joint to the axis (*c*), which rotates on the friction-wheels (*o*), and has a pot attached at (*g*). The longer axis (*m*) is used to attach a cylinder (*i*) containing germinating seedlings (*l*). If the cylinder contains

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[1] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, pp. 189, 270; Ber. d. bot. Ges., 1901, Generalvers., p. (129); Noll, Flora, 1893, p. 357; Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 459; Ber. d. bot. Ges., 1902, p. 409.

[2] As a matter of fact it is only a question whether the same effect is produced on a klinostat as when the exciting agency acts simultaneously on all sides, and from this point of view the impossibility of rigidly separating tropic and nastic reactions is of no importance. Every light ray, and also the most momentary illumination, exerts a stimulating phototropic action, and the absence of a response simply shows that the opposed stimuli balance. Hence, even when a plant is rapidly rotated on a klinostat, it is still subject to phototropic and geotropic stimulation so long as its irritability is unaltered.

[3] Sachs, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 387. On a geotropic chamber see Sachs, Flora, 1895, p. 293.

[4] See Bot. Ztg., 1887, p. 27.

a little water the seedlings are kept moist, and to ensure an even distribution of moisture wet blotting-paper may be placed around the inside of the cylinder.

If the box (*h*) is closed and a wood or cork plate attached to one of the axes, a pot may be placed on it and rotated around a vertical axis, or the cover (*b*) may be inclined at various angles and fixed by the screw-clamp (*n*) so that by means of the gimbal attachment the rod (*c*) is able to rotate around an oblique axis. A pulley-wheel can also be attached instead of the rod (*c*), and by means of a cord a glass plate may be rotated under water[1]. The apparatus is strong enough to rotate several pots at the same time if they are properly attached[2], and provided that the system is equilibrated by means of the adjustable weight (*e*) so that the same amount of work is performed at each phase of rotation. Finally, the time of a rotation may be varied from two minutes to as long as eight hours.

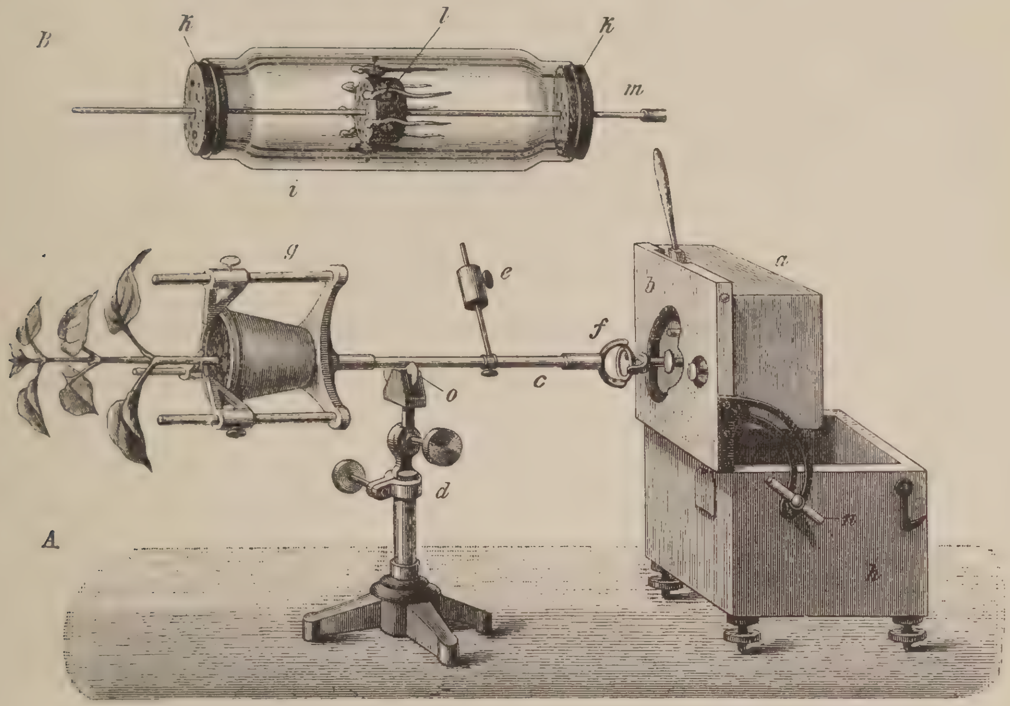

FIG. 36. Pfeffer's klinostat: *A*, showing mode of use with a potted plant; *B*, with a cylinder containing seedlings.

Fitting has recently constructed a special attachment which enables the plant to be turned through an angle of 180° at a given time, or through a lesser angle. In this way the side turned towards the light or to the ground may be suddenly placed in the opposite position and the reversal repeated at regular intervals of time[3].

The various klinostats constructed by different authors do not appear to surpass

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[1] Cf. Richter, Flora, 1894, p. 409; Klemm, Flora, 1893, p. 476. For transmission a thick circular rubber tube is best.

[2] See A. Fischer, Bot. Ztg., 1890, p. 705.

[3] A simpler intermittent klinostat was used by F. Darwin (Annals of Botany, 1892, Vol. VI, p. 245). An intermittent electro-magnetic arrangement is easily made, and full details as to the mode of use in such cases are given by Pfeffer in the Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 738.

the above instrument in accuracy and convenience. A simple form suitable for demonstration can easily be made from an ordinary American clock, either by fixing a cork plate to the finger-axis so as to get horizontal rotation, or by attaching a glass rod to it by means of stout rubber tubing, and so obtaining a horizontally-rotating rod on which seedlings may be fixed with the aid of cork rings. If the clock is fixed in a heavy frame so that it may be canted at various angles, the direction of rotation may be given varying degrees of obliquity[1].

Any rapidly rotating wheel may be used to demonstrate the action of centrifugal force[2], and slight centrifugal actions may be obtained by means of a klinostat[3]. In this way the intensity of stimulation required to produce a geotropic curvature can be determined, as well as the relationship between the intensity of stimulation and the response. It must, however, be remembered that under the action of high centrifugal forces purely physical mass-actions come in and cause the attempted curvatures to be more or less overcome and replaced by mechanical bending.

SECTION 36. **Heliotropism.**

Under this heading we may conveniently include all orienting movements produced by unilateral illumination; but since variations in the intensity of diffuse daylight may produce photonastic movements, or may cause the tone of the organ to alter, it is not always easy to say whether a particular curvature is heliotropic in character, or results from a dissimilar form of stimulatory response, or is due to a combination of factors. It must also be remembered that the position of heliotropic equilibrium may vary according to the intensity of the light, and may in some cases alter to such an extent that the direction of the curvature is reversed.

A reversal of this kind is especially well shown by those swarm-spores which react positively phototactically in weak light, but negatively photo-

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[1] Cf. F. Darwin, Linnean Soc., 1881, p. 449; Wortmann, Ber. d. bot. Ges., 1886, p. 245; Klemm, Flora, 1893, p. 472; Hansen, Flora, 1897, Erg.-Bd., p. 352; W. Oels, Pflanzenphysiol. Unters., 1893, p. 50. The mechanism used for rotating tables in shop-windows is easily made into a klinostat by changing the escapement so that the rotation is slower. Where a room at constant temperature is not available, the arrangement employed by Czapek (Ber. d. bot. Ges., 1900, p. 131) may be used to avoid effects due to changes of temperature.

[2] An apparatus driven by a water-motor, and which enables centrifugal forces up to 40 g. to be produced is described in Unters. a. d. bot. Inst. zu Tübingen, 1881, Bd. 1, p. 57. At Leipzig the apparatus used was driven by a one-horse-power gas-motor, and varying velocities obtained by the use of axes of different sizes, and of conical axes. Cf. Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 304. The centrifugal force is determined by the formula $\frac{4\pi^2 r}{gt^2}$, where $\frac{4\pi^2}{g}$ = a constant (4·024); r = radius in cms.; t = time of a rotation in seconds. On a large wheel the centring need not be so accurately performed as on a small one. On simpler forms of apparatus cf. Oels, l. c., p. 51; Detmer, Pflanzenphysiol. Practicum, 1895, 2. Aufl., p. 384; Hansen, Flora, 1893, Erg.-Bd., p. 352. Mottier, Annals of Botany, 1899, Vol. XIII, p. 326. Pfeffer has more recently used a specially constructed milk centrifuge to obtain centrifugal forces up to 4,000 g.

[3] Cf. Czapek, l. c., p. 305.

tactically when the light passes beyond a certain intensity. A similar change is also shown by the radial organs of various plants, for the filaments of *Vaucheria* and *Phycomyces*, the seedling stems of *Lepidium* and other plants grow towards the light when of moderate intensity, but as the latter increases pass through positively plagiotropic, diatropic, and negatively plagiotropic positions, finally assuming a negatively parallelotropic position of equilibrium[1]. Changes of this kind appear in certain plants and in swarm-spores when the light is of moderate intensity, but in other plants only when the intensity is considerable, and they may not be shown if the light has to be so concentrated that the plant is rapidly injured. This applies to many plants, and in others the deviation from the positively heliotropic position of equilibrium is only produced by light of an intensity which is not reached under natural conditions. The tendrils of *Vitis* and *Ampelopsis*, on the other hand, react positively heliotropically, according to Wiesner[2], only when the light is feeble, and negatively heliotropically even when only moderately strongly illuminated on one side. It does not follow, however, that every negatively heliotropic organ will show positive heliotropism when the light is weak enough. Nor is it surprising that the statements as to phototropic reactions and the phototropic positions of equilibrium should not always agree, for the tropic condition of tone varies according to the stage of development and the other external conditions[3].

After it had been shown by N. J. C. Müller[4] in the case of seedlings of *Lepidium*, by Stahl[5] in that of *Vaucheria*, and by Berthold[6] in certain marine algae that the positive heliotropic position was changed to a plagiotropic or negatively phototropic one under strong illumination, Oltmanns carried out more extended researches on this phenomenon, using at first sunlight[7] and later employing a strong arc-light as a source of illumination[8]. These experiments showed that the sporangiophore of *Phycomyces*

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[1] The positive movement is that towards the source of illumination, the negative the one away from it. Oltmanns (Flora, 1897, p. 7) regards the transversal position as an indifferent one, but there can be no doubt that it is as much the result of a stimulatory reaction as any other.

[2] Wiesner, Die heliotropischen Erscheinungen, 1880, II, p. 38.

[3] According to Oltmanns (l. c.), the young sporangiophores of *Phycomyces* react positively heliotropically to light of an intensity that causes the old sporangiophores to assume a transverse or negatively heliotropic position. In other words, the old sporangiophores are adapted to light of feeble intensity.

[4] N. J. C. Müller, Bot. Unters., 1872, Bd. I, p. 57.

[5] Stahl, Bot. Ztg., 1880, p. 412; Bot. Centralbl., 1882, Bd. XII, p. 142. Cf. Oltmanns, Flora, 1892, p. 214.

[6] Berthold, Jahrb. f. wiss. Bot., 1882, Bd. XIII, pp. 574 ff.

[7] Oltmanns, Flora, 1892, p. 214. On the gradation of the intensity of the light by the interposition of cells containing diluted indian ink cf. Oltmanns, l. c., p. 183, and Jahrb. f. wiss. Bot., 1892, Bd. XXIII, p. 416.

[8] Oltmanns, Flora, 1897, p. 1. For details of the methods cf. Oltmanns, l. c. On the removal of the heat-rays see also Pfeffer, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 711. On the use of lamps and gas-flames cf. Wiesner, l. c., 1878, I, p. 35. A heliotropic curvature is readily produced by covering the plant with a black cover having a slit or hole on one side. Cf. Sachs, Flora, 1895, p. 293.

nitens assumed a diaheliotropic position when exposed to light equivalent to 25,000 Hefner lamps, whereas an intensity of 500,000 to 600,000 Hefner lamps was required to produce the same effect on seedlings of *Lepidium sativum* and of *Hordeum*[1]. Observations under natural conditions show that the radial organs of many plants assume a positively parallelotropic position when feebly illuminated from one side, but in direct sunlight assume a more or less plagio-phototropic position[2]. The position of many dorsiventral organs alters according to the intensity of the illumination, and although the exact mode in which this altered reaction is produced is uncertain, there can be no doubt that the light-position of leaves, of the prothallia of Ferns, of the thallus of *Marchantia*, and of the plagiotropic shoots of the Ivy, are mainly the result of a heliotropic reaction. Furthermore, the movement of the chlorophyll-plate of *Mesocarpus* from the transverse to the profile position is produced as a direct response to the stimulus of light.

The positively heliotropic reaction of most seedling-stems, and of subaerial stems in general under normal conditions of illumination, is obviously a purposeful biological adaptation[3]. For in this way the leaves are brought into brighter light and, when endowed with a photometric power of reaction, set their surfaces at right angles to the direction in which the strongest diffuse light falls upon them. Positive heliotropism is also shown by the seedling-stems of twiners, whereas the older twining stem, in accordance with its habit, shows only a feeble negative or positive phototropic reaction. Most tendrils are also comparatively indifferent, although a few are aided in approaching and applying themselves to a support by their negative heliotropism.

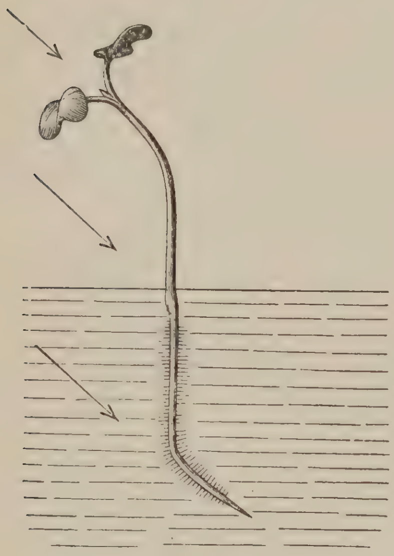

FIG. 37. Seedling of *Sinapis alba*. The hypocotyl shows a positive, the root in water a negative heliotropic curvature. The arrows show the direction of the incident rays of light.

There is also evidence of biological adaption in the fact that attaching aerial roots such as those of Aroids, Orchids, and *Hartwegia* are usually

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[1] The brightness of a Hefner-Altenach light corresponds to 1·162 German standard candles. The spermaceti candle used by Wiesner (l. c.) is equivalent to a Hefner-Altenach lamp. Oltmanns, 1897, l. c., pp. 2, 20. The cessation of growth and of heliotropic curvature observed by Wiesner with much feebler intensities of light is apparently the result of some accessory action of the gas-flames employed. It must also be remembered that the greatest heliotropic action is exercised by the more refrangible rays, so that the action of the light is not always proportional to its apparent brightness. Cf. also Wiesner, Bot. Centralbl., 1897, Bd. LXIX, p. 305.

[2] Cf. Oltmanns, Flora, 1892, p. 225.

[3] A few facts concerning stems and other organs, as well as references to the literature, are given by Wiesner, Die heliotropischen Erscheinungen im Pflanzenreich, I, 1878; II, 1880 (reprinted from Denkschriften d. Wien. Akad., Bd. XXXIX).

endowed with a negative or transversal heliotropism, whereas the longer nutritive roots which descend into the soil show a lessened power of heliotropic reaction[1]. Furthermore, the penetration of the root of *Viscum* into a host plant is brought about by the negatively heliotropic curvature of the hypocotyl[2], whereas the adult stem of *Viscum*, in accordance with its special habit, shows neither geotropic nor heliotropic irritability. In much the same way the heliotropic irritability decreases as we pass outwards from the main trunks of many trees and shrubs to the successive lateral branches. If the heliotropic irritability of a branch increases when its neighbours are removed, it is evident that the dormant irritability was suppressed or partially inhibited by the correlative and autotropic stimuli radiating from the surrounding organs. Very many subaerial runners are almost devoid of heliotropic irritability, changes in their direction of growth produced by alterations in the intensity of the illumination being due to the fact that their geotropic irritability is modified by the action of light.

Roots which grow normally in the soil are either without any heliotropic irritability or show feeble negative heliotropism, as in the cases of *Sinapis alba*, *Lepidium sativum*, and *Helianthus annuus*. The roots of *Allium sativum* and *Hyacinthus orientalis* are, however, feebly positively heliotropic[3].

Numerous instances of heliotropism in non-chlorophyllous organs are afforded by fungi. Thus the stalks of the fructifications of *Coprinus stercorarius*[4], of *C. niveus*[5], and of *Peziza fuckeliana*[6], the young stipes of *Lentinus lepideus*, the perithecia of *Sordaria fimiseda*[7], and the stalks of the perithecium-heads of *Claviceps microcephala*[8] are positively heliotropic. The same applies to the sporangiophores of *Phycomyces nitens*, *Mucor mucedo*, *Pilobolus crystallinus*, and various other Mucorineae[9], whereas the

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[1] Dutrochet, Ann. sci. nat., 1833, Bd. XXIX, p. 413; Wiesner, l. c., 1880, II, p. 76; H. Müller, Flora, 1876, p. 93; Schimper, Bot. Centralbl., 1884, Bd. XVII, p. 274; Die epiphytische Vegetation Amerikas, 1888, p. 53; Went, Ann. d. Jard. bot. de Buitenzorg, 1894, Vol. XII, p. 24; Massart, Sur l'irritabilité d. plantes supérieures, 1902, p. 60 (*Ficus*).

[2] Dutrochet, Rech. s. la structure intime, &c., 1824, p. 115; Wiesner, Sitzungsb. d. Wiener Akad., 1894, Bd. CIII, Abth. I, p. 436. Keeble, Trans. of the Linnean Soc., 1896, p. 112 (*Loranthus*).

[3] For the literature and numerous observations see Wiesner, Die heliotropischen Erscheinungen, 1880, II, p. 79; also F. G. Kohl, Mechanik der Reizkrümmungen, 1894, p. 26.

[4] Brefeld, Unters. über Schimmelpilze, 1877, Heft 3, p. 96.

[5] Hofmeister, Pflanzenzelle, 1867, p. 289; Wiesner, l. c., 1880, II, p. 89.

[6] Winter, Bot. Ztg., 1874, p. 1.

[7] De Bary and Woronin, Beiträge z. Morphol. u. Physiol. d. Pilze, 1870, 3. Reihe, p. 10.

[8] G. Kraus, Bot. Ztg., 1876, p. 505; Duchartre, Compt. rend., 1870, T. LXX, p. 779.

[9] Hofmeister, Pflanzenzelle, 1867, p. 289; Vines, Arb. d. bot. Inst. in Würzburg, 1878, Bd. II, p. 133; Wiesner, l. c., II, p. 85; K. Steyer, Reizkrümmungen bei *Phycomyces nitens*, 1901. Since *Pilobolus* curves towards the light during development, its sporangia will be thrown in this direction, and can be collected on a glass plate. Noll, Flora, 1893, p. 32. See also Sorokin, Bot. Jahresb., 1874, p. 214; Fischer v. Waldheim, ibid., 1875, p. 779; Brefeld, Bot. Unters. über Schimmelpilze,

mycelium here and in other fungi appears to possess but little heliotropic irritability. The rhizoids of *Marchantia*[1], of the prothallia of Ferns[2], and of *Equisetum*[3] afford, however, instances of unicellular organs which show a negatively heliotropic reaction even to weak illumination, while a similar reaction is shown by *Vaucheria* and by the sporangiophores of *Phycomyces* when the light is intense. The non-cellular fronds of *Caulerpa* and *Bryopsis*[4], as well as the internodes of *Chara* and *Nitella*[5], react in the same way as *Vaucheria*, and show positive heliotropism in ordinary light. Algae in general, which are not adapted to high intensities of illumination, show orienting heliotropic movements of this character[6].

Without doubt the heliotropic irritability is more or less dependent upon the stage of development and upon the general external conditions. The peduncle of *Linaria cymbalaria* is, for instance, positively heliotropic when the flower opens, but later becomes negatively heliotropic, and hence curves so as to press the ripe capsule against the wall, or into a crevice of the rock or wall on which the plant may be growing[7]. In addition, the young internodes of *Tropaeolum majus*[8] and of other plants are either positively heliotropic or indifferent, whereas the older internodes assume a positive or negative klinotropic position. We may still term a reaction heliotropic when the change of position is due to the induction of dorsiventrality, or to a related modification produced by the unilateral illumination. The change to the klinotropic position of the older internodes of the Ivy indicates, therefore, an alteration of heliotropic irritability; but, since it may also be produced by changes in other properties, direct experiment is necessary to determine the exact causation of an altered power of response. It is only in a few cases, however, that these requirements have been properly fulfilled.

SECTION 37. **The Heliotropic Action of Rays of Different Wave-length.**

The more refrangible rays are not only more effective in inducing heliotropic curvature, but also influence growth, formative activity, and

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Hefte 3, 6, 7; Zopf, Pilze, 1890, p. 204; Elfving, Einwirkung d. Lichtes auf Pilze, 1890, p. 19; Eidam, Cohn's Beiträge zur Biologie, 1886, Bd. IV, p. 212; Klebs, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 55 (*Sporodinia*); Neger, Flora, 1902, p. 228 (*Erysiphe*).

[1] Pfeffer, Arb. d. bot. Inst. in Würzburg, 1871, Bd. I, p. 88.

[2] Leitgeb, Studien über d. Entwickelung d. Farne, 1879, p. 7 (reprint from Sitzungsb. d. Wien. Akad., Bd. LXXX, Abth. 1); Prantl, Flora, 1879, p. 679.

[3] Stahl, Ber. d. bot. Ges., 1885, p. 338; Buchtien, Bibliotheca botanica, 1887, Heft 8, p. 28.

[4] Klemm, Flora, 1893, p. 472; Noll, Arb. d. bot. Inst. in Würzburg, 1888, p. 467.

[5] Hofmeister, Pflanzenzelle, 1867, p. 289; J. Richter, Flora, 1894, p. 400.

[6] Cf. Oltmanns, l. c., and Berthold, Jahrb. f. wiss. Bot., 1882, Bd. XII, pp. 573, 581; E. Winkler, Krümmungsbewegungen von *Spirogyra*, 1902, p. 20.

[7] Hofmeister, l. c., p. 292. According to Wiesner (Die heliotropischen Erscheinungen, II, p. 72) the peduncles of *Helianthemum vulgare* behave similarly at flowering and fruiting.

[8] Sachs, Experimentalphysiol., 1865, p. 41; Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 271.

movement in general more than the less refrangible rays. Hence a heliotropic curvature is performed almost as rapidly beneath an ammoniacal solution of copper hydrate, which allows mainly the blue and violet rays to pass through, as in ordinary light, whereas beneath a solution of potassium bichromate, which only allows the less refrangible rays to pass, little or no heliotropic action can usually be excited.

This applies to green and non-green cells, to cellular and non-cellular or unicellular plants, and to positively and negatively heliotropic organs[1]. The relative efficiency of the different rays is not, however, the same in all plants, and, according to G. Kraus[2], the positively heliotropic stalks of the perithecial heads of *Claviceps microcephala* react almost as rapidly under a solution of potassium bichromate as under one of cupr.-ammonia. According to Brefeld[3], *Pilobolus microsporus* behaves similarly, and the mixture of yellow and red light exercises nearly as strong a heliotropic action upon the sporangiophore of *Pilobolus crystallinus*[4] as that from the more refrangible half of the spectrum. Specific differences of this kind are known to exist in other forms of growth and movement, and the curves showing the action of the different rays of the spectrum upon these forms of vital activity need not necessarily coincide with the curve showing their relative heliotropic action. *Pilobolus* and *Coprinus stercorarius* behave as regards etiolation and formative activity similarly in yellowish-red light and in darkness, whereas the yellowish-red rays are able to excite a strong heliotropic response in them. On the other hand, both the more and less refrangible halves of the spectrum exercise approximately the same action upon the stalks of the perithecium-heads of *Claviceps microcephala* in regard both to etiolation and heliotropism.

In most cases, according to Wiesner[5], the maximum point on the curve showing the heliotropic action of different rays is reached between the violet and ultra-violet rays. The curve, as measured by the rapidity of the heliotropic response, falls gradually towards the green, sinks to nothing in the yellow[6], recommences in the orange, and rises to a small

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[1] On negatively heliotropic organs cf. Wolkoff, communicated by Hofmeister, Pflanzenzelle, 1867, p. 299 (aerial roots); Sachs, Lehrbuch, 4. Aufl., p. 810 (Ivy); Kraus, Bot. Ztg., 1876, p. 505 (aerial roots); Prantl, Bot. Ztg., 1879, p. 699 (rhizoids of fern prothalli); Wiesner, Die heliotropischen Erscheinungen im Pflanzenreich, 1878, I, p. 53. Sorokin's statement (Bot. Jahresb., 1874, p. 214) that *Mucor mucedo* and a few other fungi are positively heliotropic in blue light (cupr.-ammonia) and negatively heliotropic in yellow light (potassium bichromate) is incorrect according to other observers. Cf. Wiesner, l. c., II, p. 88.

[2] G. Kraus, Bot. Ztg., 1876, p. 505.

[3] Brefeld, Unters. über Schimmelpilze, 1881, Heft 4, p. 77; Gräntz, Ueber d. Einfluss d. Lichtes auf d. Entwickelung einiger Pilze, 1898, p. 18.

[4] Wiesner, l. c., II, p. 88.

[5] Wiesner, l. c., I, p. 50.

[6] It is worthy of note that the yellow rays exercise a certain influence on growth. Cf. Wiesner, l. c., II, p. 11.

secondary maximum in the ultra-red[1]. It can, therefore, readily be understood why, when the light is feeble, a perceptible reaction may only be produced by the more refrangible rays. It is, however, possible that in some cases only these rays are able to excite a heliotropic response.

Many researches have been performed by various authors on the heliotropic action of different rays[2]. Guillemin worked with especial care and showed that, owing to the varying absorption and dispersion of the different rays, the position of the heliotropic maximum varied according to whether prisms of quartz, rock-salt, or flint-glass were used. For these reasons it is easy to understand why the curve obtained by Guillemin, Wiesner, and other authors do not always precisely agree. The fact that Sachs could detect no heliotropic action under a solution of potassium bichromate was probably the result of feeble intensity of the light used, or of the special properties of the experimental material. Wiesner[3] found that the heliotropic action of the red and orange rays was weakened by the admixture of yellow rays. Gardner, Guillemin, and Wiesner all observed that the plants did not always set themselves precisely parallel to the incident rays, but curved somewhat towards the more active regions of the spectrum, a result only to be expected.

Polarized light acts, according to Guillemin and Askenasy, in the same way as ordinary light[4]. The non-luminous ultra-violet rays exercise a strong and the ultra-red rays a feeble phototropic action. Röntgen rays appear to exert mainly injurious actions[5], for Schober was unable to detect any tropic action of these rays on seedlings, although Joseph and Prowazek found that *Paramoecium* and *Daphnia* showed a negatively tactic reaction. The Becquerel and radium rays exercise a certain injurious action, but have no tropic influence, as far as is known[6].

SECTION 38. **Thermotropism.**

In addition to the action of the ultra-red rays which are associated with the visible part of the spectrum, dark heat rays of still greater wave-length as well as differences of temperature may produce a thermotropic curvature in certain cases. As far as our present knowledge goes, however,

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[1] According to Wiesner (Die heliotropischen Erscheinungen, 1878, I, p. 46), the ultra-red rays which pass through a solution of iodine in carbon bisulphide also act in this way.

[2] Poggioli (1817); Zantedeschi, Bot. Ztg., 1843, p. 620; Payer, Ann. d. sci. nat., 1844, 3^{e} sér., T. II, p. 99; Dutrochet, ibid., 1843, 2^{e} sér., T. XX, p. 329; Gardner, London, Edinburgh, and Dublin Phil. Mag., 1844, Vol. XXIV, p. 7; Guillemin, Ann. d. sci. nat., 1857, 4^{e} sér., T. VII, p. 154; Sachs, Bot. Ztg., 1864, p. 361; N. J. C. Müller, Bot. Unters., 1872, Bd. I, p. 57; G. Kraus, 1876, l. c.; Wiesner, Die heliotropischen Erscheinungen, 1878, I, p. 44; 1880, II, pp. 10, 87, 89. Wiesner gives a full account of the literature and also of the methods.

[3] L. c., II, p. 50.

[4] Guillemin, l. c., p. 172; Askenasy, Bot. Ztg., 1874, p. 237.

[5] Cf. Seckt, Ber. d. bot. Ges., 1902, p. 87; Joseph and Prowazek, Zeitschrift f. allgem. Physiologie, 1902, Bd. I, p. 143.

[6] A summary of all that is known in regard to the physiological action of these rays is given by K. Hoffmann, Die radioaktiven Stoffe, 1903, p. 21. See also Bohn, Compt. rend., 1903, T. CXXXVI, p. 1012.

a pronounced thermotropic irritability is present only in a few plants, and it is a natural result of the conditions of life of an ordinary plant that it should make use of thermotropic reactions only in a minor degree for purposes of orientation.

Wortmann[1] observed that seedlings of *Lepidium sativum* and *Zea Mays*, as well as the sporangiophores of *Phycomyces*, curved towards a hot iron plate emitting dark heat-rays. Steyer[2] has, however, shown that the sporangiophore of *Phycomyces* has no power of thermotropic reaction, so that the curvatures observed by Wortmann may have been due to accessory causes or were possibly heliotropic in character. Wortmann observed that the seedling-shoot of *Zea Mays* was positively but that of *Lepidium* negatively thermotropic, although the latter possesses a stronger heliotropic irritability than the former. Steyer, however, found that both plants were positively thermotropic.

Wortmann[3] has also investigated the radicles of seedlings by growing them in boxes of sawdust, one side being kept hot, the other cold. The roots of *Ervum lens* were found to be diathermotropic at 27° C., and similarly those of *Pisum sativum* did not curve out of a vertical position when at 32° to 33° C. On being placed nearer the hot side, however, the roots curved away from it, but when near the cold side showed a positively thermotropic curvature. According to Klercker[4], however, some roots only show a negatively thermotropic reaction, whereas a strong positive thermotropism is shown, according to Vöchting[5], by the peduncle of *Anemone stellata*.

The smallness of the difference in the temperature of the opposite sides, as well as the fact that either a positive or negative curvature may be produced, suffice to show that they are not due to the more rapid growth of the side exposed to heat. According to Wortmann, decapitated roots show the same reaction, and, since hydrotropic stimuli are only perceived by the root-tip, the curvatures can hardly be due to variations in the amount of moisture on the hot and cold sides. In moist sawdust there can hardly be any appreciable difference in the rate of transpiration from the two sides, whereas when an object is exposed on one side to radiant heat-rays in ordinary air, the resulting differences in the rate of transpiration might be responsible for the tropic stimulation. Apart from this effect, it is not known whether radiated and conducted heat exercise a similar thermotropic action. Hence there is no need at present to adopt

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[1] Wortmann, Bot. Ztg., 1883, p. 457.

[2] Steyer, Reizkrümmungen bei *Phycomyces nitens*, 1901, pp. 10, 20.

[3] Wortmann, Bot. Ztg., 1885, p. 193.

[4] Klercker, Die caloritropischen Erscheinungen bei einigen Keimwurzeln, 1891. (Reprint from Öfversigt af K. Vetenskaps-Akademiens Förhandlingar, Nr. 10.)

[5] Vöchting, Jahrb. f. wiss. Bot., 1890, Bd. XXI, p. 269.

Klercker's[1] term of 'caloritropism' to indicate curvatures produced by conducted heat.

SECTION 39. **Chemotropism and Osmotropism.**

Chemical stimuli not only play an important part in the general vital activity, but are often specially employed to produce tropic orienting movements. This power of reaction has, however, been more especially studied in connexion with freely motile organisms, and less is known in regard to the production of chemotropic curvatures. Among these are included all movements produced by a substance in virtue of its chemical constitution and varying distribution. When the movement takes place towards the source of the diffusing substance, or where it is more abundant, we may speak of positive chemotropism, and of negative when the curvature is in the opposite direction. Transverse chemotropism might be due to the absence of any power of response, but could only be the result of a definite chemotropic orienting stimulus when it was attempted in spite of the action of other directive agencies. Reversal is possible as in the case of heliotropism, for although a negative reaction may be produced by some substances when in extreme dilution, frequently a positive reaction becomes negative or transversal beyond a certain concentration.

An increase of concentration also involves an enhanced osmotic action, and when this acts as a tropic stimulus we have an osmotropic reaction before us[2]. A special osmotropic irritability is often shown, although comparatively high concentrations are required to excite it, and the response hitherto observed has always been negative. It is, however, not impossible that positive osmotropism may be detected in some cases[3].

Since osmotropic stimulation does not depend upon chemical quality but upon osmotic action, all substances exercise the same osmotic stimulus when in equivalent concentrations, so long as the power of perception or of reaction remains unaffected[4]. On the other hand, chemotropic stimulation is primarily dependent upon the chemical nature of the stimulating substance, and hence isosmotic solutions of different materials exercise widely dissimilar chemotropic actions. Furthermore, the chemotropic sense, like the sense of smell and taste in animals, is developed to widely dissimilar degrees in different plants. Hence a substance may be strongly chemotropic for one organism but not for another, and while a power of

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[1] Die caloritropischen Erscheinungen bei einigen Keimwurzeln, 1891, p. 767.

[2] Rothert (Flora, 1901, p. 408, footnote) suggests the terms 'osmotropism' and 'osmotaxis,' which are preferable to Massart's 'tonotaxis.' Since it is not merely a question of the attraction by food, and since all food-substances are not chemotropically active, the term 'trophotropism' suggested by Stahl (Bot. Ztg., 1884, p. 165) is highly unsuitable.

[3] Cf. Rothert, l. c., p. 403, footnote.

[4] Id., p. 413.

responding to oxygen is in many cases associated with a power of responding to peptone and other substances, it need not always be so. Furthermore, a particular organism may respond to one or a few substances, whereas another may be chemotropically stimulated by a large number of substances, though not all to the same extent. At the same time bodies of similar constitution may exert widely dissimilar physiological actions, while dissimilar substances may be comparatively alike from a chemotropic point of view. Whenever the chemotropic action depends upon acid or alkaline action it is only natural to expect that the influence of equimolecular solutions of neutral salts will partly depend upon the degree of dissociation, as in the case of poisons. The dissociated ions as well as the undissociated molecules may, quite apart from any acid or alkaline character, exercise independent chemotropic actions[1].

Either or both of these forms of irritability may be developed in the same organism, and in the latter case the two stimuli may act conjointly when a chemotropic substance is applied in considerable concentration, or when a dilute chemotropic solution has a large quantity of an indifferent soluble substance added to it. Since the stimulating chemotropic action is not directly proportional to the concentration, and since conjoint stimuli may induce changes of tone, it is not always possible to say whether the conversion of a positive into a negative response by increasing concentration is of chemotropic or osmotropic origin. That the change is a chemotropic one is, however, obvious in the case of organisms which have no osmotropic irritability, and the same applies when the tropic reversal is shown in a concentration at which isosmotic solutions of non-chemotropic salts exert no osmotropic repulsion. When a chemotropic action is only shown with high concentrations it is always accompanied by an osmotropic excitation if the organ possesses this latter form of irritability. In this way it arises that isosmotic solutions of different substances exert more or less dissimilar stimulating effect.

These forms of irritability are especially important in freely motile organisms, and often serve to lead them to nutriment or to suitable habitats, or aid them in avoiding injurious or unfavourable media. Of equal advantage are the chemotropic and osmotropic curvatures performed by the hyphae of mould and other fungi. Chemotropic stimuli also aid in directing the pollen-tube to the ovule and in bringing the antheridial

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[1] [Massart (Biol. Centralbl., 1902, Bd. XXII, p. 22) proposes the terms 'alcalio-' and 'oxytropism' for the chemotropism induced by alkalies and acids, while for the attraction exercised by oxygen the term of 'oxygenotropism' is suggested by Herbst, Biol. Centralbl., 1894, p. 694, and of 'aerotropism' by Molisch (Sitzungsb. d. Wiener Akad., 1884, Bd. XC, I, p. 111). As a holiday amusement the invention of special terms for detailed phenomena has its advantages, but for serious scientific studies the unnecessary duplication of terms is strongly to be deprecated.]

hypha of *Saprolegnia*[1] into contact with the oogonium. They probably determine the direction of growth of the fertilizing filaments of *Dudresnaya*[2], and aid in bringing about the formation and union of the conjugation tubes of Conjugatae[3]. They may also play a more or less important part in determining the union of fungal hyphae to form pseudo-parenchyma or sclerotic tissue, and also in producing and maintaining certain symbiotic associations.

It is hardly surprising that subaerial organs, such as stems and leaves, should appear usually to be devoid of any chemotropic or osmotropic irritability, for the latter could hardly be of any appreciable use for purposes of orientation in such organs. Roots, however, appear also to have developed these forms of irritability only to a limited extent, for hitherto only a certain aerotropism, or rather oxytropism, as well as a power of curving away from injurious gases, has been observed in them, while they are apparently not subject to chemotropic stimulation by nutrient solutions, or to osmotropic repulsion by concentrated saline solutions.

After Engelmann[4] had discovered that oxygen exerted a chemotactic action on certain bacteria, Pfeffer[5] studied the phenomenon and showed that a chemotactic irritability was possessed by a variety of freely motile organisms. Stahl[6] then showed the existence of a chemotropic irritability in the plasmodia of Myxomycetes, while Massart[7] established the fact that the repulsion exerted by concentrated solutions independently of their chemical nature was the result of an osmotactic reaction. A variety of researches then followed on the chemotaxis of freely motile animals and plants. Molisch ascribed the curving of the pollen-tube to the stigma to a chemotropic reaction[8] and previously examined the aerotropic curvatures of roots[9]. Miyoshi[10] then fully investigated the chemotropic curvatures of fungal hyphae and of pollen-tubes.

Miyoshi sowed the spores of fungi or pollen-grains on the under-surfaces of leaves which had been injected with water or with nutrient solutions, and then found

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[1] De Bary, Beiträge z. Morphol. u. Physiol. d. Pilze, 1881, 4. Reihe, pp. 85, 90. Cf. Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 469; Miyoshi, Bot. Ztg., 1894, p. 1.

[2] Berthold, Protoplasmamechanik, 1886, p. 282.

[3] Overton, Ber. d. bot. Ges., 1888, p. 68; Haberlandt, Sitzungsb. d. Wiener Akad., 1890, Bd. XLIX, Abth. I, p. 390.

[4] Engelmann, Bot. Ztg., 1881, p. 440; Pflüger's Archiv f. Physiologie, 1881, Bd. XXV, p. 285; 1881, Bd. XXVI, p. 541.

[5] Pfeffer, Ber. d. bot. Ges., 1883, p. 524; Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 363; 1888, Bd. II, p. 582. In the second work (1884, Bd. I, pp. 365, 469) the facts are mentioned which suggested the existence of a power of chemotropic curvature.

[6] Stahl, Bot. Ztg., 1884, p. 155.

[7] Massart, Archiv d. Biologie, 1889, Bd. IX, p. 515.

[8] Molisch, Sitzungsb. d. Wiener Akad., 1884, Abth. I, p. 111.

[9] Molisch, 1893, Bd. CII, Abth. I, p. 423; a preliminary communication in Sitzungsanzeiger d. Wiener Akad., January 17, 1889.

[10] Miyoshi, Bot. Ztg., 1894, p. 1; Flora, 1894, p. 76.

that the germ-tubes were drawn in at the stomata when positively chemotactic substances were present, but passed over the stomata along the surface of the epidermis when they were absent. The same result is obtained when the clean epidermis of an onion scale, or a thin plate of mica is bored with fine holes and laid on a mass of gelatine containing the substance to be tested. If gelatine containing a chemotropic substance is placed in a capillary tube which is brought near to a filament growing in water, the filament, if irritable, will show a chemotropic divergence towards the open end of the tube.

Miyoshi found that phosphates and ammonium-salts, and hence also meat-extract, exert a strong attraction upon *Penicillium glaucum*, *Aspergillus niger*, *Mucor mucedo*, and *Saprolegnia ferox*, which is already perceptible in solutions of 0·01 per cent. strength. Cane-sugar, grape-sugar, and dextrin are less effective, especially in the case of *Saprolegnia*, while such nutritive substances as glycerine and quinic acid exert little or no chemotropic action. In the case of pollen-tubes, however, Miyoshi found that cane-sugar, grape-sugar, and dextrin exerted an especially strong chemotropic attraction, whereas phosphate of ammonium, peptone, and meat-extract excited no positive chemotropism. It is possible that this is not always the case under all circumstances, for Lidforss found that proteids and diastase both produced strong attraction[1].

The above-named substances act in general as stimuli to bacteria, which are also attracted by potassium nitrate and sodium chloride, although these salts exercise no chemotropic action on fungal hyphae or pollen-tubes. In all cases, however, hydrochloric and other acids exercise a repellent action even in considerable dilution, and the same action is exercised by all substances when sufficiently concentrated.

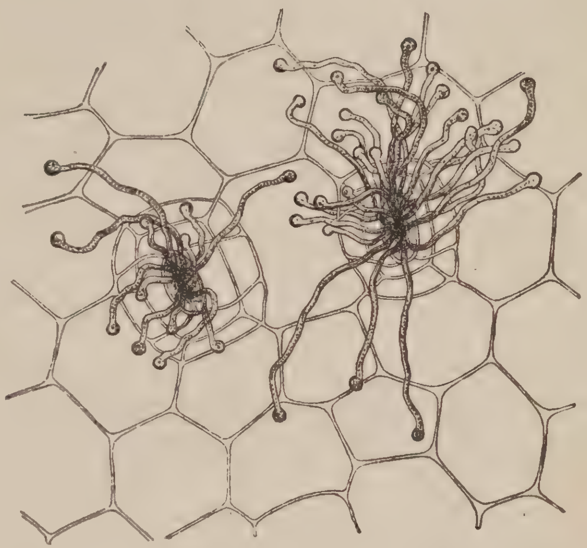

FIG. 38. A portion of the epidermis from the under side of the leaf of *Tradescantia discolor* which had been injected with a solution of cane-sugar. The germ-tubes from the spores of *Penicillium glaucum* are seen growing towards and partly into the stomata.

The penetration of the hyphae of fungi through the cell-walls of a host-plant is in part the result of chemotropic stimulation, but the whole problem of the relations and interactions of parasites and their host is one of extreme intricacy[2]. This also applies to the conduction of pollen-tubes to the ovules, which, according to Miyoshi[3],

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[1] Lidforss, Ber. d. bot. Ges., 1899, p. 236.

[2] Cf also Nordhausen, Jahrb. f. wiss. Bot., 1898, Bd. XXXIII, p. 1; Behrens, Centralbl. f. Bact., 2. Abth., 1898, Bd. IV, p. 514. On the penetration of cell-walls by bacteria cf. Buller, Die Wirkung von Bacterien auf todte Zellen, Leipzig. Dissert., 1899.

[3] Miyoshi, Flora, 1894, p. 76, and the literature there given. On the path of the pollen-tube

is brought about in the following way. The first penetration of the stigma by the pollen-tube is induced by chemotropic stimulation aided by the hydrotropism of the pollen-tube, and possibly also by aerotropic and other stimuli. The growth of the tube down the conducting tissue appears to take place independently of any chemotropic action. The actual entry at the micropyle appears to be brought about by the exudation of a stimulating material from the ovule, for the pollen-tubes penetrate the micropyles of isolated ovules injected with sugar, but not when injected with non-chemotropic solutions, or when the ovules and pollen-tubes are placed in a solution of sugar so that the action of the sugar exuding from the micropyle is masked.

Aerotropism. According to Celakovsky[1], the hyphae of *Dictyuchus monosporus* curve towards water richer in oxygen, but pollen-tubes towards water poorer in oxygen, according to Molisch[2]. Roots, on the other hand, were found by Molisch[3] to be positively oxytropic and to curve from air deficient in oxygen to air where it was more abundant. According to the same author, the one-sided accumulation of carbon dioxide, as well as the unilateral action of ether and camphor vapours, produces a negatively tropic curvature both in normal and in decapitated roots[4]. The reactions are, however, feeble, and it has yet to be shown that they take a prominent part in the orientation of roots in water and soil. It is also uncertain whether the upward growth of roots in mud or in soil whose pores are clogged with water[5] is due to oxytropism or to an alteration of the geotropic irritability produced by the deficiency of oxygen[6].

SECTION 40. **Hydrotropism.**

Many plants show tropic curvatures either towards moisture (positive hydrotropism), or away from it (negative hydrotropism). Both the main and

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cf. Dalmer, Jenaische Zeitschr. f. Naturw., 1880, Bd. XIV, p. 39; Strasburger, Jahrb. f. wiss. Bot., 1886, Bd. XVII, p. 50; Busse, Bot. Centralbl., 1900, Bd. LXXXIV, p. 209; Murbeck, Verhalten des Pollenschlauchs bei *Alchemilla* u. d. Chalazogamie, 1901, p. 7 (reprint from Lunds Universitets Årsskrift, Bd. XXXVIII).

[1] Celakovsky, Ueber d. Aerotropismus von *Dictyuchus monosporus*. Reprint, 1897, p. 8.

[2] Molisch, Sitzungsb. d. Wien. Akad., 1893, Bd. CII, Abth. I, p. 432; Miyoshi, Flora, 1894, p. 87.

[3] Molisch, l. c., 1884, Bd. XC, I, p. 194. According to Steyer (Reizkrümmungen bei *Phycomyces nitens*, 1901) the unilateral accumulation of carbon dioxide induces no tropic curvature in the sporangiophore of *Phycomyces nitens*. [Bennett (Botanical Gazette, 1904, Vol. XXXVII, p. 241) has conclusively shown that the roots of *Zea*, *Cucurbita*, *Raphanus*, *Vicia*, *Pisum*, and *Lupinus* have no aerotropic irritability, and that the curvatures observed by Molisch were hydrotropic in character.]

[4] Molisch, l. c., Vol. XC, pp. 172, 194. Cf. also Rothert, Flora, 1894, Ergzbd., p. 216.

[5] Cf. Jost, Bot. Ztg., 1887, p. 169; Goebel, ibid., p. 717; Schenck, Jahrb. f. wiss. Bot., 1889, Bd. XX, pp. 534, 564, 569; Wieler, ibid., 1898, Bd. XXXII, p. 503. On the curvatures of roots produced by deoxygenated water cf. Ewart, Trans. Liverpool Biol. Soc., 1894, Vol. VIII, p. 240.

[[6] The absence of oxygen, or the presence of poisonous gases, produces disturbances of growth often resulting in irregular curvatures, which are not always traumatropic in character. When the curvature is towards the region less deficient in oxygen, growth will be more rapid, and in this way a certain biological advantage may be gained by parts of the root system, or by some of the seedlings. It appears, however, as though the avoidance by the roots of regions poor in oxygen is in part aided by the suppression or reversal of the geotropic irritability, for on repeating the experiments described lateral roots[1] are positively hydrotropic, and hence curve towards moister soil or moister regions of the surrounding air. In this way the roots of plants growing on the sides of cliffs keep themselves buried in the soil or curve back towards it. The positive hydrotropism of the rhizoids of *Marchantia*[2] is of equal importance when the plant is growing on the sides of rocks, and the possession by the pollen-tube of this form of irritability aids it in applying itself closely to the stigma[3].

On the other hand, the sporangiophores of *Phycomyces* and of other Mucoriniae[4], as well as the stipe of *Coprinus velaris*, according to Molisch, are negatively hydrotropic. According to Steyer, however, the sporangiophore of *Phycomyces* assumes a diatropic direction of growth at a certain distance from a wet surface, whereas when further away it performs a slight positive curvature towards the region where the percentage of moisture is most to its liking. When the young sporangiophore first rises above the medium, it is strongly negatively hydrotropic (hydrophobic), and hence grows at right angles to the surface of the substance, since the moistness of the subjacent air decreases regularly in successive upward layers.

The aerial organs appear to be devoid of any hydrotropic irritability, for it is only in the case of the hypocotyl of *Linum usitatissimum* that feeble negative hydrotropism is shown[5].

For demonstration purposes seeds may be germinated in sawdust on an obliquely inclined sieve, or on the porous clay filters recommended by Molisch. Since the roots do not curve to the moist surface when the air is saturated with moisture, it is evident that differences in the percentage of moisture form the external causes inducing curvature. In the case of *Phycomyces* the culture medium, such as a slice of bread, may be covered with a sheet of mica having small holes bored through it. The sporangiophores which grow through these holes may be used for experimentation.

It is owing to their negative hydrotropism coupled with their transpiration that

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in Trans. Liverpool Biol. Soc., 1896, Vol. X, p. 191, on a klinostat, I was unable to obtain any constant and definite curvatures of the radicles away from the deoxygenated portion of the medium. The whole subject, however, well merits further investigation.]

[1] Knight (Phil. Trans., 1811, p. 212) first made it certain that the curvature of the roots to moister substrata was due to their hydrotropic irritability, which at a later date was studied in detail by Sachs, Arb. d. bot. Inst. in Würzburg, 1872, Bd. I, p. 209; and Molisch, Sitzungsb. d. Wien. Akad., 1883, Bd. LXXXVIII, Abth. I, p. 897. Further research is required on the influence of the irregular distribution of moisture upon the development of roots in soil.

[2] Molisch, l. c., p. 932.

[3] Miyoshi, Flora, 1894, p. 84.

[4] Wortmann, Bot. Ztg., 1881, p. 368; Molisch, l. c., p. 935; Dietz, Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. II, p. 478; Steyer, Reizkrümmungen bei *Phycomyces*, 1901, p. 14. The negative hydrotropism observed by Klebs (Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 55) in the sporangiophore of *Sporodinia* is disputed by von Falck (Cohn's Beiträge z. Biologie, 1901, Bd. VIII, p. 237). On the fruit-stalk of *Dictyostelium* cf. Potts, Flora, 1902, Ergzbd., p. 319.

[5] Molisch, l. c., p. 937; Dietz, l. c., p. 480. According to Vöchting, Bot. Ztg., 1902, p. 98, the shoots of potatoes are hydrotropic. Cf. Singer, Ber. d. bot. Ges., 1903, p. 175.

the sporangiophores diverge from one another when closely crowded. Frequently they may curve towards or away from a rod of metal or other material fixed upright in the culture medium[1]. According to Errera and Steyer, this is due to the rod either condensing or evolving water vapour, or changing the degree of saturation of the surrounding air by warming it[2]. There is therefore no need to assume the existence of any mysterious action at a distance, although in some circumstances other stimulatory reactions may come into play.

Even should it be found that the dissimilar rates of transpiration due to the variations in the percentage of moisture act as the stimuli to curvature there would be no need to change the term 'hydrotropism,' and still less need to invent a new one.

SECTION 41. **Mechanotropism.**

Under this head we may include all orienting movements produced in response to mechanical agencies. Thigmotropism, or haptotropism, has already been fully discussed when dealing with the irritability to contact of tendrils and certain other organs. The seismonic irritability shown in response to mechanical disturbances is not made use of for the attainment of any pronounced tropic curvatures. Nevertheless, certain curvatures due to rubbing or striking on one side may be seismonic reactions.

RHEOTROPISM. This special form of irritability by means of which plants are able to perform curvatures in response to the movement of the water in which they are growing was discovered by Jönsson[3], and is possessed by a variety of roots. The radicle of *Vicia sativa* responds especially well, according to Juel, in water moving with a rapidity of 0·3 mm. per second. For the radicle of *Zea Mays*, however, a rapidity of about 3 mm. per second is required. The extent and rapidity of the curvature is increased by a further moderate rise in the rate of flow, but is retarded when it becomes too rapid. When the current is as rapid as 500 mm. per second, a portion of the roots of *Vicia sativa* curve in the direction of the stream, probably owing to the mechanical action of the latter. According to Berg, however, at low temperatures so pronounced a change of tone takes place that the roots no longer respond positively but give a negatively rheotropic reaction. Juel found that decapitated roots also showed positive rheotropism, so that the stimulus cannot be perceived solely by the root-tip. Newcombe[4] indeed finds that the whole

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[1] Elfving, Ueber physiologische Fernwirkung einiger Körper, Helsingfors, 1890; Zur Kenntniss d. pflanzlichen Irritabilität, 1893 (reprint from Öfversigt af Finska Vet.-Soc. Förhandlingar, XXXVI).

[2] Errera, Annals of Botany, 1892, Vol. VI, p. 373; Steyer, l. c., pp. 16, 21.

[3] Jönsson, Ber. d. bot. Ges., 1883, p. 518; Berg, Studien über Rheotropismus bei den Keimwurzeln, 1889 (repr. from Lunds Universitets Årsskrift, Bd. XXXV); Juel, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 507.

[4] Newcombe, Botanical Gazette, 1902, Vol. XXXIII, p. 177; Annals of Botany, 1902, Vol. XVI, p. 429.

of the growing zone, as well as the next zone which has just ceased to grow, are able to perceive rheotropic stimuli. Among the roots examined by Berg, only those of *Soja hispida* showed no power of rheotropic reaction, whereas, according to Newcombe, a variety of roots are insensitive.

Rheotropism has also been detected in the hyphae of fungi, those of *Phycomyces* and *Mucor* being negatively and those of *Botrytis cinerea* being mainly positively rheotropic, according to Jönsson. The strip of filter-paper on which the mycelium is growing has each end immersed in a nutrient liquid, one of the vessels being slightly higher than the other. The slow movement of water thus induced is sufficient to act as a rheotropic stimulus to the hyphae.

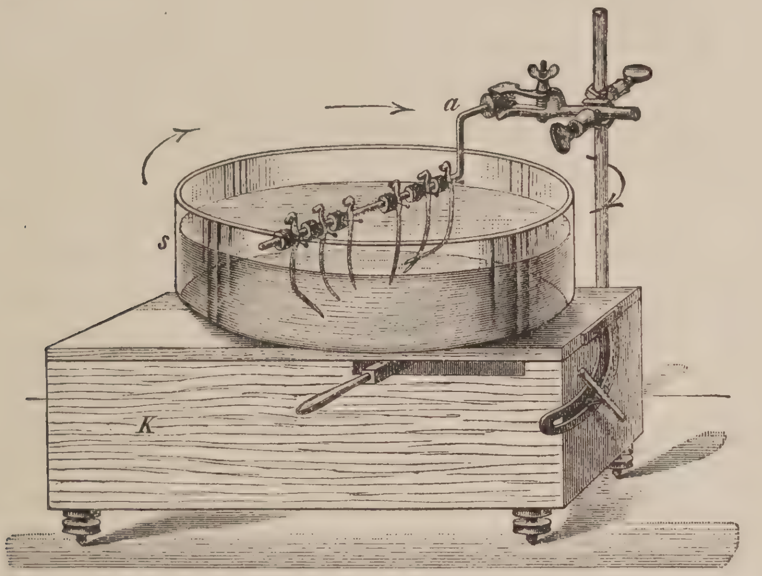

FIG. 39. Radicles of *Vicia sativa* undergoing rheotropic excitation. The arrow shows the direction of rotation, the movement of water producing the curvatures shown at the end of sixteen hours.

For purposes of demonstration the apparatus shown in Fig. 39 may be used, the glass dish containing water being rotated on a klinostat, so that the speed of the current to which the radicles are exposed will depend upon their distance from the axis of rotation. The same effect is produced when the seedlings are rotated and the vessel kept stationary, and Jönsson placed the radicles in a narrow straight stream of running water. Berg also succeeded in showing that roots show a rheotropic reaction when growing in soil.

Traumatropism. Injury causes a wound-reaction which may exercise a correlative effect upon the growth and movement of associated or remote parts. Among these are included certain tropic curvatures which are induced by local injury to the growing-points of aerial and subterranean roots, due to incision or to cauterization by heat, alkali, acid, or lunar caustic[1]. A few hours afterwards a curvature begins in the elongating

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[1] Darwin, The Power of Movement in Plants, 1880, p. 528; Spalding, Annals of Botany, 1894, Vol. VIII, p. 423; Pollock, Botanical Gazette, 1900, Vol. XXIX, p. 1.

zone of the root, away from the injured side or injurious agency. This negatively traumatropic curvature is about as rapidly produced as a geotropic one, and is shown as the result of comparatively trifling injuries, while severe injury may cause the growing apex to perform a complete coil (Fig. 40).

Since we are here dealing with a tropic stimulus which is only perceived at the root-apex, no reaction is shown when the tip of the root is removed by a transverse cut, or when it is entirely killed by the injury. The removal of an oblique slice from one side of the apex produces, however, a corresponding traumatropic curvature, while, according to Spalding[1], the incision must pass through the meristem below the root-cap in order to be effective. MacDougal[2] regards the periblem as being the irritable and responsive region, but without bringing forward any conclusive proof.

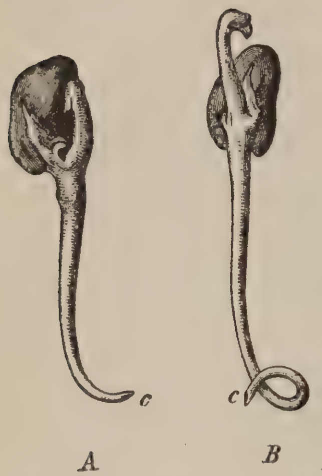

FIG. 40. Seedlings of *Vicia Faba*. The radicles have curved, as shown, sixteen hours after the application of silver-nitrate at *c*. In *B* the injury and resulting curvature are greater than in *A*.

Naturally gentle rubbing has no effect, but the energy of growth of the roots in soil is such that when in contact with stones sufficient pressure and friction might be exerted to produce a traumatropic curvature away from the hindrance. The root-apex, except in the case of the roots of *Vanilla planifolia*, does not appear to possess any thigmotropic irritability, for the curvatures observed by Darwin away from the side to which pieces of paper, glass, or mica had been attached were apparently traumatropic in origin, and were due to the means of attachment employed. Indeed the local application of alcohol or of a solution of shellac readily produces a traumatropic curvature away from the point of application.

The traumatropic stimulation is not the result of the generally occurring transitory reaction, but is due to the cessation of the correlative influences which normally radiate from the injured zone. This produces asymmetric disturbances which induce an acceleration of growth on the side opposed to the injury. Spalding found, in fact, that if the root was embedded in plaster-of-paris immediately after being injured, a traumatropic curvature was shown as soon as it was set free eight days afterwards[3]. During this

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[1] Spalding, Annals of Botany, 1894, Vol. VIII, p. 432.

[2] MacDougal, Botanical Gazette, 1897, Vol. XXIII, p. 307.

[3] Cf. Spalding, l. c., p. 426; Pfeffer, Druck- u. Arbeitsleistungen, 1893, p. 373. The curvature observed by Němec (Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 87) as the result of attaching particles of plaster-of-paris to one side of a root was possibly traumatropic in character. It is also possible, however, that a local retardation of growth might act as a tropic stimulus to the primary meristem, or that the curvature might be more or less mechanically induced.

time the general wound-reaction had mainly ceased, whereas the regeneration of the injured region was prevented by the plaster cast.

The traumatropic curvature was discovered by Darwin, and was further investigated by Spalding, who showed that certain authors were incorrect in denying the existence of any such curvature[1]. Naturally there is no question of a tropic curvature when the injury is so pronounced as to lead to the partial or complete death of the whole of the tissues on one side of the growing zone of a root or other organ, for in this case the retardation or cessation of growth on one side, and its continuance on the other, unavoidably results in a curvature. Nor is any traumatropic irritability in play when an injurious agency retards the growth of that side of the organ to which it is applied. It was in this way that the curvatures of roots were produced which Newcombe considered to be thigmotropic in character, and possibly similar curvatures may be produced by the unilateral action of poisonous gases. The true traumatropic curvatures, however, are shown by roots even when the zones of perception and response are some distance apart. The tip of the seedling leaf of *Avena*, however, which is sensitive to heliotropic stimuli does not appear to have any traumatropic irritability.

The traumatropic curvature is independent of whether the defect to which it is a response has been produced by mechanical, chemical, or electrical means. The other two mechanotropic reactions differ in that the rheotropic response is excited by a current of water, but the thigmotropic only by contact with solid bodies. It is not impossible that rheotropism, hydrotropism, and osmotropism may all be forms of the same irritability, and that the primary processes of perception may be alike in all three cases[2]. In the case of osmotropism and hydrotropism, the stimulation might arise from differences of turgor on the opposed sides of the irritable organ, produced in the first case by the differences in the concentration of the surrounding medium, and in the second by the different rates of transpiration in unequally moist air. No such differences of turgor can be responsible for the rheotropic excitation, although the unequal pressure of the water on the front and back of the root might lead to a movement of water through the tissues which might operate as a stimulus.

As far as is known, however, these three forms of irritability by no means always occur together, but are in most cases separately developed, and hence it is more probable that they are integrally distinct manifestations of irritability. Roots which are strongly hydrotropic do not appear to be osmotropic, while the osmotropic hyphae of certain fungi also show rheotropism but have no hydrotropic irritability[3]. Roots are, it is true, both

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[1] See Spalding, Annals of Botany, 1894, Vol. VIII, p. 440; Bot. Centralbl., 1883, Bd. XIII, p. 180.

[2] Cf. Juel, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, pp. 507, 533; Rothert, Flora, 1901, p. 415.

[3] Steyer, Reizkrümmungen von *Phycomyces*, 1901, p. 28. The sporangiophore of *Phycomyces* is, however, strongly hydrotropic.

rheotropic and hydrotropic, but hydrotropic stimuli are only perceived at the root-apex, whereas rheotropic stimuli are also perceived in the zone of stretching growth. Probably further researches, especially in connexion with freely motile organisms, will reveal additional instances of the occurrence of these forms of irritability single or in combination. Nothing is known as to the mode in which rheotropic, osmotropic, and hydrotropic stimuli are perceived, but it is quite possible that osmotropic stimulation may be the result of a very different form of excitation to that involved in the production of rheotropic or hydrotropic responses. On this basis it is easy to understand why transpiration is able to excite an increased development of cuticle but not the withdrawal of water due to the osmotic action of a saline solution. Elfving[1] found that no curvature was induced in the strongly hydrotropic sporangiophore of *Phycomyces* by the impact of a stream of saturated air, but this empirical fact permits of no conclusions as to the nature of a hydrotropic excitation.

SECTION 42. **Galvanotropism.**

Since many freely motile organisms are strongly galvanotactic, it might be expected that the organs of fixed plants would often be capable of galvanotropic curvature. Hitherto, however, this form of irritability has only been detected in the radicles of seedlings, which according to some authors are positively, and according to others negatively galvanotropic[2]. Brunchhorst considers that these contradictory results are due to the fact that when the current is weak the curvature is towards the kathode, but when strong towards the anode. This latter positive curvature is, according to Brunchhorst, traumatropic in character, being due to the injury of the anodal side of the root by the strong current. Further researches are, however, required to determine whether this is actually the case, and also to elucidate more thoroughly the observed phenomena.

Additional investigation is also needed concerning the negatively directed curvatures produced on the sporangiophore of *Phycomyces*, according to Hegler[3], by the action of the Hertzian electrical waves, also concerning the negative curvatures observed by Lepellier[4] away from

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[1] Elfving, Zur Kenntniss d. pflanzlichen Irritabilität, 1893, p. 4.

[2] Elfving, Bot. Ztg., 1882, p. 257; Müller-Hettlingen, Pflüger's Archiv f. Physiol., 1883, Bd. XXXI, p. 201; Brunchhorst, Ber. d. bot. Ges., 1884, p. 204; Notizen über d. Galvanotropismus, 1889 (reprint from Bergens Museums Aarsberetning); Rischawi, Bot. Centralbl., 1885, Bd. XXII, p. 121. [None of the methods used, even by Brunchhorst, is wholly satisfactory. See Ewart and Bayliss, Proceedings of the Royal Society, Nov., 1905.]

[3] Hegler, Ueber die physiologische Wirkung der Hertzischen Elektricitätswellen auf Pflanzen, 1891 (reprint from Verhandlg. d. Ges. deutscher Naturf. u. Aerzte in Halle).

[4] Letellier, Bull. de la Soc. bot. de France, 1899, T. VI, p. 11. Steyer (Reizkrümmungen bei *Phycomyces*, 1901, p. 17) obtained negative results with *Phycomyces*. On the action of statical electricity cf. also Danilewsky, Die physiolog. Fernwirkungen der Elektricität, 1902; Loeb, Pflüger's Archiv f. Physiol., 1897, Bd. LXVII, p. 483; Bd. LXIX, p. 99.

regions of high electrical potential. Should these responses prove to be tropic in character[1] it remains to be seen whether the action of electrical waves corresponds to that of an electrical current[2], and also whether the varying magnetic permeabilities of the different constituents of the cells and tissues[3] may render magnetotropic responses possible in a sufficiently strong magnetic field.

According to Brunchhorst[4], the curvature produced by a strong current is shown when the root is decapitated, but not the true galvanotropic curvature in the opposite direction produced by a weak current. The latter is shown when only the tip of the root is submerged in water or touches a wet flannel[5] through which the current is passing. Hence only the tip of the root seems capable of the perception of a negatively galvanotropic stimulus[6].

SECTION 43. **Autotropism and Somatotropism.**

It was long ago observed by Dutrochet[7] that the sporangiophores of *Mucor*, *Phycomyces*, and *Pilobolus*, and of other fungi placed themselves at right angles to the substratum from which they had emerged. The phenomenon was further studied by Sachs and by Dietz[8]. The latter author concluded that the escape from the substratum was regulated by thigmotropic excitation whereas Steyer[9] denies the truth of this statement. Sachs supposed that seedling-stems would, in the absence of any other excitation, set themselves at right angles to a block of moist turf in which they were germinated; but Dietz has shown that this is not the case[10]. The position assumed by the sporangiophores of the fungi mentioned is primarily the result of their negative hydrotropism, since their position of equilibrium is reached when they are parallel to the direction of diffusion of the water-vapour from the substratum. Negatively heliotropic organs would assume similar positions around a strong centre of illumination. This apparent action of the substratum causes the young sporangiophores to grow at first vertically outwards from the sides of the piece of bread, whereas when they grow longer their geotropic stimulation becomes relatively

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[1] [The true nature of these *galvanogenic* curvatures has been recently investigated by Ewart and Bayliss, Proceedings of the Royal Society, Nov., 1905.]

[2] Induction-shocks act on tendrils like mechanical stimuli (Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1885, Bd. I, p. 504), and in much the same way upon protoplasmic streaming. (Cf. Ewart, Protoplasmic Streaming in Plants, 1902, p. 88.)

[3] Ewart, l. c., pp. 45-9.

[4] Brunchhorst, Ber. d. bot. Ges., 1884, p. 204.

[5] Müller-Hettlingen, Pflüger's Archiv f. Physiologie, 1883, Bd. XXXI, p. 201.

[6] Cf. Rothert, Flora, 1894, Erg.-bd., p. 213.

[7] Dutrochet, Rech. anat. et physiol., 1824, p. 100.

[8] Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 221. Dietz, Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. III, p. 478.

[9] Steyer, Reizkrümmungen bei *Phycomyces*, 1901, p. 27.

[10] Dietz, l. c., p. 480.

stronger and causes them to curve upwards. This is due to the fact that the intensity of the hydrotropic excitation diminishes rapidly as the distance from the source of moisture increases. The young sporangiophores are also geotropically excitable, and if they are subjected to strong centrifugal action they curve outwards almost as soon as they emerge from the substratum. Similarly, an upward curvature is at once shown if they develop in saturated air so that they are geotropically but not hydrotropically excited.

Orienting actions of this character may arise from living as well as from dead parts, if these evolve moisture. Pollen-tubes and parasitic fungi are attracted in this way into living tissues, and it is largely owing to stimuli of this kind that the stem of the Mistletoe and the sporophores of parasitic fungi set themselves in a definite position, which is usually nearly at right angles to the surface of the stem upon which they are growing.

In all symbiotic associations not only formative but also directive interactions are exercised by the symbionts upon each other. These relationships are of the utmost complexity in the higher plants, for by them are determined not only the development and point of origin of shoots, roots, hairs and leaves, but also the tendency to a particular direction of growth of each organ in regard to the main axis. This autotropism[1] naturally only finds full expression in the absence of all external directive factors, but even when these are in play the position assumed is the result of their co-operation with the autotropic tendencies. Organs may be either auto-orthotropic as in the case of the primary root and stem, or auto-campylotropic as in the case of the leaves and other lateral appendages. The term autotropism may be used in the general sense to correspond with that of automorphosis, and this terminology renders the use of the words rectipetality and curvipetality unnecessary. These terms were indeed used by Vöchting[2] more especially in connexion with flowers.

Every disturbance of equilibrium excites reactions which tend to its restoration, and it is in this way that an organ is brought back into its original position after temporary stimulation has induced movement. Experiments illustrating this fact have been carried out by various investigators[3], and more especially Baranetzsky has shown that the return

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[1] The term 'Eigenrichtung' was suggested by Pfeffer (Pflanzenphysiol., 1. Aufl., 1881, Bd. II, p. 286; Die Reizbarkeit der Pflanzen, 1893, p. 19), and may be translated by 'autotropism.'

[2] Vöchting, Bewegungen der Blüthen und Früchte, 1882, pp. 31, 192. Cf. also Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 313. The terms 'autonasty,' 'autoepinasty,' and the like are less suitable, since the positions assumed are to be regarded as the result of the action of internal directive stimuli. Noll used the word 'morphaesthesia' to indicate the tendency to assume definite relations of symmetry (Sitzungsb. der Niederrhein. Ges. für Natur- und Heilkunde, 15. Jan. 1900), but the term is a quite unnecessary one.

[3] Vöchting, l. c., 1882, pp. 31, 182, 192; F. Darwin and Pertz, Annals of Botany, 1892, Vol. VI, p. 247; Czapek, l. c., 1895, p. 308; Kohl, Ber. d. bot. Ges., 1898, p. 169; Baranetzsky, Flora, 1901,

movement may involve a few transitory oscillations. The return movement can naturally only be performed when the power of growth or of expansion is retained, but it is worthy of note that the growing apex of an auto-orthotropic shoot or root continues to grow in a straight line even when the parts immediately behind are permanently curved or forcibly bent, and the attempted autogenic straightening prevented. It follows that the autotropic reaction is strictly localized to the part affected, and hence it is not surprising to find that autotropic return curvatures may be performed by decapitated roots [1].

Autotropic stimuli may, however, affect parts a greater or less distance away by the aid of the correlative mechanism, and indeed the removal of an organ such as the terminal shoot of a Conifer may affect the autotropism as well as the geotropic irritability of neighbouring branches. It is owing to some autotropic action at a distance of this character that the lateral branches and roots assume at first their autotropic position, but are more affected by the geotropic stimulus as they increase in length. The lateral roots always ultimately assume the same plagio-geotropic position independently of the angle which they assume in regard to the parent axis. Dutrochet was therefore in error in assuming that the plagiotropic position of the lateral roots was the resultant of their positive geotropism and their tendency to set themselves at right angles to the main root. It is, however, quite possible that the lateral roots may possess a feeble geotropic irritability as soon as they emerge externally.

A lateral shoot will only return to its original position when capable of an autotropic curvature. So long as no mechanical hindrances intervene, this is the case with hairs and with the lateral roots of second, third, and higher orders, for these have no geotropic irritability, and orient themselves in regard to the main root at angles determined by their autotropism. The same applies to the lateral roots of the first order when developed on a rotating klinostat, for they then grow out for the most part at right angles to the main root; whereas under normal conditions they usually form acute downwardly-facing angles with the perpendicular main root [2].

The orienting actions radiating from living and dead substrata were first recognized by Dutrochet [3], and were studied more fully by Sachs [4]. Dutrochet erroneously concluded that the autotropic angle was

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Erg.-Bd., p. 143. See also Bonnet, Nutzen d. Blätter, 1762, p. 170; Dutrochet, Mémoires, &c., Bruxelles, 1837, p. 320; Ann. d. sci. nat., 1844, 3e sér., T. II, p. 98; Müller, Flora, 1876, p. 91; Darwin, The Power of Movement in Plants.

[1] Czapek, l. c., p. 322.

[2] Sachs, Arb. d. bot. Inst. in Würzburg, 1874, Bd. I, pp. 596, 615.

[3] Dutrochet, Rech. anat. et physiol., 1824, p. 101.

[4] Sachs, Arb. d. bot. Inst. in Würzburg, 1874, Bd. I, p. 598; 1879, Bd. II, p. 217.

always a right angle, and considered that the directive action of the substratum was due to the mass attraction of the latter. Van Tieghem[1] supported this view, but its incorrectness was shown by Sachs[2], and the whole subject was discussed in a manner according with our present views in the first editions of Pfeffer's Physiology. Various authors then brought forward instances of the elimination of curvatures by autotropic action. No precise determination is, however, possible at present of the complex factors involved in all autotropic responses, for the same problems are involved as in growth and formative activity in general.

The fact that alterations in the tissue-strains, as well as in the tension of the plasmatic membranes, may affect growth affords no evidence as to the origin of the autotropic curvatures, and hence it is impossible to follow Noll[3] in his attempt to ascribe these curvatures to the result of the changed strains in the tissues and plasmatic membranes. Klercker assumed that the removal of the curvature was the mechanical result of the continuance of equal growth on the opposed sides, but Czapek[4] has shown the insufficiency of this view.

PART III

THE CONDITIONS FOR AND CHARACTER OF TROPIC STIMULATION

SECTION 44. **Instances of the Separate Localization of Perception and Response.**

Usually the effect of tropic stimulation is strictly localized and conducted to only a short distance from the directly excited region[5]. In addition, separated organs, or even fragments of organs, may still remain capable of tropic response; and hence the existence of a power of transmitting tropic stimuli from the percipient organs to the motory zones was overlooked until Darwin's researches were made[6].

In all tropic action at a distance the intervening ductory processes are such as to regulate the curvature to the direction of incidence of the exciting agency upon the percipient organ. This is still the case when the motory zone is not directly excitable, and can only be indirectly stimulated

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[1] Van Tieghem, Bull. de la Soc. bot. de France, 1876, T. XXIII, p. 56.

[2] Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 224.

[3] Noll (Biol. Centralbl., 1903, Bd. XXIII, p. 403).

[4] Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 320.

[5] Cf. Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 263; 1898, Bd. XXXII, p. 248; Kohl, Mechanik der Reizkrümmungen, 1894.

[6] Darwin, The Power of Movement in Plants, 1880, p. 523.

through the percipient zone, as well as when the stimulus merely spreads more or less from the directly excited responding zone to surrounding responsive regions. If in the latter case a particular zone lose the power of growth and response, it may still remain capable of receiving stimuli and transmitting them to neighbouring active zones. A separation of perception and response also occurs when a portion of a growing zone loses the power of perception, or when the meristem-cells at a growing apex develop a special irritability before their rapid stretching growth begins, and lose it as soon as this rapid growth commences. This is actually the case in the growing apex of the root, for the power of receiving geotropic stimuli is lost as soon as the tissue-differentiation begins. In other cases, however, a special irritability is absent from the primary meristem, and only appears as the tissues differentiate.

The importance of these relationships was pointed out by Pfeffer[1], but many observers denied the accuracy of Darwin's investigations[2]. Although certain of the experiments were not altogether satisfactory, the correctness of Darwin's conclusions was established by Czapek, and our knowledge of the localization of the phototropic irritability was considerably amplified and extended by Rothert[3]. As in other cases, the division of labour is not always complete, so that one zone may be more perceptive, the other more responsive. In such generalized organs direct and indirect tropic stimuli may co-operate in producing a particular response.

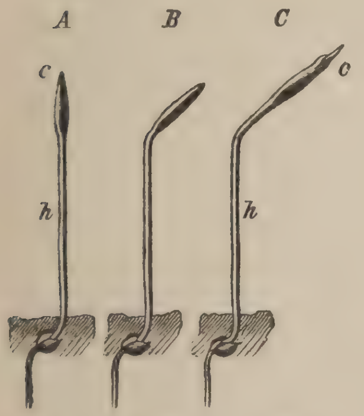

FIG. 41. Seedlings of *Panicum miliaceum*. *A* unstimulated. *B*, after shorter, *C*, after longer heliotropic stimulation from the right. *c*, cotyledon. *h*, hypocotyl.

The heliotropic curvature of grass seedlings is especially instructive, and was studied in detail by Rothert. In the cases of *Setaria viridis, Panicum miliaceum,* and a few other Paniceae only the cotyledons are perceptive, whereas the pronounced curvature is produced in the hypocotyl which is not directly excitable. The hypocotyl of *Sorghum vulgare,* however, possesses a feeble phototropic irritability. The same applies to the subapical portion of the cotyledon[4] of *Avena sativa*, which performs the heliotropic curvature in this plant, mainly in response to the indirect excitation arising from the highly irritable tip of

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[1] Pfeffer, Pflanzenphysiologie, 1881, Bd. II, p. 327.

[2] Cf. the literature given by Rothert, Flora, Ergzbd., 1894, p. 179; Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 244.

[3] Rothert (Cohn's Beiträge zur Biologie, 1896, Bd. VII, p. 3).

[4] The same terms are used as by Rothert, without expressing any view as to the still doubtful morphological nature of these organs. The term coleoptile, or cotyledonary sheath, may be used instead of cotyledon, and mesocotyl instead of hypocotyl. Cf. Goebel, Organography, Vol. II, 1905, p. 408.

the cotyledon. The tip of the hypocotyl of many cruciferous seedlings, or that of the epicotyl of *Vicia sativa*, is more irritable than the basal regions; but in other seedlings, such as those of *Tropaeolum*, *Solanum*, and *Coriandrum*, and the organs of very many adult plants, the heliotropic sensibility is fairly evenly distributed.

The above examples of localized perception are also instances of the transmission of tropic stimuli, but the same is shown in the peduncle of *Brodiaea congesta*, one of the Liliaceae, although the perceptive and responsive zones are not separately localized. Thus a phototropic stimulus radiates in three hours to a distance 6 cms. from a directly illuminated area. A somewhat less pronounced transmission is shown by the stems of *Linum usitatissimum* and *Coleus*, whereas most plant-organs have only a feeble power of conducting heliotropic stimuli. The stem of *Galium purpureum*, however, not only affords an instance of the ready transmission of stimuli, but is also able to receive and transmit the latter even when the power of response is lost. Thus the basal parts of the internodes which remain longer capable of growth and curvature may be excited indirectly by stimuli applied to the apical non-growing region which has lost the power of curvature[1].

Similarly, geotropic stimuli perceived by the root-tip are transmitted to the actively growing zones behind, which are not directly excitable. The tip of the root itself is, however, able to perform slight geotropic curvature[2], and forms the percipient organ for hydrotropic, and possibly also for negatively galvanotropic[3] and heliotropic stimuli. As regards the latter, however, Rothert[4] was unable to obtain sure results, nor do the experiments of Darwin[5] and of Kohl[6] form sure proof of the localization of the heliotropic irritability in the root-tip. Traumatropic curvatures are also usually directed from the root-apex, although the parts behind may be directly excited as well, and indeed all tropic irritability need not of necessity be localized in the root-tip. Thermotropic, aerotropic, rheotropic, and thigmotropic stimuli may, in fact, be perceived by the curving regions, and these may often be the only parts capable of direct excitation. The localization of the heliotropic irritability to the tip of the cotyledon of certain Grasses does not, therefore, necessarily indicate that the geotropic irritability will be similarly localized, although experiment has shown that this is the case. The power of perception is retained by the tip of the cotyledon after it has ceased to grow, whereas in the primary meristem of roots the geotropic irritability disappears when stretching growth commences.

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[1] Rothert, l. c., p. 139.

[2] Czapek, Jahrb. f. wiss. Bot., 1900, Bd. XXV, p. 361.

[3] [On the true nature of this irritability see Ewart and Bayliss, Proc. Roy. Soc., Sep., 1905.]

[4] Rothert, l. c., p. 140; Flora, 1894, Ergzbd., p. 207.

[5] Darwin, l. c., p. 413.

[6] Die Mechanik d. Reizkrümmungen, 1894, p. 26.

When one considers that the power of tropic reaction has been developed for the purpose of bringing the various organs of the plant into different positions suitable to the performance of their special functions, it is evident that the organs will not only have dissimilar irritabilities but also that the area over which a stimulus may spread must be restricted. Otherwise the tropic stimulation of a stem might spread to the root and cause it to perform unsuitable curvatures. In general the purpose of tropic curvature can be attained when the perceptive and active zones are not separated. Hence it is only in special cases that any such separation is shown, or that a pronounced power of transmitting tropic stimuli is developed. The special heliotropic irritability of the apical parts of various seedlings may be of use in rendering possible a curvature towards the light as soon as the tip emerges above ground, the stimulus spreading to and stimulating the parts below the ground. Similarly, it is evidently a purposeful adaptation which leads to the tip of the root receiving geotropic stimuli and regulating the growth of the region behind so that it assumes a proper position. The importance of such localization must, however, not be overestimated, since equally rapid and appropriate orientation is possible when the power of perception is evenly distributed over the whole of the active zone. Teleological considerations must, indeed, never be pressed too far, and they would lead us to conclude that the movement of the leaf-stalk into a phototropic position would be best induced by the directive action of the lamina. As a matter of fact, the heliotropic sensibility appears never to be restricted to the lamina, and its orientation seems always to be due to the co-operation of a variety of factors.

The power of transmitting tropic stimuli across small distances which may surpass the breadth of the organ affected must always be present, for all the cells are not equally irritable, and yet growth activities must be excited in the responsive tissues corresponding to the extent of the induced curvature. In the case of dorsiventral tendrils in which the convex surface is not directly excitable, the stimulus to increased growth must be transmitted from the concave to the convex surface, and probably the same applies to tendrils in general, since it is always the outer side not in contact whose growth in length is accelerated. In addition, *Mucor* and *Caulerpa* afford instances in which the different parts of a cell are endowed with dissimilar tropic irritabilities, and Steyer[1] has shown that in the case of *Phycomyces* the heliotropic sensitivity is restricted to the apex of the sporangiophore. Hence localized unilateral illumination beneath the growing zone produces no heliotropic reaction, either because this zone has no power of perception or because it is unable to transmit the stimulus to the growing zone and so direct the growth of the latter.

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[1] K. Steyer, Reizkrümmungen bei *Phycomyces* 1901, p. 6.

The localization of the heliotropic irritability is most readily determined, since the direction and point of application of the light is easily controlled. Thus Darwin and Rothert found that unilateral illumination of the seedling of *Panicum* produced no curvature when the cotyledon was covered with tinfoil, but that the full curvature of the hypocotyl took place when the cotyledon was exposed, but the hypocotyl wrapped round with tinfoil. These experiments can be performed without injury and without placing the plant under abnormal conditions, and Rothert has shown that the normal power of reaction is not affected by the enclosure in tinfoil.

According to Vöchting [1], illumination of the lamina of *Malva verticillata* is able to operate as a directive stimulus to the darkened petiole, causing the upper pulvinar portion to move so that the leaf is placed in a diaphototropic position. Since, however, the petiole is also capable of a heliotropic response, under normal circumstances its curvature is the result of direct and indirect heliotropic excitation. Czapek [2] finds that darkening of the lamina of *Cornus sanguinea*, *Linaria cymbalaria* and *Viola odorata* prevents any phototropic orientation, whereas Rothert [3] was unable to detect any phototropic direction of the leaf-stalk by the lamina of *Tropaeolum minus*, and the same was found by Krabbe [4] to apply to the leaves of *Fuchsia* and *Phaseolus*. Finally, Ewart [5] has shown that the folding together of the leaflets of various Leguminosae in strong light takes place when the laminas are darkened but the pulvini exposed, but not when the laminas are exposed to light and the pulvini darkened. The various factors concerned in the orientation of leaves are by no means clearly determined, and it is not certain whether Czapek [6] is correct in ascribing to the laminas of certain leaves a power of perceiving geotropic stimuli and transmitting them to the leaf-stalk.

The perception of geotropic stimuli by the apex of the root. Darwin [7] found that decapitated roots lost the power of reaction, whereas a curvature took place when the decapitation followed previous geotropic induction. Although the geotropic irritability is temporarily suspended as the result of injury, the opposition to Darwin's views was largely unjustified, and Czapek [8] showed conclusively that the same results could be obtained in the absence of an injury. The growing apex was caused to grow in a bent glass tube closed at one end so that the apical region was kept permanently at right angles to the growing zones behind, the segments derived from the apical meristem expanding backwardly out of the tube. The seedlings were at first rotated on a klinostat, and then arranged so that the apical region pointed

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[1] Vöchting, Bot. Ztg., 1888, p. 519.

[2] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 274. Further research is needed in this direction.

[3] Rothert, Cohn's Beiträge z. Biologie, 1896, Bd. VII, p. 121.

[4] Krabbe, Jahrb. f. wiss. Bot., 1889, Bd. XX, p. 256.

[5] Ewart, Annals of Botany, 1897, Vol. XI, p. 452 seq. The same was found by Oltmanns and by Macfarlane (Flora, 1892, p. 234; Bot. Centralbl., 1895, I, p. 136) to apply to the pulvini of *Robinia pseudacacia*.

[6] Czapek, l. c., p. 274.

[7] Darwin, The Power of Movement in Plants, 1880, p. 523.

[8] Czapek, l. c., 1895, Bd. XXVII, p. 243. The lateral roots behave similarly (l. c., p. 263).

vertically downwards, but the rest of the root was horizontal. No curvature followed, but when the root was placed as in Fig. 42, *A*, within twenty-four hours a curvature had taken place as at *B*, so that the tip pointed downwards. It follows, therefore, that the growing zones behind the apex which perform the curvature are incapable of directly perceiving geotropic stimuli.

To obtain successful results, the roots must be able to slip easily into the glass tubes, since otherwise disturbances of growth ensue, such as prevented Wachtel and Richter from obtaining any positive results [1]. The experiments when properly performed are, however, fully satisfactory; and Czapek [2] has shown that exactly the same phenomena are shown after the removal of the tube if the apex of the root remains permanently bent for a time.

The special geotropic irritability of the root-tip is also shown by the fact that the active zone curves beyond the vertical when the apical part is kept permanently horizontal [3]. This method was used by F. Darwin [4] to show that the cotyledon of a seedling of Panicum not only perceives heliotropic, but also geotropic stimuli (Fig. 43). This method is, however, unable to determine whether the power of perception is totally absent from the responding zones, and it is not surprising that, owing to the abnormal conditions, the plant is not always able to bring the irritable region into the normal position of equilibrium [5].

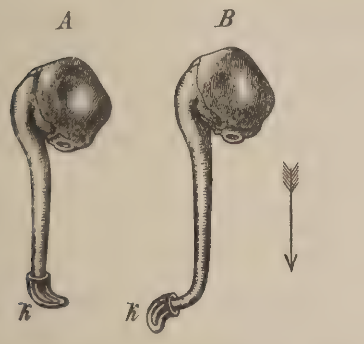

FIG. 42. Seedlings of *Lupinus albus* (smaller size). The seedling (*A*) has been removed from the klinostat after the apex is fixed in the glass cap *k*, and after twenty-four hours has curved so as to place itself parallel with the perpendicular line shown by the arrow.

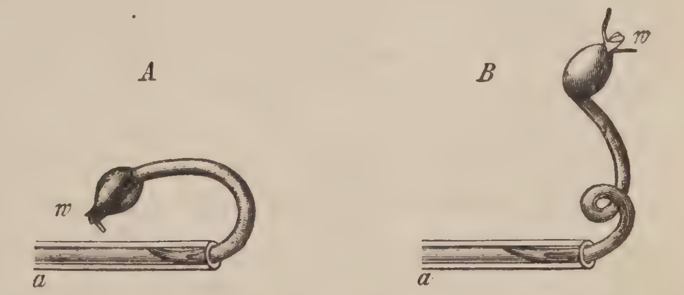

FIG. 43. Seedlings of *Setaria italica*. The roots have been cut away down to the rudiments *w*, the cotyledon fixed in the glass tube *a*, and the seedling is then placed horizontally. In *A* the hypocotyl has curved through 180°, and at *B* has formed a complete coil. (Twice enlarged.)

The hydrotropic irritability was not conclusively shown by Darwin's [6] experiments

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[1] Cf. Czapek, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 312; and the reference to Wachtel's work in the Bot. Ztg., 1899, p. 227; Richter, Zur Frage nach der Function der Wurzelspitze, 1902.

[2] Czapek, l. c., p. 336.

[3] F. Darwin, Proceedings of the Cambridge Philosophical Society, 1901, Vol. XI, p. 133; Linnean Soc. Journal, 1902, Vol. XXXV, p. 266.

[4] F. Darwin, Annals of Botany, 1899, Vol. XIII, p. 568. The special geotropic irritability of the tip of the cotyledon was suggested by certain observations of Rothert (Cohn's Beiträge z. Biologie, 1896, Bd. VII, p. 189) and of Czapek (Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 254). Massart (Sur l'irritabilité d. plantes supérieures), 1902, has applied this method to various roots and shoots.

[5] Cf. Miehe, Jahrb. f. wiss. Bot., 1902, Bd. XXXVII, p. 590.

[6] Darwin, The Power of Movement in Plants, 1880, p. 180. Cf. Rothert, Flora, 1894, Ergzbd., p. 208.

to be localized in the root-apex. Molisch[1] was, however, able to obtain a curvature when the root was enveloped right up to the tip in moist tissue-paper, while Pfeffer[2] found that, if only the extreme tip was clothed in moist paper while the rest of the root was exposed to hydrotropic stimulation no curvature followed. Hence the power of perceiving hydrotropic stimuli is developed in the root-apex alone.

The heliotropic and geotropic irritabilities are not equally distributed throughout the sensitive apex of the cotyledon of Gramineae, and presumably the geotropic irritability of the root-apex gradually disappears in the differentiating tissues. Czapek[3] found that the length of the geotropically irritable zone in the roots of *Lupinus* and *Faba* was about 1·5 millimetres. If a less zone than this is included in the terminal limb of the glass cap, a curvature takes place when the apex is placed vertically, since the horizontal region just behind is geotropically excitable. Hence the power of perception cannot be restricted to the extreme tip of the growing-point or to the calyptrogen layer. The conclusion of Fritsch and Němec, that perception is localized in the root-cap, is based partly upon faulty experiments and partly upon incorrect ideas as to the process of stimulation[4]. Czapek concludes that the whole of the meristem and of the young tissues abutting upon it is capable of perceiving geotropic stimuli. According to Wachtel[5], the geotropic irritability returns to decapitated roots where the apical meristem is regenerated[6]. The removal of the epidermis from the cotyledons of Gramineae[7] does not prevent them from perceiving geotropic stimuli.

It is difficult to determine by operation whether certain tissues are more highly excitable than others, since the removal of the other tissues may not only affect the power of response, but may also result in traumatropic curvature. Rothert[8] found the removal of the tip of the cotyledon of *Panicum* or *Avena* caused the geotropic and heliotropic irritabilities to be entirely suspended for a few hours. At the same time, growth is retarded, but not to such an extent as to cause the cessation of a curvature which had already begun or which had just been induced. Similarly, transverse or longitudinal incisions or punctures in the root-apex inhibit the geotropic irritability for a few hours or even a couple of days, although the percipient organ is neither removed nor destroyed. It is not surprising that the irritability should return sooner after such an incision has been made than when the root-apex is entirely removed[9]. Owing to the fact that the injury excites an energetic process of regeneration, it is difficult or impossible by operative experiments to determine the part played by different tissues in the perception of stimuli. It is hardly to be

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[1] Molisch, Sitzungsb. d. Wien. Akad., 1883, Bd. LXXXVIII, Abth. 1, p. 897.

[2] Cf. Rothert, l. c., p. 212; Czapek, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 316.

[3] Czapek, loc. cit., 1895, Bd. XXVII, p. 262; Ber. d. bot. Ges., 1901, Generalvers., p. 117.

[4] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 230; Ber. d. bot. Ges., 1901, pp. 117, 119.

[5] Cf. Czapek, l. c., 1901, p. 118.

[6] Cf. also Němec, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 98; Fünfstück's Beiträge z. wiss. Botanik, 1901, Bd. IV, p. 193.

[7] Czapek, l. c., 1898, p. 255.

[8] Rothert, Cohn's Beiträge z. Biol., 1896, Bd. VII, pp. 191, 211.

[9] Czapek, l. c., 1898, p. 202; l. c., 1901, p. 118; Němec, l. c., p. 97.

expected that the removal of the tip of the root and of the cotyledon of a Grass should produce exactly the same effect, since in one case we are dealing with undifferentiated meristem, and in the other with a nearly adult differentiated tissue. Hence, any incision into the root-apex temporarily inhibits its irritability, whereas the complete removal of the tip of the cotyledon of a Grass is required, according to Rothert, to produce the same effect.

The traumatic inhibition of the heliotropic and geotropic sensibilities on the one hand, and the retardation of growth on the other, are two distinct reactions to the same external agency. It is only possible to demonstrate the conduction of stimuli leading to both forms of response when the zone of action is directly excitable, but nothing is known as to the inherent character of the phenomenon. Nevertheless, the removal of the apex of the cotyledon of *Avena* must either entirely inhibit the power of perception of heliotropic stimuli or must prevent the awakened sensation progressing to the induction of movement. According to Rothert[1], the inductory processes once begun are not stopped by the injury, but progress, and are propagated to the active zones. After only short exposure to unilateral illumination, a heliotropic after-effect is shown in spite of the removal of the tip of the cotyledon, and leads to a curvature. In roots, however, prolonged induction is required before any geotropic after-effect is shown, and in such cases the ductory processes might already have reached and affected the active zones before the sensitive apex was removed. Darwin[2], for instance, decapitated the roots after they had been kept for one to one-and-a-half hours in a horizontal position. Czapek[3] has shown why this after-effect cannot be used to demonstrate the localization of the geotropic irritability in the root-apex, and has also found that short induction periods may produce perceptible after-effects[4]. It is, however, always possible that the processes of induction themselves may be affected by traumatic agencies, and hence probably arose the fact that Czapek[5] was unable to detect any geotropic after-effect in the roots of *Lupinus*. Nor is it surprising that a short period of induction may not be able to overcome the existent tendencies and the effects of decapitation, and hence may fail to produce any after-effect. Owing to the fact that Němec[6] did not consider this possibility, his experiments fail to determine whether the injury entirely suppresses the geotropic excitability of the root, or whether the sensory processes are still excited up to a certain point. Decapitated parts, even when in a condition of traumatonus, are still capable of reaction, and may indeed be capable of certain tropic responses.

The conduction of stimuli usually occurs over a short distance only, even when the transference is from one organ to another, as from the cotyledon to the hypocotyl of *Panicum*. Copeland[7] suggests that the positively geotropic curvature of certain

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[1] Rothert, l. c., p. 200.

[2] Darwin, The Power of Movement in Plants, 1880, p. 525.

[3] Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 252.

[4] Czapek, ibid., 1898, Bd. XXXII, p. 219.

[5] Czapek, l. c., 1895, p. 252.

[6] Němec, Fünfstück's Beiträge z. wiss. Bot., 1901, Bd. IV, p. 186.

[7] Copeland, Botanical Gazette, 1901, Vol. XXXI, p. 410.

hypocotyls and cotyledons is due to processes of induction transmitted from the sensory region of the root-apex.

Tropic stimuli are only slowly conducted, as are most stimuli in plants. Under favourable conditions a heliotropic stimulus may travel at a rate of 1 mm. to 2 mm. in five minutes in the case of *Avena* and *Brodiaea*[1], while the geotropic excitation may pass from the root-apex at a rate of 1 mm. in five minutes[2]. Stimuli must travel in sensitive tendrils over at least 18 mm. in five minutes, as measured by the difference in time between the application of a stimulus to the concave side and the commencement of the acceleration of growth on the convex side and resultant curvature[3]. Presumably the stimulus may spread in all directions where conducting tissue is available; but, according to Rothert[4], heliotropic stimuli travel mainly in the basipetal direction in the cotyledon of *Avena*. Since the latter has only two longitudinal vascular bundles, it is easy to cut these and show that the heliotropic stimulus is able to travel through the fundamental parenchyma[5]. According to Czapek[6], the same is true for geotropic stimuli, although it does not follow that here and in other cases the vascular bundles are devoid of all power of conducting stimuli. In addition, the cortical tissue of roots is able to transmit geotropic[7] and traumatropic[8] stimuli, for curvatures can still be produced in the active zone when only a strip of living cortex is left between the stimulated apex and the growing zones behind. No geotropic reactions can, however, be excited in a node of *Tradescantia fluminensis* by stimulation of the next younger node if the continuity of the vascular bundles is broken[9]. Probably also the stimuli involved in the regulation of translocation mainly travel through the vascular bundles.

Geotropic[10] and traumatropic[11] stimuli are still able to travel from the apex of the root to the active zone and to produce a normal curvature when a pair of incisions are made in the path of the stimulus on opposite sides one above the other and past the median line. This shows that the stimulus may have followed a curved path and may be capable of lateral

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[1] Rothert, l. c., pp. 137, 209.

[2] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 219.

[3] H. Fitting, Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 610.

[4] Rothert, l. c., p. 52.

[5] Rothert, l. c., pp. 63, 209.

[6] Czapek, l. c., 1898, Bd. XXXII, p. 255.

[7] Czapek, l. c., p. 220.

[8] Pollock, Botanical Gazette, 1900, Vol. XXIX, p. 24.

[9] Miehe, Jahrb. f. wiss. Bot., 1902, Bd. XXXVII, p. 527.

[10] Czapek, l. c., 1898, p. 220. Cf. also Němec, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 96. Němec states in another paper (Fünfstück's Beiträge z. wiss. Bot., 1901, Bd. IV, p. 207) that the stimulus does not travel beyond an incision in the active zone of the root. See also Němec, Die Reizleitung u. die reizleitenden Structuren, 1901, p. 134.

[11] Pollock, l. c., p. 24.

transference, but how this is produced is quite uncertain. We may, however, conclude with reasonable certainty that the protoplasmic communications play an important or even essential part in the conduction of stimuli. The fact that stem and roots are incapable of any geotropic reactions when plasmolysed does not afford conclusive proof[1], since the treatment probably acts by suppressing the growth reaction. The fact that the influence of the external conditions upon the rapidity and readiness of transmission of stimuli corresponds to their influence upon perception and sensation indicates that the former also is a vital phenomenon[2]. The possibility of the transverse conduction of stimuli is probably owing to the presence of interprotoplasmic communications on the side walls, their distribution being such as to restrict the stimuli to particular paths[3]. There appears, however, to be a certain time block at each passage from cell to cell, and it is for this reason that longitudinal propagation is always more rapid in tissues composed of elongated cells than transverse propagation. The times usually given for the transference of stimuli include the latent period of response, but by eliminating this Ewart found that traumatic stimuli inducing streaming travelled at rates of 1 mm. to 2 mm. per minute at 30° C.[4] Within the long cells of *Chara* and *Nitella*, a much more rapid prolongation of stimuli inhibiting streaming is shown when the time of reaction is excluded, for they travel at a rate of 1 mm. to 8 mm. per second at room temperatures[5].

The protoplasmic fibrillae which Němec[6] considered to be the channels for the transmission of tropic stimuli may favour the transmission in a special direction. According to Němec, they become more strongly marked as the result of stimulation, and, if so, this may explain why a continuous stimulation may spread further than a single excitation. The fibrillae do not, however, form a continuous conducting system, nor are they always present[7], while in the latter case stimuli may be transmitted as rapidly, or even more rapidly, than when they are present[8]. Czapek[9] found that reducing substances increased in amount in geotropically-excited root-

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[1] Strasburger, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 578.

[2] Czapek, ibid., 1898, Bd. XXXII, p. 221.

[3] Cf. Strasburger, l. c., 1901, Bd. XXXVI, p. 493; Kienitz-Gerloff, Ber. d. bot. Ges., 1902, p. 93.

[4] Ewart, The Physics and Physiology of Protoplasmic Streaming in Plants, 1903, p. 105.

[5] Ewart, l. c., p. 103.

[6] Němec, Die Reizleitung und die reizleitenden Structuren, 1901, p. 135; Biol. Centralbl., 1901, Bd. XXXI, p. 529.

[7] Haberlandt, Sinnesorgane im Pflanzenreich, 1901, p. 150; Biol. Centralbl., 1901, Bd. XXXI, p. 369; Ber. d. bot. Ges., 1901, p. 569. On the conduction of stimuli in nerves cf. Verworn, Das Neuron in Anatomie und Physiologie, 1900. See also the summary by Boruttau, Zeitschr. f. allgem. Physiol. von Verworn, 1901, Bd. I, p. 129.

[8] Ewart, l. c., 1903, p. 102.

[9] Czapek, l. c., p. 208 u. Ber. d. bot. Ges., 1901, Generalvers., p. 122.

apices, and that this effect spreads from the excitable zone. We are, however, probably dealing with a secondary reaction, resulting from the primary processes of sensation and induction.

SECTION 45. **Instances of Autogenic and Aitiogenic Changes of Irritability.**

The special irritabilities of stems, roots, and other organs cannot come into being before the primordial rudiments are developed, and in many cases may only appear when a certain stage of development has been reached. Thus stems and leaves while in the bud, or when just escaping from it, usually show no geotropic or heliotropic irritability. In addition, the nodes of stems do not at first possess any geotropic irritability, while those of *Dianthus bannaticus* only develop this irritability when fully grown[1]. In the case of *Spirogyra*, Bacteria, and other asomatophytes only embryonic cells are available, while the geotropic perception and reaction of mould-fungi is restricted to the embryonic growing apex of the hypha. Furthermore, the geotropic irritability of the apical meristem of a root is lost in the elongating segment-cells, whereas in other cases a tropic sense may persist after the power of reaction has been lost. Automatic changes of tropic irritabilities are also frequently used to produce curvatures under constant external conditions, and periodic movements may be normally induced by regular autogenic changes of tone.

In addition, changes of the external conditions may induce changes of tone resulting in modifications in the character or rapidity of tropic reactions. It has already been mentioned that the heliotropic reaction of seedling-stems is suppressed by a partial pressure of oxygen which still permits of geotropic stimulation and curvature, while in air rarefied enough to suppress curvature no perception of a tropic stimulus or after-effect are possible. According to Czapek[2], however, the root of *Lupinus* is able to perceive a geotropic stimulus in the entire absence of free oxygen. A root kept in a horizontal position at 0° to 2° C. for twenty-four hours in oxygenless air showed on a klinostat a curvature due to the geotropic induction on returning to ordinary air and room temperature.

Low temperatures retard geotropic reaction sooner than geotropic sensation[3], so that roots of *Lupinus* placed horizontally for eighteen hours at 0° to 2° C. perform a geotropic curvature when returned to a more favourable temperature as the after-effect of the previous induction. The curvature is, however, not very pronounced, partly owing to the lowered

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[1] Barth, Die geotropische Wachsthumskrümmung der Knoten, 1894, pp. 8, 28. The same applies to the development of irritability in tendrils and in the pulvini of *Mimosa* and other plants.

[2] Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 277.

[3] Czapek, l. c., p. 272; Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 195.

irritability due to the low temperature, and partly owing to the fact that the power of reaction may be temporarily depressed. Similar results were obtained by Czapek by the sufficiently intense action of chloroform, carbon dioxide and caffeine.

According to Czapek[1], the receptivity of geotropically-sensitive organs continually rises as the temperature does, so that the relationship between receptivity and temperature is represented by an ascending curve, as is that between respiration and temperature, whereas the growth-curve falls beyond a certain optimum temperature. The injury of the cotyledon of *Avena*, and of the root-apices of a variety of plants, produces a transitory inhibition of the power of perception, but not always of the power of conducting stimuli, while the power of perceiving tropic stimuli is still retained when growth is mechanically prevented by embedding in a plaster cast.

The inhibition of the power of perception or reaction is an instance of the aitiogenic modification of tropic properties; but, in addition, changes of tone may be induced which cause alterations in the position of equilibrium under the same constant stimulus. Both diffuse and unilateral stimuli may directly and indirectly produce changes of tone, and a particular tone may either rapidly appear owing to the changed conditions or may gradually result from the conditions prevailing during development. These considerations apply to existent organs, although external influences may also induce a formation of organs with specific powers of reaction. No sharp distinction can, however, be drawn, since the modification of tone may only appear in the portions of the organ developed under the new conditions, or, in the case of a Bacterium, in the new individuals. Cultivated plants often show varied powers of reaction under different conditions, and Vöchting[2] found that the flowers of *Impatiens parviflora* and the cleistogamic flowers of *Linaria spuria* possessed no power of geotropic orientation when developed in feeble light. The cultural conditions also apparently exercise a pronounced effect upon the power of reaction of Bacteria and other micro-organisms[3], while in certain cases races may be developed with particular tactic or tropic properties.

Although injuries may cause a transitory depression or inhibition of the geotropic and heliotropic irritabilities, pieces of stems and roots are usually capable of tropic reaction. Nevertheless, the injury probably may either affect the rapidity of reaction, or produce a correlative modification or suppression of the position of equilibrium or of the power of tropic reaction. In certain cases, however, the removal or prevention of growth of an organ may produce profound changes of irritability in neighbouring

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[1] Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXXII, pp. 198, 303.

[2] Vöchting, ibid., 1893, Bd. XXV, pp. 179, 189.

[3] Cf. Rothert, Flora, 1901, p. 416.

ones, causing tropic curvatures often directed towards the replacement of the missing organs.

If the apex of *Picea excelsa* or of other Coniferae is embedded in a plaster cast, one or more of the side-shoots bend upwards and more or less completely replace the main axis [1]. *Chara* behaves similarly [2], while in many other plants a certain lessening in the geotropic angle of the side-shoots is produced by the removal of the apical shoot [3]. According to Strasburger [4], the effect extends to lateral shoots of *Picea pungens* grafted upon the main axis of *Picea excelsa* when the apex of the latter is embedded in a plaster cast. Similar changes of position may be produced by the infection of the axis with parasitic fungi [5]. In many cases, however, in which sympodial axes are normally produced by the non-development of the terminal bud, the required directive actions probably result from self-regulation rather than from any modification of the geotropic irritability [6]. On the other hand, the upward curvature of the previously horizontal apex of a rhizome to form an annual upright shoot seems to result from a change of the original diageotropic irritability into a negatively geotropic one, and this change is correlated with the conversion into a leafy and flowering shoot [7]. A change of the geotropic irritability not only occurs in sympodial rhizomes, but also in uniaxial ones, and is produced or hastened by the removal or bending of the subaerial shoots [8]. No such change is, however, produced in the rhizome of *Adoxa moschatellina* by the removal of the flowering axes [9].

The removal of the apex of the main root also causes the lateral roots to grow more directly downwards, owing to a change in their geotropic tone, without their reaching a vertical position [10]. Vöchting [11] found that, when the apical portion of the tap-root of a beet was transplanted into the position of a lateral root, it grew in a plagiotropic position, whereas a lateral root transplanted into the cut end of the main root assumed a positively parallelotropic position. Apparently the irritabilities were reversed in these cases by the correlative influence of the new associations. Němec [12] also found that the removal of the terminal leaflet of a compound leaf influenced the position of the lateral leaflets to a certain extent.

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[1] Kunze, Flora, 1851, p. 145; Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 280; Busse, Flora, 1893, p. 144.

[2] Richter, Flora, 1894, p. 416.

[3] Vöchting, Organbildung, 1884, Bd. II, p. 32.

[4] Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 588.

[5] Darwin, The Power of Movement in Plants.

[6] Cf. Goebel, Vergl. Entwickelungsgesch. d. Pflanzenorgane, 1883, p. 192.

[7] Cf. Goebel, l. c., p. 193; Organography, Vol. II, 1905, p. 25.

[8] Cf. Goebel, Bot. Ztg., 1880, p. 818; Organography, Vol. I, 1900, p. 172; Vol. II, 1905, p. 463 (*Sparganium*, *Sagittaria*, *Circaea*, *Scirpus maritimus*, &c.); Sachs, Arb. d. bot. Inst. in Würzburg, 1880, Bd. II, p. 484 (*Cordyline*, *Yucca*); Elfving, ibid., 1880, Bd. II, p. 489; C. Kraus, Flora, 1880, p. 54; Vöchting, Bot. Ztg., 1895, p. 95 (Potato).

[9] Goebel, Bot. Ztg., 1880, p. 791.

[10] Sachs, Arb. d. bot. Inst. in Würzburg, 1874, Bd. I, p. 622; Darwin, The Power of Movement in Plants, 1880, p. 187; Vöchting, Organbildung, 1884, Bd. II, p. 35; Boirivant, Ann. sci. nat., 1898, 7e sér., T. VI, p. 315.

[11] Vöchting, Transplantationen am Pflanzenkörper, 1892, p. 34.

[12] Němec, Ueber die Folgen d. Symmetriestörung bei zusammengesetzten Blättern, 1902 (reprint from Bull. internat. de l'Acad. de Bohême).

The pronounced geotropic reaction of a node on the stem of *Tradescantia virginica* is somewhat decreased when the internode between it and the next younger node is severed, and is entirely suppressed in the case of *Tradescantia fluminensis* and *T. zebrina*. According to Kohl[1], this is due to the fact that, as in roots and the cotyledons of grasses, the perceptive and reacting zones are separately localized, the young node perceiving the geotropic stimulus and transmitting it to the next older one. Miehe[2] has shown that a geotropic curvature is produced in the third horizontal node of an intact plant when the next younger second node is placed vertically by bending the internode. If the third node is placed vertically, no curvature results in it, but instead a geotropic reaction is awakened in the horizontal younger second node. Furthermore, the geotropic irritability of the third node is diminished when the second node is placed in carbon dioxide or in a plaster cast, so that its growth and functional activity are depressed or stopped. It follows, therefore, that the removal of the younger node awakens positive geotropism in the next older node, and that the same effect can be produced by placing the node in a vertical position; and to produce a complete change of tone the entire younger node with its bud must be removed. The remaining portion of the internode then dies and is thrown off. The older node loses its geotropic irritability when the continuity of the internodal vascular bundles is broken, so that these must serve for the transmission of the correlative interactions concerned. It is possible that the correlative stimulatory actions in question are derived from the distribution and diffusion of certain of the products of metabolism.

Vöchting[3] found that after removing the flower of a poppy, or the capitulum of *Tussilago Farfara*, the temporary positively geotropic power of reaction of the peduncle was arrested, whereas the negative geotropism and the autotropism were unaffected. Since the same effect is produced by the removal of the ovary only of the poppy, the correlative influences which modify the geotropic tone seem to have their origin in this part of the flower. According to Wiesner[4], moreover, the upward curvature of a horizontally-placed inflorescence axis of *Digitalis* and other plants no longer occurs when the flowers have been fertilized. The decapitated peduncle of a Poppy still remains capable of growth, whereas, according to Scholtz[5], the removal of the flower of *Clematis cylindrica* or of *Dahlia variabilis* causes the peduncle to lose the power of growth, and hence also of geotropic reaction.

Changes of geotropic tone may also be responsible for the absence of torsion in the internodes of *Philadelphus* and *Deutzia* when the pair of leaves at the upper end of the internode are removed[6]. Similarly, Noll[7] observed that the removal of the apex of the inflorescence of an orchid resulted in the neighbouring ovaries undergoing no torsion.

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[1] Kohl, Bot. Ztg., 1900, p. 1.

[2] Miehe, Jahrb. f. wiss. Bot., 1902, Bd. XXXVII, p. 527.

[3] Vöchting, Beweg. d. Blüthen u. Früchte, 1882, pp. 107, 126; Scholtz, Cohn's Beiträge z. Biologie, 1892, Bd. V, p. 371.

[4] Wiesner, Biol. Centralbl., 1901, Bd. XXI, p. 803.

[5] Scholtz, l. c., p. 387.

[6] De Vries, Arb. d. bot. Inst. in Würzburg, 1872, Bd. II, p. 273; Schwendener u. Krabbe, 1892, Ges. bot. Mitth., Bd. II, p. 309.

[7] Noll, Arb. d. bot. Inst. in Würzburg, 1887, Bd. III, p. 368.

SECTION 46. **Changes of Irritable Tone** (*continued*).

The thermonastic and photonastic curvatures produced by changes of illumination or temperature are either the result of indirect changes in the geotropic tone or are due to the action of gravity in producing physiological dorsiventrality in the responding organ. When the latter is the case a response may be shown at first on the klinostat, but when none is shown it still remains to be determined whether the actual curvature involves a labile ephemeral induction or a modification of the geotropic tone. Definite results may be obtained in the future, but it is worthy of note that an increased reaction following a rise in the intensity of the directive agency might merely be the result of its enhanced dorsiventral inductive action. Probably both changes of tone and inductive actions are utilized separately and in various combinations by different plants for special purposes. The increase in the intensity of a diffuse stimulus may modify the tropic action of the same agency. This occurs whenever an increase in the intensity of diffuse illumination or in concentration so alters or weakens the tropic sensitivity to unilateral illumination or to the unequal distribution of a chemical substance that a change of position results.

Instances of the influence of illumination upon the geotropic irritability are afforded by the subterranean runners of *Adoxa moschatellina*, *Trientalis europaea*, and *Circaea lutetiana*, which are diageotropic in darkness, but curve downwards when illuminated, even if already embedded in the soil. The curvature is accelerated in *Adoxa* by the fact that illumination hastens or awakens the growth of the previously darkened runner[1]. It is also owing to a change of their geotropic irritability that the runners and other shoots of a variety of plants become approximately vertical in darkness, but assume plagiotropic to horizontal positions under diffuse illumination of increasing intensity[2]. Illumination also causes a certain geotropic downward curvature of the lateral roots, causing the angle between them and the main root to diminish by about 20° to 30°[3]. Czapek found that this reaction was no longer shown when the apex was covered with tinfoil, so that the tonic stimulus of light is only perceived by the growing apex.

The geotropic angle of the lateral roots is somewhat lessened by a rise of temperature[4], which also affects the geotropic position of certain shoots and leaves. In dorsiventral organs, however, aitionastic curvatures may complicate matters, and it is always possible that changes of the heliotropic tone may be induced by alterations in the diffuse external conditions. No researches have, however, been performed in this direction, although it is certain that not only the phototropic, but also other tropic positions of equilibrium may be more or less modified by the diffuse action of

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[1] Stahl, Ber. d. bot. Ges., 1884, p. 391.

[2] Czapek, Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, Abth. i, p. 1234; Oltmanns, Flora, 1897, p. 24; Goebel, Organography, Vol. I, 1900, p. 93; Maige, Ann. sci. nat., 1900, 8^{e} sér., T. XI, p. 248.

[3] Czapek, l. c., 1895, Bd. CIV, Abth. i, p. 1245; Stahl, l. c., 1884, p. 393.

[4] Czapek, l. c., p. 1251; Sachs, Arb. d. bot. Inst. in Würzburg, 1874, Bd. I, p. 624.

temperature illumination, nutrient and non-nutrient substances, as well as other agencies[1]. The geotropic position of the lateral roots, and in some cases also of the primary root, may change somewhat according to the cultural conditions, but this result is probably of complex origin. When insufficiently supplied with water, however, certain radicles do not curve vertically downwards, but assume a more or less plagio-geotropic position[2]. According to Neljubow, the presence of the acetylene and ethylene of coal-gas in the air around a seedling-stem of *Pisum sativum* causes it also to assume a plagio-geotropic position[3].

The response produced by conjoint stimuli is rarely the sum of their actions when applied singly, even when the power of response remains unaltered, and assuming that both sensations are separately excited and remain distinct until movement is excited. As a matter of fact, it is highly probable that any kind of tropic stimulation affects the tone of the plant and its power of response to other tropic stimuli. The power of response to other stimuli naturally need not be suppressed, and in fact geotropically-excited plants remain capable of response to heliotropic stimuli and vice versa. The energetic response to particular stimuli might, however, render the plant temporarily irresponsive to special tropic agencies, either owing to a temporary suppression of excitability or of the responsive mechanism. In other cases the conditions for the production of a particular irritability might involve preceding tropic excitation. This actually applies to *Cuscuta*, which develops no contact-irritability when rotated on a klinostat, since the required tone needs the inductive action of gravity for its production.

A complete or nearly complete inhibition of one form of irritability by the functional exercise of another has not hitherto been detected, although intense stimulation usually depresses the excitability more or less. Changes of tone may, however, be produced by the combined tropic action of two dissimilar stimulatory substances. In addition, when a radial tendril is touched on both sides the excitations extinguish each other and no response is produced. Such actions may either affect the intermediate stages between sensation and response, or the primary sensation, as in the case of *Cuscuta*. Noll[4] considers changes of tone to be due to the former, and Czapek[5] to the latter, but the arguments of both authors are inconclusive.

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[1] A few additional instances are given by Massart, Sur l'irritabilité d. plantes supérieures, 1902, p. 13; Klebs, Willkürliche Entwickelungsänderungen bei Pflanzen, 1903, p. 93.

[2] Sachs, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 445; Elfving, Beitr. z. Kenntniss der Einwirkung der Schwerkraft auf Pflanzen, 1880, p. 32; Czapek, l. c., p. 1252; Němec, Jahrb. f. wiss. Bot., 1896, Bd. XXXVI, p. 91.

[3] Neljubow, Beihefte z. bot. Centralbl., 1901, Bd. X, p. 128; Singer, Ber. d. bot. Ges., 1903, p. 175.

[4] Noll, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 495; Ueber heterogene Induction, 1892, p. 56.

[5] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 246; Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, Abth. i, p. 337.

The fact that geotropic excitation does not inhibit the heliotropic irritability leaves it undetermined whether the two excitations fuse or proceed to separate motory responses. Teleological considerations lead to the conclusion that the excitations summate so that a single motory response is produced, and positive evidence of this could readily be obtained if the two stimulatory reactions had latent periods of response of very unequal length. According to Müller [1] the respiratory activity decreases during the performance of a geotropic curvature, but the experiments are not altogether satisfactory. The geotropic and heliotropic curvatures of growing organs do, however, occur without any acceleration of the average rate of growth, so that the respiratory activity need not increase. When, however, as in the nodes of grasses, growth is induced by geotropic induction, not only is the power of heliotropic curvature gained but also the respiratory activity of the awakened nodal cells may be raised.

The co-operation of geotropic and heliotropic stimuli in orienting an organ was first observed by Dutrochet and by Mohl, and their interaction was studied in detail by Müller-Thurgau and by Wiesner [2]. Pfeffer [3] pointed out that during such co-operation changes of tone might modify the results observed, and a variety of instances of such action have been subsequently obtained. It is of course possible to invent special terms to indicate the different ways in which changes of tone may be produced, but such terms are quite unnecessary and afford no explanation of the phenomena observed. This applies even to the term 'heterogeneous induction' used by Noll [4], who has unfortunately failed to recognize the general importance of tone and of the changes of tone due to internal and external factors [5]. The discussions of Herbst and of Driesch [6] as to whether special terms are needed when the change of tone is not due to the external conditions, or when it is connected with special responses, are without value.

Exact determinations of the actual relationships are extremely difficult, and hence it is not surprising that Czapek and Noll should have obtained opposite results with seedlings [7]. According to Czapek, geotropic induction does not affect the heliotropic

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[1] N. J. C. Müller, Fünfstück's Beitr. z. wiss. Bot., 1898, Bd. II, p. 267; Arct. Fünfstück's Beitr. z. wiss. Bot., 1903, Bd. V, p. 145.

[2] Dutrochet, Recherches anat. et physiol., 1824, p. 92; Mohl, Vegetabilische Zelle, 1851, p. 140; Müller-Thurgau, Flora, 1876, p. 94; Wiesner, Die heliotropischen Erscheinungen im Pflanzenreich, 1878, I, pp. 55, 63.

[3] Pfeffer, Pflanzenphysiologie, I. Aufl., 1881, Bd. II, p. 338.

[4] Noll, Heterogene Induction, 1892. Cf. also Noll, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 496.

[5] Cf. Pfeffer, Die Reizbarkeit der Pflanzen, 1893, p. 22.

[6] Herbst, Biolog. Centralbl., 1894, Bd. XIV, p. 733; Driesch, Die organischen Regulationen, 1901, p. 19, footnote.

[7] Czapek, Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, Abth. i, p. 372: cf. also Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 271; Noll, Heterogene Induction, 1892, p. 56; Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 494.

irritability, nor heliotropic induction the geotropic irritability, whereas Noll states that heliotropic excitation inhibits the geotropic irritability. Feeble lateral illumination produces a complete, or nearly complete, assumption of the position of heliotropic equilibrium in many organs, the geotropic tendency being easily overcome; but this may be merely the result of a strong development of the heliotropic irritability, coupled with an inherently feeble geotropic irritability. Possibly, however, the geotropic irritability may be partially or entirely suppressed by strong heliotropic excitation in those organs which are especially dependent upon the assumption of appropriate light positions. In any case various tropic responses of roots and other organs, such as those due to hydrotropic and rheotropic actions, appear to take place unaffected by gravity, since the latter may exercise little or no effect upon the position assumed, and is also unable to prevent a traumatropic stimulus producing a complete coil at the growing apex. In addition, Klebs has shown that hydrotropic stimuli readily overcome the heliotropic irritability of *Sporodinia grandis*[1].

SECTION 47. **Minimal Stimuli and the Latent Periods of Induction and Reaction.**

Owing to the varying degrees of irritability in different organs towards the same and to different tropic stimuli, a feeble intensity may act as an excitation in one case, whereas in others a response may be produced only when the stimulus is intense. Zoospores afford instances of the almost complete absence of any latent period, the response to stimuli being shown almost instantaneously, whereas in the case of tropic curvatures the latent period is rarely less than a few minutes, and is often from one-half to several hours in duration.

Once the curvature has begun it continues for a longer or shorter time after the stimulus has ceased to act, and an after-effect may be shown if the stimulus is removed just before the curvature has begun. It follows, therefore, that a perceptible interval of time elapses between perception and response, although it remains an open question whether the delay lies in the progress of the sensory excitation or in the awakening of the motory reaction. When the perceptive and responsive zones are separately localized, the slow transmission of tropic stimuli interposes an additional delay.

A response presupposes a sufficient intensity of excitation, and naturally a stimulus of very short duration may fail to produce any reaction. Since a summation of transient stimuli is possible when they are repeated at definite intervals of time, it is evident that each is perceived, and that its inductive action has not faded away before the next stimulus comes. Wiesner[2] found, for instance, that the hypocotyl of

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[1] Klebs, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 56.

[2] Wiesner, Die heliotropischen Erscheinungen, 1880, Bd. II, pp. 25, 87.

Lepidium sativum, when successively laterally illuminated for one second and darkened for two seconds during a period of twenty-five minutes, performed as strong a heliotropic curvature as when continuously illuminated for the same time from the side. It will probably also be possible by using super-optimal intensities of illumination to produce more rapid curvature by intermittent than by continuous illumination. In Wiesner's experiment the same result was obtained in both cases owing to the fact that the reaction is only increased up to a certain limit by increasing intensities of light. Naturally when the intervals between the successive periods of stimulation are unduly prolonged no response may be shown, although periods of one second of strong illumination and fifteen to thirty seconds darkness ultimately prove effective. A striking instance of the varying degrees of summation is afforded by the sensitive leaflets of various Leguminosae. Thus the leaflets of *Mimosa pudica* fold together fully when alternately exposed to strong sunlight for two seconds and shaded for two seconds, although the movement is slower than under continuous exposure. If for two seconds in sunlight and four seconds in the shade in regular succession, the leaflets rise up through angles of 15° to 20° only, while under alternating periods of one second exposure and ten seconds shade the leaflets remain fully expanded[1]. If an opaque wheel with an indented rim is rotated between the object and the source of illumination, the alternating periods of exposure and darkness may be made excessively short, but nevertheless a response is still shown if the light is sufficiently intense, so that the shortest flash of light can be perceived by the plant.

Similar summation appears to be possible in all the tropic reactions hitherto investigated. Noll[2] found, for instance, that geotropic induction lasting for five minutes produced no effect, but that a curvature was induced when for three hours the seedling was placed alternately horizontally for five minutes and vertically for twenty-five minutes. It can, indeed, hardly be doubtful that a feeble continuous tropic stimulus which is unable to produce any perceptible response is, nevertheless, perceived as a feeble sensory excitation, which is incapable of overcoming the autotropic tendencies and self-regulatory activities of the organism.

Minimal stimuli. The minimal intensities of light required to produce a heliotropic response have been investigated by Darwin, and subsequently by Wiesner and Figdor[3], who placed the plant in a dark room at varying distances from a candle-flame. Under favourable conditions Figdor found that the sensitive hypocotyls of

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[1] Ewart, The Effects of Tropical Insolation, Annals of Botany, 1897, Vol. XI, p. 449.

[2] Noll, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 463. Cf. also Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 206; Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, Abth. I, p. 1217; Darwin and Pertz, Annals of Botany, 1892, Vol. VI, p. 245; 1903, Vol. XVII, p. 93; Jost, Biol. Centralbl., 1902, Bd. XXII, p. 175.

[3] Darwin, The Power of Movement in Plants; Wiesner, Die heliotropischen Erscheinungen, 1878, Bd. I, p. 40; Figdor, Sitzungsb. d. Wien. Akad., 1893, Bd. CII, I, p. 45.

Lepidium sativum and *Lunaria biennis* responded heliotropically to light of intensity equivalent to 0·0003 of a standard candle, those of *Helianthus annuus* and *Mirabilis jalapa* to an intensity of 0·016 of a standard candle, whereas the etiolated shoots of *Salix* required an intensity of 10·16 units, and still stronger lateral illumination is necessary to produce a perceptible heliotropic curvature in less sensitive plants.

It is, therefore, not impossible that plants may be capable of a heliotropic response to bright moonlight[1], and they are able to detect and react to differences of illumination imperceptible to the human eye. The strongest action is exercised by the blue and violet rays, as well as by the ultra-violet rays, so that in this respect also the photic sensitiveness of the plant surpasses that of the human eye. In addition, the most sensitive plants may show a heliotropic reaction under an intensity of illumination which produces no perceptible browning in a sensitive chloride of silver paper[2]. Wiesner has shown the importance of eliminating the action of gravity, and as well as that the sensitivity varies according to the cultural conditions[3].

The *geotropic irritability* also varies greatly, as can be shown by substituting varying centrifugal forces. In this way Czapek[4] found that sensitive radicles and seedling-stems performed slight curvatures in response to a centrifugal force equivalent to 0·001 g. The extreme sensitivity of certain tendrils to contact-stimuli has already been discussed, and comparatively slow currents of water may excite a rheotropic curvature. The power of many micro-organisms of responding to the presence of the minutest traces of stimulatory substances is in part correlated with their minute size, but it also indicates a high degree of sensitivity.

Reaction and induction periods. The most rapid tropic responses appear to be shown by tendrils, for a curvature may become perceptible five to twenty seconds after stimulation. The pulvini of *Lourea vespertilionis*[5], and of a few other plants, show the commencement of a heliotropic reaction within one minute, and under favourable conditions the sporangiophores of *Phycomyces* may begin to curve towards the light in one to three minutes[6]. Usually, however, the time required to produce a heliotropic reaction is at least seven to fifteen minutes even in the case of very sensitive objects such as the seedlings of *Phalaris*, *Avena*, and *Sinapis*, while more than an hour is required by the strongly reacting seedling-stem of *Vicia sativa*[7]. The time required for a heliotropic reaction appears, however, to be shorter, on the whole, than that required for a geotropic reaction, which appears never to be less than twenty to thirty minutes[8].

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[1] Musset, Compt. rend., 1890, T. CX, p. 201. Cf. Bay, Bot. Ztg., 1891, p. 178.

[2] Wiesner, Sitzungsb. d. Wien. Akad., 1893, Bd. CII, I, p. 347; Bot. Centralbl., 1897, Bd. LXIX, p. 305.

[3] Wiesner, Die heliotropischen Erscheinungen, 1878, Bd. I, p. 54; cf. also Figdor, l. c., p. 58; Oltmanns, Flora, 1892, p. 231.

[4] Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 307; 1898, Bd. XXXII, p. 190.

[5] Cf. Pfeffer, Periodische Bewegungen, 1875, p. 63. The leaflets of *Mimosa* and other Leguminosae may begin to fold up one or two seconds after strong sunlight has fallen upon them. Ewart, The Effects of Tropical Insolation, Annals of Botany, 1897, Vol. XI, p. 449.

[6] Cf. Oltmanns, Flora, 1897, p. 11.

[7] Darwin, The Power of Movement in Plants; Wiesner, Die heliotropischen Erscheinungen, 1878, Bd. I, p. 37; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 185.

[8] Cf. Czapek, l. c., p. 184; Darwin, l. c., p. 422; Sachs, Flora, 1873, p. 321.

The time required for induction is naturally shorter than that necessary for the commencement of a reaction to constant stimulation[1], for, if the latter ceases before the reaction begins, an after-effect resulting in a response is shown. Thus Czapek found that the length of the geotropic induction period was twenty minutes at 25° C. in the case of various radicles, whereas the time of reaction was thirty minutes[2]. Czapek found no shorter geotropic induction period than fifteen minutes, whereas the heliotropic induction period of sensitive seedlings lies between seven and twenty minutes, and in the case of the epicotyl of *Phaseolus* is as long as fifty minutes. The relative lengths of the induction and reaction periods probably vary somewhat even in the same plant according to the external conditions.

It is evident, therefore, that a sensory excitation begins the moment the stimulus is applied, and reaches a maximal value in a longer or shorter time under continuous stimulation. In addition, a curvature would be perceptible sooner were it not for the delay in bringing the motor mechanism into play. It is mainly for this reason that freely motile organisms are capable of rapid response, for here the excitation merely modifies a pre-existent activity.

After-effects. If the stimulus acts longer than the minimal induction period, the after-effect is naturally increased. Sachs[3] found that if a negatively geotropic stem was placed horizontally until a curvature just began it continued to curve strongly when placed vertically, and the after-effect lasted from one to three hours. Similar results were obtained by Müller and Wiesner[4] by heliotropically stimulating seedlings until curvature just began. An after-effect is probably never entirely absent, though it is not always pronounced. Freely motile organisms, for instance, on the removal of a phototactic stimulus progress for a moment in the original direction. It was probably owing to the result of the mode of experimentation adopted that Sachs was unable to obtain any after-effects in roots, for Czapek found that they showed after-effects extremely well[5]. The amount of the after-effect is, however, not directly proportional to the intensity and duration of the induction, although in general the after-effect is increased by prolonged exposure in the case of objects showing marked reactions[6]. Various other after-effects are known, both periodic and non-periodic; but these are discussed in connexion with growth, daily periodicity, and heredity.

SECTION 48. **The Relation between the Intensity of Stimulus and the Resultant Excitation.**

In general an increase in the intensity of the stimulus produces a greater excitation, enlarging the amplitude of movement, and at the same time shortening the times of induction and reaction. The relationship, however, is by no means a simple one, and cannot be represented by

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[1] Cp. Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 183.

[2] Czapek, l. c., p. 184; in regard to the nodes of *Tradescantia* cf. Kohl, Bot. Ztg., 1900, p. 19.

[3] Sachs, Flora, 1873, p. 325.

[4] Müller, Flora, 1876, p. 89.

[5] Wiesner, Die heliotropischen Erscheinungen, 1878, Bd. I, p. 61, and 1880, Bd. II, p. 87.

[6] Sachs, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 472.

any general formula. Apart from other considerations, this is bound to result from the fact that increases of temperature, illumination, or of chemical action may deaden or inhibit sensation and motility, and may finally produce death. Even within moderate limits the intensity of the stimulus may modify not only the sensitivity and power of reaction, but also the time of reaction and the ultimate position of equilibrium. Thus intense unilateral illumination causes the positive phototaxis of swarm-spores to become negative, and varying intensities of light suffice to convert the positively heliotropic reaction of many rooted plants, and even of their radial organs, into a plagiotropic or negatively heliotropic one. Similar changes of reaction are known in the case of thermotropic, chemotropic, hydrotropic, and galvanotropic stimuli. In addition, increasing intensities of centrifugal action produce a lessening of the geotropic angle of the lateral roots[1], and cause in diageotropic rhizomes an inward curvature, so that if the mass of the earth were suddenly increased they would curve downwards[2]. These responses are physiological in character, although intense centrifugal action may produce purely mechanical curvatures. An already stimulated organ is less responsive than an unstimulated one, and hence, to produce a perceptible increase in the reaction, the stimulus must be increased by a greater amount than suffices in the first instance for the primary reaction. This applies not only to tropic but to other forms of irritability, and to animals as well as to plants. Weber's law is, in fact, of general application, for in plants also a definite relation exists between the intensity of an existent stimulus and the additional intensity required to produce a perceptible reaction[3]. For instance, man can detect changes of illumination of not less than one-hundredth of the existing intensity, while in the case of *Phycomyces* the change must be at least one-fifth. Thus this fungus under diffuse illumination equivalent to five units will show a heliotropic curvature when exposed to an increase of illumination of one unit on one side, whereas in diffuse light of 100 units intensity an increase on one side of twenty units will be necessary.

That the excitation increases less rapidly than the stimulus producing it was shown by Sachs, Elfving, and Schwarz, in regard to geotropic, and by Wiesner in regard to heliotropic stimuli[4]. Pfeffer's[5] researches on chemotactic irritability then

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[1] Cf. Sachs, Arb. d. bot. Inst. in Würzburg, 1874, Bd. I, p. 607. Cf. also Pfeffer, Pflanzenphysiologie, 1881, Bd. II, p. 334; Elfving, Beitrag zur Kenntniss d. Einwirkung der Schwerkraft auf die Pflanzen, 1880, p. 33 (reprint from Acta Soc. Scient. Fennic., Bd. XII); Schwarz, Unters. a. d. bot. Inst. zu Tübingen, 1881, Bd. I, p. 80.

[2] Czapek, Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, p. 1233.

[3] For details see Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 395.

[4] Wiesner, Die heliotropischen Erscheinungen im Pflanzenreiche, 1878, Bd. I, and 1880, Bd. II.

[5] Pfeffer, Ber. d. bot. Ges., 1883, p. 524; Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 395; 1888, Bd. II, p. 633.

established the application of Weber's law to plants, and its extension to the chemotropism of fungi and pollen-tubes was shown by Miyoshi, to phototropism by Massart, and to geotropism by Czapek[1].

Pfeffer placed freely motile organisms in water or in solutions of stimulatory materials, and determined the excess concentration required in capillary tubes to produce a chemotactic attraction. In the case of the sperms of Ferns[2], the liquid in the tube must contain thirty times as much malic acid as that outside, and in the case of *Bacterium termo*[3], about three to four times as much meat-extract as in that outside. Thus 0·001 per cent. of meat outside requires at least 0·003 per cent. inside, and 1 per cent. outside needs 3 per cent. inside the tube to produce a chemotactic attraction of the bacterium used. Miyoshi found that a five times greater concentration was required to attract pollen-tubes, and a ten times greater concentration to produce a chemotactic attraction in the case of *Saprolegnia*.

Massart[4] placed the sporangiophores of *Phycomyces* between two constant sources of illumination, and determined at what relative distances from the two sources a curvature was just produced. Since the intensity of the light is inversely proportional to the square of the distance, it is easy to calculate how much more strongly one side must be illuminated than the other to produce a heliotropic curvature. A difference of illumination of one-fifth was found to be necessary; so that plants are less sensitive than man, who is able to detect a difference of illumination of one-hundredth. We are, however, only able by our sense of touch to detect increases or decreases of weight of one-third, and similar relationships hold good in regard to our sense of smell and of warmth. It must, however, be remembered that in the case of the plant our only evidence of perception is an actual response, and that a feeble stimulus might be perceived but not be able to excite any curvature.

Not only may the diffuse action of light or of chemical substances weaken the tropic irritability, but also the performance of a response may have the same effect. This is shown by the fact that as a tropic stimulus increases in intensity the time of reaction is at first rapidly but subsequently slowly shortened. Thus Czapek[5] found that the time of reaction of a root of *Lupinus* exposed to centrifugal action equivalent to 0·001 and to 1 g. fell from six hours to one-and-a-half hours, but only decreased to forty-five minutes when the centrifugal force rose to 40 g. The times of induction afford, in fact, an indication of the relationship between the excitation and the intensity of the stimulus. Diffuse and tropic actions probably do not influence the excitability in precisely the same way; but no investigations have

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[1] Miyoshi, Bot. Ztg., 1894, p. 21; Flora, 1894, p. 81; Massart, La loi de Weber, etc. Bull. de l'Acad. royale de Belgique, 1888, 3e sér., T. XVI, No. 12; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 191; 1895, Bd. XXVII, p. 305.

[2] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 397.

[3] Pfeffer, l. c., 1888, Bd. II, p. 634. The fact that the stimulation of bacteria is due to phobochemotaxis is immaterial.

[4] Id. Massart used the light reflected from a single lamp by a pair of mirrors at varying distances.

[5] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 191; 1895, Bd. XXVII, p. 305.

been made in this direction, and it is often difficult to raise the intensity of a tropic stimulus without increasing its diffuse action.

Similar relationships hold good for non-tropic stimuli, although in many cases the diminished excitability under increasing intensity of stimulation is accompanied by special peculiarities[1]. Growth and other functions, under rising temperatures, or increasing aeration or nutrition, increase at first rapidly and then more slowly as the optimum is approached. Precisely similar curves are given by the action of unnecessary or poisonous substances, and, in fact, every agency when sufficiently intense produces a lessened response or excitation. Similarly, movements which alter with increasing stimulation may be represented by angular curves. The apex of the curve does not correspond to the optimum point on a growth-temperature curve, since beyond it the response is reversed instead of continuing of like kind but lessened quantity[2].

Considering the complicated nature of the reactions involved, it is hardly surprising to find that the relationship between the intensity of the stimulus and the degree of excitation should show many divergences[3] from Weber's law, according to which the stimulus must increase in geometric procession to produce an arithmetical progression of the excitation, or, in other words, that the excitation is proportional to the logarithm of the stimulus[4]. In accordance with the logarithmic curve, the excitation at first increases rapidly when the minimal intensity of stimulation is passed, but subsequently more slowly with equal increases of intensity. In regard to plants, there can be no doubt that the phenomenon is a physiological one, although Fechner considered it to be of psychic origin in the case of man. It is, therefore, inadvisable to use the term 'psycho-physical law' as was done by Fechner. In spite of this, however, the comparative effects of the receipt of a shilling upon a pauper and upon a millionaire may be used as an explanatory illustration.

As in other cases, the change of tone with increasing intensity of stimulation is undoubtedly the result of a modification of the power of sensation, and if this has no effect upon another stimulatory reaction, it is evident that the two stimuli act upon different sensory mechanisms[5]. This applies more especially to chemotropic excitations, and Rothert[6] has, in fact, shown that the attractive actions exercised upon *Amylobacter* by meat-extract and by ether involves different powers of sensation, for the attractive action of meat-extract is unaffected by the presence of 1·6 per cent. of ether inside and outside the capillary.

A change of tone in a particular irritability may, however, also arise from stimulation involving an entirely dissimilar sensory perception, and hence direct conclusions can only be made with caution from changes of tone. The chemotropic action of malic acid upon the sperms of Ferns is weakened in solutions already

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[1] See Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, pp. 406, 506, 521; Correns, Flora, 1892, pp. 107, 150.

[2] On Phobophototaxis cf. Rothert, Flora, 1901, p. 401.

[3] According to Mendelssohn (Centralbl. f. Physiol., 1903, Bd. XVII, p. 11), the thermotropic excitation is proportional to the temperature.

[4] Cf. Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 401 seq., and 1888, Bd. II, p. 638.

[5] Cf. Pfeffer, l. c., 1888, Bd. II, p. 648.

[6] Rothert, Flora, 1901, p. 387.

containing this acid or maleic acid, so that both probably effect the same sensation[1]. The same conclusion applies in the case of bacteria, when the attractive action of dextrin is equally lowered in solutions of dextrin and of meat-extract[2]. Various bacteria are attracted by potassium-salts, meat-extract, and other substances in a similar manner, whereas the attractive action of oxygen is shown only in the case of certain forms, and appears to depend upon the development of a special sensory excitability. When different stimuli excite the same response, we must, in the first instance, presuppose the existence of dissimilar sensory perceptions, which in other cases may be singly developed.

SECTION 49. **The Conditions for Stimulation and its Progress.**

In parallelotropic and plagiotropic organs the conditions for stimulation are given when the organ is displaced from its normal position. When a parallelotropic organ is inverted, however, slight autotropic curvatures cause one side to be more stimulated than the other, and the organ curves more and more rapidly out of the labile inverted position of equilibrium into a normal stable one. In all cases the tropic stimulation results from the unequal application of the external agency, and none is exercised when the latter is uniformly distributed or acts equally in all directions. Hence a plant placed between and equidistant from two equal sources of illumination would show no heliotropic curvature, and the same would be the case in a geotropic root placed between two planets exercising the same mass-attraction upon it.

Tropic irritability, therefore, depends upon a power of differential sensation, that is a power of detecting differences in the intensity of the exciting agency[3] or in its direction of application, although the detailed mode of response may vary according to the irritability affected, and, in fact, unilateral illumination may exercise more than one kind of orienting action. Indeed, certain organisms may respond to differences in the intensity of the illumination, others to the direction of the incidental rays, while the action of gravity can only be of the latter character, since its intensity is the same at all points inside and outside an organ.

Although the conditions are simpler in radial organs than in dorsiventral ones, Loeb is incorrect in supposing that symmetrically disposed points are exposed to equal intensities of the orienting agency when a radial organ has assumed its proper orientation[4]. The assumption of a new tropic position by an organ in response to displacement always

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[1] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 397.

[2] Id., 1888, p. 635.

[3] Cf. Pfeffer, Pflanzenphysiol., 1. Aufl., Bd. II, p. 329, u. Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 477. Nagel (Bot. Ztg., Ref., 1901, p. 297) has no grounds for supposing that only phobotactic organisms possess a discriminatory sense.

[4] Loeb, Pflüger's Archiv f. Physiologie, 1897, Bd. LXVI, p. 441; Vergleichende Gehirnphysiologie, 1899, p. 4.

involves a certain change of tone, which, however slight, must inevitably result from the altered conditions. Noll's objections to this conclusion are based upon a one-sided consideration of the external relationships[1]. It is, in fact, true that a lowered heliotropic sensibility results either from a general increase of illumination or from an increase of illumination parallel to the long axis of a parallelotropic organ. As an instance of such action it may be mentioned that Hering found a general retardation of growth in length to occur in inverted plants or organs, and similarly the growth excited in the node of a grass by the diffuse horizontal action of gravity is inhibited by the parallelotropic action of gravity. Tropic stimuli often exercise more than one effect, so that the resultant position may be due to the co-operation of two or more activities, as, for instance, in the plagiotropic prothallia of Ferns, where the continuance of the labile dorsiventral induction affords at the same time an instance of the maintenance of a special tone appropriate to the position assumed. The tropic excitation due to a change of position usually rapidly increases to a certain limit, as the angle of divergence from the normal position increases. In the case of parallelotropic organs the maximal angle of divergence from the normal position is 180°, but in that of plagiotropic organs not more than 90°. The maximal excitation in the case of certain parallelotropic organs, and possibly of all, is not reached until the divergence is greater than 90° C., but it is quite possible that in some cases the tropic excitation may be greater when the organ is at right angles to the orienting agency, as was, in fact, concluded to be the case by Sachs, and also by Bateson and Darwin[2]. This view is supported by Massart[3], but Elfving, on the other hand, supposed that the maximal geotropic excitation is exercised when the main root is inverted[4]. It is, however, quite certain that the geotropic stimulus is not directly proportional to the sine of the angle of divergence, i.e. to the component of the force of gravity acting at right angles to the stem, although an approximate correspondence may be shown when the divergences are small. Czapek[5] found, however, that the maximal geotropic action was exercised when all the parallelotropic organs examined by him were diverted from their normal positions through angles of 140° to 160° C. The increase of excitation was evidenced in the first instance by the rapidity of reaction.

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[1] Noll, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 487. Cf. Pfeffer, Die Reizbarkeit d. Pflanzen, 1893, p. 19; Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. I, p. 476; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 195; G. Haberlandt, Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 468; Noll, Ber. d. bot. Ges., 1902, p. 416.

[2] Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 240; Flora, 1873, p. 325; Bateson and F. Darwin, Annals of Botany, 1888, Vol. II, p. 65.

[3] Massart, Sur l'irritabilité d. plantes supérieures, 1902, p. 28.

[4] Elfving, Beiträge z. Kenntniss der Wirkung d. Schwerkraft auf Pflanzen, 1880, p. 32.

[5] Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, pp. 283, 297; 1898, Bd. XXXII, p. 193.

Thus roots slowly responded to a displacement of as little as 2° C., and more rapidly to one of 20° C. An increased divergence beyond this did not further accelerate the reaction, but nevertheless, after equally long periods of geotropic induction, the most pronounced after-effects were shown by roots placed at angles of 140° to 160° C. to their normal positions. Using the same method, Pertz[1] was able to show that the node of a grass-haulm experienced a negatively geotropic excitation when the stem was inverted and reverted for equal lengths of time, while maintaining the same angle with the horizontal. Czapek found that beyond angles of 140° to 160° C. the excitation again decreased, until a labile position of equilibrium was reached in a precisely inverted position, so that when placed on a klinostat no geotropic after-effect was shown if the root or stem had been prevented from diverging from the vertical position during its exposure to the action of gravity[2]. Under natural conditions an inverted root always makes slight autonomic curvatures from the vertical, which render possible a geotropic excitation leading to the return to the normal direction of growth.

If the apex of a shoot is fixed in a horizontal position, and the base left free to move, the negatively geotropic reaction of the active zones causes it to curve upwards, but no reaction is shown if the apex is bent upwards into a vertical position. When the apex is fixed, however, in an inverted vertical position, the circumnutation of the free portion renders geotropic excitation possible, so that the free end bends upwards. If the apical segment of a horizontally-placed shoot is fixed at the middle of the active zones both the free ends curve upwards[3]. If, however, the apex of a root is fixed in a normal vertical position, the free basal portion performs no curvature since the apex alone is capable of perception, whereas when the apex is fixed in a horizontal position the free portion curves continually owing to the continuous excitation, just as when the tip of a cotyledon of *Panicum* is held in a horizontal position.

Diageotropic rhizomes behave in a similar way, but respond more rapidly to an upward displacement than to a downward one of similar extent[4]. The radial lateral roots of the first order behave similarly, and hence if a lateral root is displaced and then slowly rotated, it assumes its proper position, owing to the fact that it is more strongly excited during the upper phase than during the lower one[5]. The excitation increases

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[1] Pertz, Annals of Botany, 1899, Vol. XIII, p. 620.

[2] Czapek, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 291; Ricôme, Compt. rend., 1903, T. CXXXVII, CCIV.

[3] Cf. Frank, Beiträge z. Pflanzenphysiologie, 1868, p. 80; Noll, Heterogene Induction, 1892, p. 22; Hochreutiner, Actes du Congrès Botanique de Paris, 1900, p. 39; Massart, l. c., 1902, p. 31.

[4] Czapek, Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, I, p. 1231.

[5] Czapek, 1895, l. c., p. 1213; Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 244. Cf. also Schober, Bot. Ztg., 1897, p. 7.

steadily with progressive upward or downward displacement, and attains a maximal value when the upward displacement reaches about 90° C., so that the angle with the perpendicular is one of 150° to 160° C., which is about the same as that which produces the maximal geotropic excitation of a parallelotropic main root. In vertical positions the lateral roots behave similarly to diageotropic rhizomes, being in a condition of labile equilibrium both when the apex points vertically upwards and when it is directed vertically downwards. It does not, however, follow that all plagiotropic organs will behave similarly. Dorsiventral organs also have only one position of stable equilibrium, and it appears that the geotropic excitation does not increase with equal rapidity when they are inclined upwardly and downwardly[1].

SECTION 50. **Perception and Response.**

Even if the geotropic excitation proves to be due to the sinking of the denser particles in the cells, we should only have found the internal stimulus and should be as far as ever from understanding the mode of physiological perception. The same applies when galvanotropism is found to be due to the electrolytic action of the current producing the conditions for chemotropic excitation[2], or if the unilateral illumination were found to create changes of surface-tension which acted as the immediate agencies in producing a heliotropic curvature. Changes in the configuration of the protoplasm may also be of importance in inducing a particular movement or in enabling it to be performed, but they give no insight into the mode of perception. Local accumulations of the protoplasm are also often merely the result of a realized curvature, or are accessory to the reaction.

Kohl and Wortmann have actually observed accumulations of the protoplasm on the concave sides of organs performing geotropic, heliotropic, and thigmotropic curvatures[3]. Elfving[4] has, however, shown that the accumulation follows the curvature, and is also produced as the result of forcible bending, so that it is possibly the mechanical result of the hindrance interposed to the movement of the protoplasm. Wortmann[5] assumed that in multicellular organs performing tropic curvatures the protoplasm travelled to the concave side and largely accumulated there, but Noll and Kohl[6] have shown that this is not the case.

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[1] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 195.

[2] See Ewart and Bayliss, Phil. Trans., 1905.

[3] Kohl, Bot. Hefte von A. Wigand, 1885, Bd. I, p. 161; Wortmann, Bot. Ztg., 1887, p. 803; 1888, p. 469; 1889, p. 491.

[4] Elfving, Zur Kenntniss d. Krümmungserscheinungen, 1888, Sep. a. Öfversigt af Finska Vet. Soc. Förhandlingar, Bd. XXX; Bullot, Ann. de la Soc. belg. de Microscopie, 1897, Bd. XXXI, p. 71; Mitschka, Ber. der bot. Ges., 1897, p. 164. Cf. also Noll, Flora, 1895, Ergzbd., p. 38; Haberlandt, Oestreich. bot. Zeitschr., 1889, p. 5.

[5] Cf. Godlewski, Bot. Centralbl., 1888, Bd. XXXIV, p. 83.

[6] Cf. Noll, l. c., and Arb. d. bot. Inst. in Würzburg, 1888, Bd. I, p. 531; Kohl, Die Mechanik der Reizkrümmungen, 1894, pp. 27, 35.

In certain cases at least a tropic excitation may be produced without the direct co-operation of the nucleus, and presumably the ectoplasmic membrane plays a prominent part in the perception of tropic stimuli[1]. Streaming cells in which only the peripheral layer of protoplasm is at rest may be capable of a tropic response, but this is not an entirely satisfactory proof that the perception is solely due to the peripheral membrane, since an altered configuration of the streaming protoplasm may be maintained by the continued action of a tropic stimulus in spite of the regular change. The chloroplastids in a streaming cell of *Elodea* are, indeed, capable of phototropic orienting movements in spite of their circulation around the cell. Contact-stimuli naturally primarily affect the ectoplasmic membrane, and cells are capable of tropic response when the protoplasm is reduced to a thin layer of ectoplasm, while cilia composed solely of ectoplasm perceive stimuli. None of these facts, however, affords any conclusive proof of the localization of irritability in the peripheral layer, and as a matter of fact the whole of the cytoplasm is irritable and capable of reaction. Probably the different parts, including the nucleus, commonly co-operate in perception and response, or in the former alone. The ectoplasmic membrane is only relatively a permanent structure, and its irritability is undoubtedly not alike in all cases.

Both plagiotropic and parallelotropic orientation may result from a single tropic perception, in spite of the assumption of Sachs and de Vries that a plagiotropic response to a single orienting agency must always be due to the antagonism of opposing tendencies to movement. The fact that an autogenic or aitiogenic conversion of a positive into a negative tropism is possible does not show that the cells and tissues contain both negatively and positively reacting elements, as was supposed to be the case by Wiesner[1]. Even when the orientation is due to two separate stimuli these may fuse to a single impulse and excite only one tendency to movement. A change in the degree of sensitivity may or may not affect the tropic position assumed in response to the conjoint action of two orienting agencies. Czapek formerly considered the plagiotropism of lateral roots and of diageotropic rhizomes to result from the co-operation of their positive and transversal geotropism[2], but now considers that their plagio-geotropic position is assumed in response to a single tropic excitation. Czapek's arguments are mainly based upon the dissimilar behaviour of roots bent upwards and downwards through equal angles, and upon the increase of the positively geotropic movement on exposure to rising

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[1] Wiesner, Die heliotropischen Erscheinungen, 1880, Bd. II, p. 21. Cf. Pfeffer, Osmotische Untersuchungen, 1877, p. 211.

[2] Czapek, Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, 1, p. 1257. Cf. Noll, Sinnesleben d. Pflanzen, 1896, p. 86 (reprint from Ber. d. Senkenberger naturforsch. Ges. in Frankfurt).

intensities of centrifugal action. Sachs is evidently incorrect in supposing the lateral roots to be only very feebly geotropic, since when bent downwards they soon curve back to their proper plagio-geotropic position[1].

Our knowledge of the human eye or ear affords a good instance of how the most intimate familiarity with the structure and localization of the organs of perception fails to reveal the processes of sensation and perception. Even if the electrical vibrations which we call light excited syntonic electrical surgings in the rods and cones of the retina with whose length their wave-length harmonizes, and even if the fibres of Corti's organ resonated to the sound-waves travelling in the lymph of the inner ear, we should still have advanced no further than when we found that the curvature of a tendril was induced by the pressure of discrete particles upon the sensitive epidermis. Hence, to speak of the heliotropic organs as forming a field of heliotropic sense, and the geotropic ones as forming one of geotropic sense, is simply to clothe facts already known in a new dress, which does not conceal our ignorance concerning their intimate causation. Noll's[2] attempts to elaborate stimulatory fields in cells or tissues, which would theoretically produce the results actually observed, are devoid of scientific value, and are in the first instance based upon the untenable assumption that the orientation of the organ is directly dependent upon the position of the supposed stimulatory fields in regard to the direction of the orienting agency. Discussions of this kind, based on supposed physical analogies, are usually highly misleading. It is possible to make mechanical arrangements which will assume definite positions of equilibrium according to the direction of incidence of light, gravity, or of contact-stimuli, and which will return to the same position when disturbed; but no direct conclusions can be made upon a basis of this kind as to the mode of orientation in the living organism. In other words, mechanical models may serve to direct attention to vital phenomena, but afford no explanation of them in the absence of any proof of a similarity of mechanism.

SECTION 51. **Instances of Specific Tropic Irritability.**

THIGMOTROPISM affords a very good instance of the localization of irritability, since a gentle touch which is insufficient to produce any perceptible deformation in the epidermal cells stimulates the peripheral layer of protoplasm and creates an excitation which spreads to the opposite side. Diffuse contact on all sides does not excite the transitory accelera-

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[1] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 248.

[2] Noll, Heterogene Induction, 1892, p. 18; cf. also Fitting, Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 619.

tion of growth which accompanies curvature, and this applies not only to radial but also to physiologically-dorsiventral tendrils. In the latter case, therefore, both sides are sensitive to contact, but in different ways, for only stimulation of the concave side is able to produce a curvature. Further research is, however, necessary to elucidate this phenomenon and to determine wherein the difference between the two surfaces lies.

RHEOTROPISM, TRAUMATROPISM, and HYDROTROPISM have already been shown to be special irritabilities involving distinct powers of perception.

GEOTROPISM. Gravity and centrifugal force probably act indirectly, the changes of pressure or of the position of the parts in the cell due to their altered direction acting as the stimulus exciting curvature. That the pressures external to the cell are immaterial is shown by the fact that unicellular organisms show geotropic responses, and that a root will curve down into mercury against an upward pressure. It is, however, uncertain whether the pressure of the fluid or of the solid contents of the cell acts as a stimulus, and it does not follow that the relationships are the same in all organisms, or that plants must behave in the same way as certain lower animals whose perception of and orientation in regard to gravity appear to be due to the pressure exercised by solid bodies such as statoliths and otoliths in special 'auditory' sense-organs.

By the term geotropism we merely indicate the power of response to a particular tropic stimulus, and hence the same term would still be used if this form of irritability proved to be due to some kind of internal contact stimulation[1]. In the same way the term magneto-tropism would be used if a tropic response was produced by the action of a magnet upon internal particles of iron or upon the substances of varying magnetic permeability of which the plant-cell is composed[2]. As a matter of fact, plants, like man, seem to be devoid of any direct power of perception of gravitational forces.

Knight[3] was probably the first to suggest that geotropic curvatures were caused by the distribution of materials of varying specific gravity in the plant, although according to Treviranus the same idea was previously put forward by Astruc[4]. Knight, however, seems to have assumed that the mass-attraction of gravity directly produced a downward plastic curvature of the root, and was unaware that the root will grow downwards in mercury or against considerable resistances. Negative geotropism Knight considered to be the result of the denser nutrient sap collecting on the under side of the horizontally-placed stem, causing this side to grow more rapidly and hence producing an upward curvature of the apex. Hofmeister[5] accepted this

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[1] Cf. Verworn, Allgemeine Physiologie, 1901, 3. Aufl., p. 467.

[2] Cf. Ewart, On Protoplasmic Streaming in Plants, Clar. Press, 1903, p. 45.

[3] Knight, Phil. Trans., 1806, Pt. I, p. 104.

[4] Treviranus, Physiologie, 1838, Bd. II, p. 599.

[5] Hofmeister, Allgemeine Morphologie, 1868, p. 629.

view of Knight's, and considered that the positive geotropism of the root was due to the *less* dense nutrient materials collecting on the upper side of a horizontally-placed main root and favouring the growth of this side. On this assumption it is difficult to see how the nutrient materials would reach the apex of the root when vertical.

The theories of Traube and of Cisielski[1] were mainly based upon observations made on precipitation membranes. Their general trend was that the tensions due to mass-attraction, and the thickening of the walls due to more favourable nutrition, were responsible for both negative and positive geotropism. Dutrochet[2] endeavoured to explain the phenomena as being due to the co-operation of endosmotic actions with the tissue-strains, and with the distribution of nutrient materials resulting from anatomical considerations and their relative densities. Mohl and Hofmeister[3] showed, however, that anatomical structure has nothing to do with geotropic irritability, but all these authors failed to recognize that gravity and also light acted merely as exciting stimuli.

It is only necessary to clothe these mechanical views of Knight, Dutrochet, and Hofmeister in a modern dress[4] by supposing that the moving materials act as stimuli instead of nutritively to arrive at the recent hypotheses of Berthold, Noll, Němec, and Haberlandt[5]. These authors agree in supposing that the physical sinking of the denser bodies in the cells, and the changes of pressure thereby produced, act as the immediate causes of the tropic excitation. If analogy is any guide, it seems, however, more probable that the excitation is the result of an internal contact-stimulus. Possibly the strong thigmotropic excitability of the ectoplasmic membrane in the epidermal cells of tendrils is transferred to the endoplasmic membrane on the side walls of the cells in parallelotropic organs, and to the membrane on the end walls in plagiotropic ones. In the vertical and horizontal positions the hydrostatic pressures on the end and side walls of an elongated cell alter slightly, but it is not easy to see how these changes could act as the stimulating actions regulating geotropic curvatures, nor how they could mechanically affect growth as Sachs suggested[6]. The maximal differences of hydrostatic pressure in the longest root-cells are extremely small, and in virtue of Weber's law they cannot possibly produce any

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[1] Traube, Bot. Ztg., 1875, p. 67: cf. Pfeffer, Osmot. Unters., 1877, p. 215; Cisielski, Cohn's Beiträge z. Biologie, 1872, Bd. II, Heft 2, p. 23.

[2] Dutrochet, Ann. sc. nat., 1833, 1re sér., T. XXIX, p. 413; Mémoires, etc., Bruxelles, 1837, p. 292.

[3] Hofmeister, Jahrb. f. wiss. Bot., 1863, Bd. III, p. 178.

[4] Pfeffer, Period. Bewegungen, 1875, p. 147.

[5] Berthold, Protoplasmamechanik, 1886, p. 73; Noll, Heterogene Induction, 1892; Němec, Ber. d. bot. Ges., 1900, p. 241; 1901, p. 310; Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 80; Ber. d. bot. Ges., 1902, p. 339; Haberlandt, Ber. d. bot. Ges., 1900, p. 261; 1902, p. 189; Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 447. A summary is given by Jost, Biol. Centralbl., 1902, Bd. XXII, p. 161.

[6] Pfeffer, Period. Bewegungen, 1875, p. 149.

perceptible excitation, since they merely add to or subtract from the enormously greater internal osmotic pressure[1]. Noll has recently suggested that the centrosphere with its centrosome may act as the percipient organ for detecting the direction of gravitational stimuli, but the fact that the centrosphere and centrosome do not appear to be permanent organs of the cells of flowering plants suffices to show the danger of putting forward hypotheses unsupported by experimental evidence[2].

Any local discrete pressure produced by the accumulation of the starch-grains or other bodies might act as an internal stimulus, and the deformations and changes of configuration due to the rearrangement of the denser and lighter particles might be equally effective. In the former case the cell-mechanism of the plant would resemble that of the equilibratory organs of certain animals[3]. These possess statocysts or otocysts in which lie dense particles, statoliths or otoliths, and the latter pressing on the under inner surface of the otocyst excite sensory reactions directed towards the maintenance of the normal position of the otocysts and of the organism. Kreidl even found that the insertion of particles of iron in place of the usual otoliths caused the organisms to orient themselves in regard to a magnet[4]. It is, however, not known whether the side walls of the otocyst are sensitive, but not the ventral wall, or whether only the latter is irritable. In the former case movement would follow until the otocyst experienced no excitation, whereas in the latter case it would be directed towards the renewal of the normal constant tonic stimulus radiating from the otocyst.

According to Němec and Haberlandt, the excitation in plant-cells is usually due to the starch-grains, although other bodies may become effective in fungal hyphae and other organs possessing geotropic irritability but devoid of starch-grains. No sure proof of such action has, however, been brought forward as yet, for the fact that when a cell is reversed the starch-grains fall from one end to the other with the required rapidity merely shows that the supposed stimulatory action is not an impossible one. Jost has, indeed, shown that none of the arguments put forward by Němec is conclusive, while Němec's conclusion that the power of perception of geotropic stimuli is restricted to the starch-bearing columella of the root-cap is negatived by the fact that the excitable apical region is usually about 1·5 mm. long.

Haberlandt[5] found that the stems of certain plants which had become

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[1] Noll, Ber. d. bot. Ges., 1902, p. 425.

[2] Noll, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 502; Ber. d. bot. Ges., 1902, p. 403.

[3] Cf. Noll, Das Sinnesleben d. Pflanzen, 1896, p. 71; Bethe, Biol. Centralbl., 1894, Bd. XIV, p. 95; Steiner, Centralbl. f. Physiol., 1898, Bd. XII, p. 775; Laudenbach, ibid., 1900, Bd. XIII, p. 586; Ilyin, ibid., 1901, Bd. XIV, p. 361; Haberlandt, Ber. d. bot. Ges., 1902, p. 448.

[4] Kreidl, Sitzungsb. d. Wien. Akad., 1892, Bd. CI; 1893, Bd. CII.

[5] Haberlandt, l. c., 1902, p. 193; Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 447.

free from starch after prolonged exposure to low temperatures also lost their geotropic irritability, but regained it at favourable temperatures simultaneously with the reappearance of the starch. Haberlandt supposes that these observations afford definite proof of the function of starch-grains as the agents for geotropic excitation, but it is quite possible that the solution and regeneration of the starch might merely form accidental accompaniments of the disappearance and restoration of the geotropic irritability[1]. It has yet to be found whether the geotropic irritability of starchless organs is similarly affected by low temperatures. The geotropic irritability is modified by many factors, and Darwin found that the heliotropic reaction is also weakened at low temperatures, though to a less extent than the geotropic one[2]. Irritability in general seems to be affected by low temperatures, and it is quite possible that in certain cases a tropic sensibility may only be fully restored some time after growth has been resumed under renewed favourable conditions.

Haberlandt[3] found that the nodes of *Tradescantia virginica* lost their power of geotropic response when the cortex included the endodermis or starch-layer, and concludes that the latter is the seat of geotropic perception. The effect might, however, be the direct result of the injury inhibiting the geotropic irritability, or removing tissue essential for the production of a curvature[4]. On the other hand, the fact that weak centrifugal action incapable of producing any displacement of the starch-grains may act as an excitation to curvature does not disprove Haberlandt's views, for the starch may exert local pressure without being displaced[5]. The short period of presentation required during intermittent excitation to produce a response affords no argument one way or the other. Gentle shaking, which might be supposed to cause the starch-grains to exert a greater contact stimulus, does actually accelerate the geotropic reaction[6], but here also other actions may be involved besides the apparent one. Naturally also the ascent of air-bubbles or of oil-globules in the cell might act as an excitation as well as the descent of the denser starch-grains.

A local accumulation of protoplasm such as might be responsible for the geotropic excitation does not appear to be produced by the usual intensity of gravity, or at least not in all plants. Němec[7] observed that in

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[1] Additional arguments against Haberlandt's conclusions are given by Noll, Ber. d. bot. Ges., 1902, p. 423.

[2] F. Darwin, Proceedings of the Royal Society, 1903, Vol. LXXI, p. 362.

[3] Haberlandt, Ber. d. bot. Ges., 1900, p. 269.

[4] See Jost, Biol. Centralbl., 1902, Bd. XXII, p. 174.

[5] Cf. Jost, l. c., 1902, Bd. XXII, p. 176; Haberlandt, Ber. d. bot. Ges., 1902, p. 191.

[6] Haberlandt, l. c., 1903, p. 489; Darwin, l. c., 1903, p. 366.

[7] Němec, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 147: cf. Jost, l. c., p. 177. On the appearance of certain minute bodies at the tips of the rhizoids of *Chara* cf. Giesenhagen, Ber. d. bot. Ges., 1901, p. 227; Jost, l. c., p. 173; Němec, Ber. d. bot. Ges., 1902, p. 351.

the cells of a displaced root the protoplasm accumulated at the points from which the starch-grains had moved, but this was probably the direct result of the displacement of the starch.

Jensen[1] supposes that, in the case of freely motile organisms, their geotactic irritability is the result of their response to the differences of pressure at varying depths, which enable them to orient themselves in regard to the perpendicular. Jensen forgets, however, that the maximal differences of pressure capable of affecting the organism at a given time are exceedingly small. On the other hand, the gravitational acceleration is only constant so long as the organism is moving with uniform velocity along a straight path, which is never the case. Every time the velocity changes, or the direction of motion alters, the organism experiences an increase or decrease of the geotropic stimulus. These changes, though relatively feeble, might well act as directive stimuli.

Owing to the subordination of the individual cells in each tissue or organ their potential powers of sensation and response are not always fully represented in every response. Hence when the growth in length of a curving radial organ is accelerated on the convex side, retarded on the concave one, and unaffected in the middle lamella, this does not justify Noll's conclusion that a corresponding distribution of sensibility is involved in the responsive cells[2]. A precisely similar distribution of the growth-activity is shown in curving unicellular organs, and a tissue composed of such cellular organs would undoubtedly show the same differences of growth, for a tendency to curvature on the part of the individual cells can only find external expression when the rate of growth of convex and concave sides undergoes appropriate alteration.

It is therefore impossible to follow Noll, or even Němec and Haberlandt, in ascribing the realized reaction to the unequal distribution of irritability in the individual cells, or in their radial and longitudinal walls. Nor does it follow that the different cells of a *Pandorina* possess dissimilar irritabilities because they are at varying angles with the incident rays when the colony is phototactically oriented. In plagiotropic positions the starch-grains collect at the lower corners of the cells, but this does not afford any explanation of the plagiotropic irritability, as Němec supposes[3]. There can be no doubt that, as in the case of tendrils, each organ responds as a whole to geotropic excitation, but the regulation of the individual cells is probably an extremely complex phenomenon. Czapek[4] has attempted to explain this regulation as being due to the pressures and stresses which

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[1] Jensen, Bot. Centralbl., 1893, Bd. LVI, p. 21.

[2] Noll, Heterogene Induction, 1892, p. 31. Cf. also Jost, Biol. Centralbl., 1902, Bd. XXII, p. 169; Haberlandt, Ber. d. bot. Ges., 1903, p. 470; Němec, Ber. d. bot. Ges., 1902, p. 359.

[3] Němec, l. c., 1901, p. 310.

[4] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 236; Ber. d. bot. Ges., 1901, p. 123.

the cells exert upon each other in virtue of their weight, tendency to growth, and mode of union, but in rejecting these conclusions Noll and Jost[1] have forgotten that Czapek was merely attempting to give a comprehensible means of arriving at the required regulation.

There can be little doubt that, as in all vital phenomena, not only the motory but also the sensory processes are connected with chemical changes, and Czapek has, in fact, found that such changes do occur as the result of tropic stimulation. Since they begin before any reaction is shown they appear to be more or less directly related to the process of sensation. The change is evidenced by an increased reducing action upon an alkaline solution of silver in the geotropically stimulated root-apex, as well as by the reduced oxidatory action upon readily oxidizable reagents such as guiacum. The change is propagated from the sensitive apex to the elongating zones behind, reaches its maximum about the time curvature begins, and then dies slowly away again, so that by the completion of the curvature the tissues are once more normal. Czapek's later researches appear to show that the silver reduction is due to homogentisinic acid, and that the latter is produced by the oxidation of tyrosin. Normally the acid appears to undergo further oxidation, which is, however, suspended in the presence of antioxydase ferments[2]. These are produced on geotropic stimulation and are responsible for the accumulation of the reducing substances in the cell. The latter might, however, equally well be the result of an increased productive activity only indirectly connected with the tropic stimulation.

Similar results have been obtained with hydrotropically stimulated roots and also with the heliotropically stimulated seedling stems of a few plants. The increased reducing action is not, however, produced by diffuse illumination, or in roots from which the sensitive apex ($1\frac{1}{2}$ mm.) has been removed, so that the result is due to tropic stimulation. It does not, of course, follow that all plants will react in the same way, and to all forms of stimulation; but if these changes prove to be a constant accompaniment of tropic stimulation they may serve as indications of the latter when the power of movement is absent, or when the stimulation is not intense enough to excite it. Czapek found that the reducing substances appeared in equal quantity on both convex and concave sides of a curving root, so that the unequal distribution of growth appears to have a different origin.

PHOTOTROPISM. Phototropic excitation is dependent not only upon

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[1] Cf. Noll, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 465; Jost, Biol. Centralbl., 1902, Bd. XXXII, p. 165.

[2] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 208; Ber. d. bot. Ges., 1901, p. 122; 1902, pp. 454, 464; 1903, pp. 229, 243. Cf. also Noll, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV., p. 485.

[3] On antiferments cf. Czapek, Ber. d. bot. Ges., 1903, p. 229.

a difference in the intensity of illumination, but also upon the direction of the light rays, owing to the fact that it is only those rays of light which penetrate the cells and tissues which operate as stimuli. Hence a beam of light must exert a lessened stimulatory action when it falls at an oblique angle to the surface of the plant, since less light will penetrate and more be reflected. It is, however, impossible to say whether the sensitive cells respond to the direction of the light rays or to their relative intensities on different surfaces. In the case of tendrils the directive action of the support is the result of the tendril's own activity in bringing fresh surfaces into contact, while chemotropic, osmotropic, and possibly also galvanotropic stimulation depend upon the distribution of differences of concentration rather than upon the direction of diffusion of stimulatory materials.

Sachs and Müller[1] concluded that the light rays acted as stimuli in virtue of their direction, but without bringing any definite proof forward[2]. The arguments of Darwin, Wiesner, and Oltmanns do not, however, definitely show that only differences in the intensity of the illumination act as stimuli[3]. The results obtained by using angular prisms filled with humic acid[4], or indian ink and glycerine gelatine[5], are inconclusive. A beam of light falling upon the plant after passing through a prism so arranged that the intensity of the light is diminished at right-angles to the direction of propagation has only to induce a slight curvature of the plant to produce the same intensity of illumination on both sides[6]. If the beam falls on the plant at an acute angle, a phototropic movement occurs even when the prism is so placed that the plant must curve towards the less bright portion of the beam. The same occurs in the case of freely motile organisms, whose direction of locomotion is in fact determined by the phototropic orientation of the body. Strasburger performed experiments of this kind with zoospores, and Oltmanns with freely motile and rooted plants. Similar results are obtained with organisms creeping on a substratum and exposed to an oblique beam. Many motile lower animals can also be induced in the same way to move towards regions where the illumination is feebler if the beam is so arranged that the feebler portion of the beam is towards its source[7]. If a plant is directed towards a strong source of illumination, feeble light falling at right angles

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[1] Sachs, Arb. d. bot. Inst. in Würzburg, 1880, Bd. II, p. 487; H. Müller, Flora, 1876, p. 92.

[2] Cf. Pfeffer, Osmotische Untersuchungen, 1877, p. 213; Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 478.

[3] Darwin, The Power of Movement in Plants, 1881, p. 398; Wiesner, Bot. Ztg., 1880, p. 456; Oltmanns, Flora, 1892, p. 183.

[4] Cf. Strasburger, Wirkung d. Lichtes und der Wärme auf Schwärmsporen, 1878, p. 35.

[5] Oltmanns, Jahrb. f. wiss. Bot., 1892, Bd. XXIII, p. 416; Flora, 1892, p. 183.

[6] Cf. Pfeffer, Pflanzenphysiol., I. Aufl., 1881, Bd. II, p. 373; Elfving, Die photometr. Bewegungen d. Pflanzen, 1901 (Öfvertryck af Finska Vet. Soc. Förhandlingar, Bd. XLIII).

[7] Cf. Nagel, Bot. Ztg., 1901, Abth. ii, p. 289, and the literature there quoted.

to it will here also produce a curvature towards the weaker light. Darwin[1] found that when one side of a plant was smeared with indian ink the plant curved away from that side in diffuse light owing to the fact that more light penetrated on the unsmeared side. Even this experiment, however, does not afford sure proof that the difference in the intensity, and not the direction of the light-rays, acts as the orienting stimulus.

It is quite possible that light may induce chemical changes or variations of surface-tension capable of acting as stimuli, but it is by no means certain whether Loeb[2] is correct in ascribing the phototactic movements of animal organisms to the direct action of changes of surface-tension produced by light. Quincke[3] has recently observed that the precipitations produced by alkaline carbonates in solutions of calcium salts turn towards the light, so that light may exercise a direct physical orienting action. No protoplasmic aggregation or displacement has as yet been established as a precedent to phototropic or phototactic response. Vines supposed that light directly depressed the motility of the protoplasm, while Wiesner supposed that it increased the power of stretching in the cell-walls of the illuminated sides, but neither of these hypotheses has any value as an explanation of heliotropism[4]. Similarly, historical interest alone attaches to de Candolle's[5] view that the curvature towards light is due to the partial etiolation of the shaded side. Organs which are not etiolated in darkness are, however, capable of heliotropic reaction, while negatively heliotropic organs may grow more rapidly in darkness; and in this case it is the exposed side which grows more rapidly during heliotropic curvature. Further, when the zones of perception and action are some distance apart the curvature may take place when the active zone is not illuminated at all. Wolkoff[6] assumed that negative heliotropism was produced by the refraction and concentration of the light-rays in the tissues upon the shaded side, so that this side was the more strongly illuminated one; but this quaint idea is totally incorrect. In any case phototropism and phototaxis are simply general terms for orienting movements produced by light, and it does not follow that precisely the same irritability and mode of response are involved in all cases. Yerkes[7] has suggested the term 'photopathy' for orienting movements due to differences of illumina-

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[1] Darwin, The Power of Movement in Plants, 1881, p. 398.

[2] Loeb, Einleitung in d. vergleichende Gehirnphysiologie, 1899, p. 128: cf. Nagel, Bot. Ztg., 1901, p. 294.

[3] Quincke, Annal. d. Physik, 1902, Folge iv, Bd. VII, p. 742.

[4] Vines, Arb. d. bot. Inst. in Würzburg, 1878, Bd. II, p. 145; Wiesner, Heliotropische Erscheinungen im Pflanzenreiche, 1880, Bd. II, p. 21: cf. also Godlewski, Bot. Ztg., 1879, p. 113.

[5] A. P. de Candolle, Physiologie végétale, 1832, T. III, p. 1083.

[6] See Hofmeister, Pflanzenzelle, 1867, p. 293; Sachs, Lehrbuch d. Botanik, 1874, 4. Aufl., p. 810.

[7] Cf. Nagel, Bot. Ztg., 1901, Abth. ii, pp. 291, 298.

tion, while 'photocliny' might be used to indicate responses due to the direction of the incident rays, but the terms are premature at present.

CHEMOTROPISM. Chemotropic stimulation is dependent upon the direction of diffusion in so far as the latter produces the differences of concentration to which the organism responds[1]. It is, however, uncertain whether the stimulatory substance must actually penetrate, or whether the mere contact with the ectoplasmic membrane produces the chemical action, or modification of surface-tension, which forms the first stage of perception. Many strong excitants do not appear to penetrate the protoplast, or at least do so with difficulty, but an apparent impermeability may allow of the penetration of traces of the substance sufficient to excite internal stimulation. Even when the substance readily penetrates, the stimulation may occur either during or after absorption.

OSMOTROPISM. The maximal osmotic action is exercised by impermeable substances, which may also be expected to exert the greatest osmotropic action. It is, however, uncertain whether the tropic stimulus is due to the unequal withdrawal of water, to the movement of water through the cell, to the osmotic pressures, or to surface-tension. It is also possible that a readily penetrating substance might exercise a tropic excitation, for any unequal distribution in the external medium will also be produced in the cell. A variety of observations upon freely motile organisms seem, however, to show that readily penetrating substances exercise little or no osmotropic action. Since, however, osmotaxis may arise in more than one way, it is possible that organisms may exist which are especially responsible to readily penetrating substances.

PART IV

THE MECHANISM OF TROPIC MOVEMENT

SECTION 52. **The Progress and Mode of Movement.**

All tropic curvatures produced by the aid of growth naturally cease to be performed when the power of growth is lost, whereas the presence of pulvini capable of variation movements renders possible various tropic responses in adult organs[2]. It is, however, not known whether pulvini may possess other tropic irritabilities in addition to those of geotropism and heliotropism, although no heliotropic variation curvatures appear to occur

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[1] For details see Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. II, p. 650; 1884, Bd. I, p. 475.

[2] Pfeffer, Periodische Bewegungen, 1875, p. 63. On the pulvini of Marantaceae cf. Schwendener, 1896, Gesammelte Abhandlungen, Bd. II, pp. 203, 210; Debski, Anzeiger d. Akad. d. Wiss. in Krakau, Juli 1895.

in unicellular organs. Any awakening of growth will naturally restore the power of nutation curvature, and it is for this reason that grass-stems, which have ceased to grow while erect, perform an upward geotropic curvature when placed horizontally[1]. That two reactions are involved is shown by the fact that on the klinostat, when the action of gravity is uniformly distributed, no geotropic curvature is produced, whereas the awakening of growth[2] enables a heliotropic response to be made to unilateral illumination.

According to Barth[3], the stem-nodes of *Dianthus bannaticus* behave similarly, while Miehe[4] found that the adult nodes of *Tradescantia fluminensis* remained capable of geotropic response. In most cases, however, the heliotropic and geotropic irritabilities appear to be lost with the normal cessation of growth. Before this happens tropic stimulation may often cause a more or less marked acceleration of growth, such as is also shown when those parts of tendrils where growth has fallen to a minimum are subjected to contact stimulation. Leaves, especially when they possess pulvini, may, however, remain capable of heliotropic and geotropic response for weeks or months after the leaf appears to be fully grown[5]. Preuss even found that a leaf of *Codiaeum Wendlandi* eight months old remained capable of reaction. Ultimately the power of reaction is lost in all cases, and even in the nodes of grasses the power of renewed growth is not indefinitely retained. The total amount of growth is in all cases limited, and hence a grass-node can only perform one or two geotropic curvatures. The production of two successive curvatures in opposed directions appears, however, to result in a greater total growth than when the unilateral action of gravity is eliminated on the klinostat.

FIG. 44. Portion of haulm of *Triticum vulgare* showing the geotropic curvature produced twenty-four hours after it had been placed in a horizontal position.

Usually the power of geotropic curvature is restricted to the normal

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[1] Sachs, Arb. d. bot. Inst. in Würzburg, 1872, Bd. I, p. 204; de Vries, Landw. Jahrb., 1880, Bd. IX, p. 473; Pfeffer, Druck- und Arbeitsleistungen, 1893, p. 390; Barth, Die geotropische Wachsthumskrümmung der Knoten, 1894, p. 30.

[2] Elfving, Ueber das Verhalten d. Grasknoten am Klinostat, 1884 (Öfvertryck af Finska Vetenskaps Societetens Förhandlingar, Bd. XXVI); Barth, l. c., p. 33.

[3] Barth, l. c., p. 27.

[4] Miehe, Jahrb. f. wiss. Bot., 1902, Bd. XXXVII, p. 532.

[5] Möbius, Festschrift f. Schwendener, 1899, p. 40; Preuss, Die Beziehungen zwischen dem anat. Bau und d. physiol. Function d. Blattstiele und Gelenkpolster, 1885. Cf. also Frank, Die natürl. wagerechte Richtung von Pflanzentheilen, 1870, p. 50.

growing zone[1], the lengths of the growing and curving zones corresponding. It is, however, possible that the power of curvature may be temporarily retained by the zones which have just ceased to grow, although Kohl's[2] experiments do not suffice to show that this is a common phenomenon. Woody twigs of *Aesculus*, *Tilia*, and other plants of one or more years' age, and which have long ceased to grow in length, may still remain capable of slow geotropic curvature when displaced from their normal position[3]. Apparently the geotropic excitation awakens a corresponding tendency to growth in the cambium and younger tissues, the energy of which is sufficient to produce a gradual bending of the inactive and woody parts. The existence of any power of geotropic reaction in the adult petioles of *Hedera helix*[4] is disputed by Frank[5], and doubt also attaches to Hofmeister's statement[6] that the adult petioles of *Hedera* and adult portions of the roots of *Ranunculus aquatilis* are capable of heliotropic curvature. Errera's[7] statement that the trunks of large trees may perform geotropic curvatures does not require discussion, since to produce the required bending moment the cambium would need to develop pressures of several hundred atmospheres to compress and extend the inactive tissues.

Every tropic curvature naturally depends, not only upon the nature of the excitation, but also upon the plant's power of reaction. Hence etiolated stems are usually capable of more rapid geotropic curvature than normal ones, owing to their more rapid rate of growth[8]. Hence also growth-curvatures appear earlier in the more rapidly growing zones than in the older ones even when the same degree of excitation is assured in both cases. Other factors come into play, however, in determining the further progress and final character of the curvature. Among these are included the mechanical resistance to curvature and the counteraction excited by its realization, as well as the altered orientation of the organ in its new position and the changes of the power of reaction and response with the progress of development. Thin organs will naturally curve more rapidly than thick

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[1] Sachs, Flora, 1873, p. 324; H. Müller, Flora, 1876, p. 65; Wiesner, Bewegungsvermögen der Pflanzen, 1881, p. 45; Rothert, Cohn's Beiträge z. Biologie, 1896, Bd. vii, p. 152. In the case of fungi and rhizoids cf. Haberlandt, Oesterr. bot. Zeitschr., 1889, p. 3 of reprint; Zacharias, Ber. d. bot. Ges., 1890, Generalvers., p. 57; Flora, 1891, p. 489; Oltmanns, Flora, 1897, p. 9; Steyer, Reizkrümmungen bei *Phycomyces*, 1901, pp. 6, 25.

[2] Kohl, Mechanik d. Reizkrümmungen, 1894, p. 13. Cf. Rothert, Biol. Centralbl., 1895, Bd. xv, p. 596.

[3] Vöchting, Organbildung im Pflanzenreiche, 1884, Bd. ii, p. 85; Frank, Lehrbuch d. Botanik, 1892, Bd. i, p. 470; Meischke, Jahrb. f. wiss. Bot., 1899, Bd. xxxiii, p. 363, footnote; Jost, Bot. Ztg., 1901, p. 20; Baranetzsky, Flora, 1901, Ergzbd., pp. 202, 213; Wiesner, Sitzungsb. d. Wien. Akad., 1902, Bd. cxi, Abth. i, p. 796.

[4] Hofmeister, Pflanzenzelle, 1867, p. 285; Bot. Ztg., 1869, p. 95.

[5] Frank, Bot. Ztg., 1868, p. 644.

[6] Hofmeister, Pflanzenzelle, 1867, p. 289.

[7] Report of British Association. Cambridge, 1904.

[8] Wiesner, Die heliotropischen Erscheinungen, 1880, Bd. ii, p. 7; H. Müller, Flora, 1876, p. 91; Darwin, The Power of Movement in Plants, 1881, p. 493.

ones, granted that the differences in the rate of growth on the opposed sides are the same in both cases, while the weight of the organ will favour or retard curvature according to the direction of the latter in regard to gravitational attraction.

When a radial shoot is placed in a horizontal position its negatively geotropic upward curvature[1] begins first in the more actively growing zone, so that the curvature does not exactly follow the arc of a circle. As the apex curves upwards it is more and more withdrawn from the stimulating action of gravity, but nevertheless it curves beyond the vertical, partly owing to the persistence of the geotropic induction and partly because the lower zones are still inclined to the perpendicular and hence continue to curve. The apical region then performs a return curvature by which it becomes straightened after one or more oscillations[2]. Ultimately only the basal portion remains curved although the reaction began latest in this region, and only progressed slowly in it. It is, however, by no means surprising that in many cases the excess curvature and resultant oscillation should not in all cases be perceptible.

FIG. 45. Shoot of *Impatiens glanduligera* showing phases of geotropic curvature (*a–e*). From photographs.

Changes of position produced by torsion are readjusted in a similar manner. Thus when young leaves of *Fraxinus*, *Robinia*, and other plants are turned upside down, the orienting torsion begins first at the tip of the leaf and then progresses basally, so that the apex passes beyond the appropriate position and is caused to perform a return torsion[3]. Since the torsion and retorsion progress basally, the twisting curvature is ultimately restricted to the basal zone, as can easily be seen in the leaves on drooping branches of the Ash and Weeping Willow, which must curve through 180° in order that the upper and under surfaces may gain their appropriate

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[1] Cf. Sachs, Flora, 1873, p. 324; Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 453; Bd. III, Plates; H. Müller, Flora, 1876, p. 88; Kohl, Mechanik d. Reizkrümmungen, 1894, p. 11; Rothert, Cohn's Beiträge z. Biologie, 1896, Bd. VII, pp. 161, 210; Meischke, Jahrb. f. wiss. Bot., 1899, Bd. XXXIII, p. 338. On the cinematographic representation of curvature see Pfeffer, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 741.

[2] Baranetzsky, Flora, 1901, Ergzbd., pp. 145, 159.

[3] Schwendener and Krabbe, 1892 (Schwendener's gesammelte Abhandlungen, Bd. II, p. 288).

positions. A similar progress of geotropic torsion or curvature may be shown by the stalks of flowers.

Although the curvature usually begins first in the more actively growing zones exceptions may occur. Thus, when the tip only is irritable, as in the cotyledons of *Avena*, the curvature begins first in the regions bordering upon it, and later in the further removed most actively growing zones[1]. This is, however, the natural result of the slow transmission of the tropic stimulus, and similarly geotropic curvature begins first just behind the percipient apex[2], although shortly afterwards the curvature is most marked in the most actively growing zone a little further away from the apex (Fig. 46, *B*). Later still, the curvature is transmitted basally, while the zones 2 and 3 (Fig. 46, *C*) which have elongated most have nearly become straight again[3]. These facts were correctly interpreted by Frank[4], whereas Hofmeister[5] erroneously concluded that no curvature took place in the most actively growing zones.

Similar relationships were found by Sachs, Müller, and Rothert to exist in the case of heliotropic organs, for here also the whole growing zone appears to be capable of curvature. According to Wiesner, the basal growing portion of seedling-stems does not react heliotropically, but merely shows a mechanical bending due to the weight of the curving portion above[6]. Rothert has, however, shown that this is not the case, and that all the growing zones are capable of heliotropic response. Presumably the same applies to all forms of tropic curvature, although further investigation is needed in this direction[7].

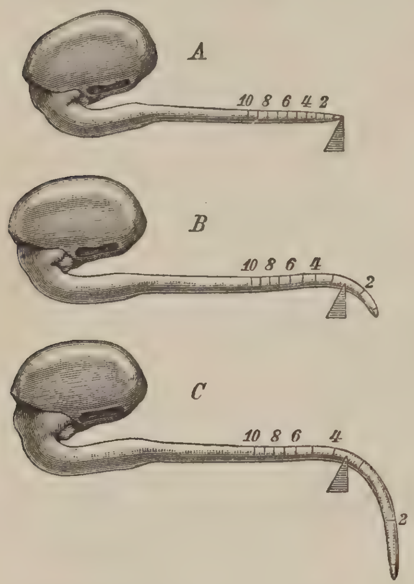

FIG. 46. Seedlings of *Lupinus albus* showing geotropic curvature. The horizontally-placed radicle in *A* has its terminal ten millimetres marked, and after three hours has curved as in *B*, and after eight hours as in *C*.

The power of tropic reaction is, however, not always localized in the most actively growing zones, as is shown by the existence of variation-movements, and by those nodes in which the awakening of growth is due to the tropic stimulus. In addition, the amount of the reaction depends

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[1] Darwin, The Power of Movement in Plants, pp. 421, 477; Rothert, Cohn's Beiträge z. Biologie, 1896, Bd. VII, pp. 163, 211.

[2] Cf. Czapek, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 361.

[3] For details see Sachs, Arb. d. bot. Inst. in Würzburg, 1874, Bd. I, pp. 440, 454, 612; Cisielski, Cohn's Beiträge z. Biologie, 1872, Bd. I, p, 4; N. J. C. Müller, Bot. Ztg., 1869, p. 390.

[4] Frank, Beiträge z. Pflanzenphysiologie, 1868, p. 10.

[5] Hofmeister, Jahrb. f. wiss. Bot., 1863, Bd. III, p. 96.

[6] Wiesner, Das Bewegungsvermögen d. Pflanzen, 1881, p. 45. Cf. Rothert, l. c., pp. 141, 152.

[7] On traumatropism cf. Pollock, Botanical Gazette, 1900, Vol. XXIX, pp. 17, 50; on rheotropism, Juel, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 530.

upon the degree of irritability, and the latter may not be fully developed in the most actively growing zones, or may be entirely absent from them even when the powers of perception and reaction are not localized. The maximum irritability appears commonly to be attained by nodes after the grand period of growth has been passed, and this has been definitely proved to be the case in the nodes of *Tradescantia* by Barth and Kohl[1], while the nodes of *Dianthus bannaticus*, and of a few grasses, only acquire their special geotropic irritability after their normal growth has ceased. It is owing to changes in the distribution of the altered irritability that the positively heliotropic curvature of the stem of *Tropaeolum majus* takes place mainly in the zone of most active growth, whereas the negatively heliotropic curvature is performed by the older but still growing regions. The fact that in other cases the heliotropic curvature begins in the most actively growing zone affords no evidence of the existence of two special kinds of negative heliotropism as suggested by H. Müller[2]. Since tropic irritability is always lost beyond a certain stage of development, it is possible that in certain cases it may disappear before growth in length has ceased, although in all the plants hitherto examined the whole growing-zone remained irritable.

In the case of the haulms of grasses, two or more nodes co-operate in producing the geotropic upward curvature of a horizontally-placed stem, since the internodes are inactive, and a single node is unable to curve sufficiently to make the stem erect. Other plants which possess motile nodes behave similarly, the geotropic response being performed mainly or entirely by the nodes. The special geotropic irritability of the nodes of *Mercurialis* was observed by Bonnet[3] a century and a half ago, but the general nature of the phenomenon was only established by the researches of de Vries[4] and later authors, while Wiesner[5] has investigated the heliotropic irritability of the nodes of certain plants.

The rapidity of reaction. This is most pronounced in the case of sensitive tendrils, for they may perform a considerable curvature in a few minutes when thigmotropically excited. It takes one or more hours for a thin actively growing stem to become erect when geotropically excited, while thicker or less irritable stems may require one or more days to attain

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[1] Barth, Die geotropischen Wachsthumskrümmungen d. Knoten, 1894, p. 19; Kohl, Mechanik d. Reizkrümmungen, 1894, p. 21.

[2] H. Müller, Flora, 1876, pp. 70, 93.

[3] Bonnet, Nutzen d. Blätter, 1762, p. 68.

[4] De Vries, Landw. Jahrb., 1880, Bd. IX, p. 473; Rützow, Bot. Centralbl., 1882, Bd. IX, p. 81; Briquet, Monographie du Genre *Galeopsis*, 1893, p. 60; Barth, Die geotropischen Wachsthumskrümmungen der Knoten, 1894; Kohl, Bot. Ztg., 1900, p. 1 (*Tradescantia*); Westermaier, Ueber gelenkartige Einrichtungen an Stammorganen, 1901; Miehe, Jahrb. f. wiss. Bot., 1902, Bd. XXXVII, p. 527 (*Tradescantia*).

[5] Wiesner, Die heliotropischen Erscheinungen, 1880, Bd. II, p. 32.

the same end [1]. The reaction begins at first slowly, then attains a maximum rapidity, and slowly decreases again. At the same time the apex extends regularly or in jerks, and describes a simple or complicated curve in space according to circumstances [2].

A tendency to curvature can naturally only find expression when it is able to overcome the internal and external resistance. A rise of the internal resistance due to the production of wood or sclerenchyma will render the active tissues capable of only feeble curvature or of none at all. Similarly, by determining the exact external resistance required to prevent curvature a measure is obtained of the energy of movement [3]. The latter is considerable in all movements produced by heterauxesis, and hence a horizontal shoot is able to overcome a considerable statical moment in curving upwards. To prevent movement the statical moment due to the organ's own weight usually needs to be increased from four to thirty times [4], so that under normal conditions the plant works with a considerable margin of safety. Usually also the rapidity of curvature is not affected by fractional increases of the normal statical moment or even by doubling it [5]. Exactly the same applies to the influence of a resistance upon rectilinear growth, and in both cases a relatively considerable increase of resistance is required to lessen the rate of growth or curvature perceptibly. Similarly, a man may climb a mountain as rapidly with a small load as with none at all, whereas when heavily laden he must climb slowly in order to be able to perform the greater work required.

No upward geotropic curvature is possible when a shoot is unable to support its own weight, but nevertheless, as in the case of the hanging free ends of the stems of climbers, the basal part bends mechanically downwards, while the apex turns upwards. That is the natural result of the tendency to upward curvature coupled with the fact that the statical moment at any point is proportional to the length of free stem beyond it. Hence such shoots assume a double curvature or S shape, such as may also be produced in normally erect stems, when they are subjected to sufficiently intense centrifugal forces [6].

The statical moment in the case of the basal growing zone of the peduncle of the Hyacinth may amount to 6 kilograms, in that of the lowest nodes of a ripe stem

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[1] Cf. Sachs, Flora, 1873, p. 327; Darwin, The Power of Movement in Plants. On heliotropic curvatures see H. Müller, Flora, 1876, p. 88, and Wiesner, Die heliotropischen Erscheinungen, 1878, Bd. I, p. 68.

[2] Darwin, l. c., pp. 495–512.

[3] On dynamometers see Pfeffer, Period. Bewegungen, 1875, p. 9; Druck- und Arbeitsleistungen, 1893, p. 251; Meischke, Jahrb. f. wiss. Bot., 1899, Bd. XXXIII, p. 345.

[4] Meischke, l. c., p. 362.

[5] Id., p. 364.

[6] F. Schwarz, Unters. a. d. bot. Inst. zu Tübingen, 1881, Bd. I, p. 80. Cf. also Baranetzsky, Flora, 1901, Ergzsbd., p. 186.

of Barley to 5 kilograms, and to no less than 130 kilograms in the case of a Maize-stem[1]. Meischke also measured the maximal pressure exercised by curving organs against fixed resistances, and found that usually the basal nodes are able to take part in the geotropic erection of the shoot. In the case of *Avena*, however, they only begin to curve when the upward bending of the more apical portion has lessened the statical moment exercised upon them. The internal resistance increases as the curvature progresses, so that less external energy of movement is available, and in the haulms of most Grasses complete erection requires the co-operation of several nodes.

Thin tendrils naturally are incapable of exercising any pronounced pressure when curving, and in the case of the stiffer tendrils of *Bauhinia*, *Strychnos*, *Vanilla*, and other plants, a considerable internal resistance must be overcome before any considerable external pressure can be exercised. Coiled hooks and tendrils which undergo secondary thickening exercise sufficient pressure to strangulate the branches they have clasped[2], and become extremely rigid, whereas relatively thin fruit- and flower-stalks (Apple, Snowdrop, Fuchsia) are mechanically bent by the weight of the organ they support[3]. The peduncles of the Poppy are able to support the rather heavy bud, and hence can perform active geotropic curvatures both negative and positive in character. Most peduncles are, in fact, rigid enough to support the flowers and flower-buds in any position, whereas the fruits, especially when succulent and heavy, naturally tend to assume a more pendent character.

The downward curvature of the root is always an active one, although Knight[4], Hofmeister[5], and more lately Saposchnikow[6] and Letellier[7], have considered it to be a passive plastic bending produced by the root's own weight. This obsolete idea is, however, sufficiently disproved by the fact that the root may curve against resistances equivalent to more than its own weight[8], and that it may curve downwards into mercury against an upthrust of about ten times the weight of the part submerged[9].

A free root cannot exercise any great pressure owing to the readiness with which it becomes laterally displaced, and because of the plastic properties of the growing

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[1] Pfeffer, Druck- u. Arbeitsleistungen, 1893, p. 395; Meischke, Jahrb. f. wiss. Bot., 1899, Bd. XXXIII, p. 337. On the capacity for work in geotropically excited pulvini cf. Pfeffer, Periodische Bewegungen, 1875, p. 145.

[2] Ewart, on Contact Irritability, Ann. du Jard. bot. de Buitenzorg, Vol. XV, 1898, p. 187.

[3] Cf. Vöchting, Die Bewegungen d. Blüthen u. Früchte, 1882, p. 192; Wiesner, Sitzungsb. d. Wien. Akad., 1902, Bd. CXI, Abth. i, p. 744.

[4] Knight, Phil. Trans., 1806, I, p. 104. Bazin appears, according to Duhamel, Naturgesch. d. Bäume, 1765, Bd. II, p. 109, to have attempted a similar explanation.

[5] Hofmeister, Jahrb. f. wiss. Bot., 1863, Bd. III, p. 102; Bot. Ztg., 1868, p. 273, and 1869, p. 57. Wigand suggested (Botan. Unters., 1854, p. 3) that the downward curvature of the part was due to the distensive enlargement of the cells on the under side, but Hofmeister has shown that this is not the case (Jahrb. f. wiss. Bot., Bd. III, p. 80).

[6] Saposchnikow, Bot. Jahrb., 1887, Bd. I, p. 225.

[7] Letellier, Essai de statique végétale, 1893.

[8] Johnson, Linnaea, 1830, Literaturberichte, p. 148; Frank, Beiträge z. Pflanzenphysiologie, 1868, pp. 21, 35; N. J. C. Müller, Bot. Ztg., 1871, p. 719; Sachs, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 450; Pfeffer, Druck- u. Arbeitsleistungen, 1893, p. 271; Wachtel, Bot. Centralbl., 1895, Bd. LXIII, p. 309; Meischke, Jahrb. f. wiss. Bot., 1899, Bd. XXXIII, p. 366.

[9] Sachs, l. c., pp. 431, 451.

zones. The radicle of *Vicia Faba* may, however, develop a pressure of 13 grams at its apex when in perpendicular contact, and one of 1·5 to 2·2 grams when the contact is oblique[1]. The maximal pressure is naturally only obtained after a certain length of time, and if the resistance is suddenly removed a rapid curvature due to the released strains is produced. This is more pronounced in the case of variation than of growth movements, since in the case of the latter the plasticity of the tissues and the regulation of growth prevent the attainment of any pronounced strain, so that the attempted curvature is only completed some time after the removal of the resistance to it[2]. Hofmeister supposed that negative heliotropism required high, and positive heliotropism low, tissue-strains, but these conclusions are based upon incorrect ideas as to the importance of the strains in the tissues for tropic curvature, and there is no evidence in support of his conclusions[3].

SECTION 53. **The Mechanism of Curvature.**

Since the rigidity of the pulvinus of *Phaseolus* remains constant when a negatively geotropic curvature is performed as the result of the reversal of the plant, it follows that the expansive energy of the compressed ventral side which is now uppermost must decrease in exactly the same degree that the expansive energy of the under side increases[4]. If this were not the case a pronounced decrease of rigidity must ensue, since the force of curvature may amount to a pressure of one to three atmospheres. The plasmolytic experiments of Hilburg[5] showed in fact that the osmotic pressure does actually fall in the upper side of a reversed pulvinus and rises in the under half, the observed differences approximating to 1 per cent. of potassium nitrate, which is amply sufficient to produce the required energy of movement. The same takes place, according to Hilburg, during the heliotropic curvature of the pulvinus of *Phaseolus*.

Thigmotropic growth-curvatures involve a pronounced transitory acceleration of the average rate of growth, whereas, according to Sachs and Müller, the mean growth appears in many cases to be somewhat retarded during heliotropic and geotropic curvature. In the case of the nodes of grasses and of other plants geotropic curvature involves a pronounced acceleration of the mean rate of growth, but it has not been determined whether the growth is also more rapid than in the case of nodes in which growth but not curvature has been excited by rotation on a klinostat. The same question has also to be answered in the case of those nodes which retain the power of slow growth when the stem is vertical.

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[1] Cf. Pfeffer, l. c., p. 270.

[2] Sachs, Flora, 1873, p. 207; de Vries, Sur les causes des mouvements auxotoniques, 1880, p. 14 (reprint from the Archives Néerlandaises, Vol. XV); Pfeffer, Druck- und Arbeitsleistungen, 1893, p. 402.

[3] Cf. Pfeffer, l. c., 1893, p. 426.

[4] Pfeffer, Periodische Bewegungen, 1875, pp. 140, 145.

[5] Hilburg, Unters. a. d. bot. Inst. zu Tübingen, 1881, Bd. I, p. 31.

It depends upon circumstances as to whether the total length of the concave side increases or decreases during curvature. A shortening of the concave side always occurs during the variation movements of pulvini, and usually also during the nutation curvatures of thick and slowly growing organs, whereas the concave side may in some cases actually lengthen during the curvature of stems and roots capable of active growth. This is due to the fact that during the relatively slow progress of the reaction the general elongation of the curving zone is sufficient in amount to be perceptible. Hence rapid curvatures might be expected to produce a shortening of the concave side, and this is absent or hardly perceptible in tendrils because the thigmotropic excitation simultaneously awakens a pronounced general acceleration of growth. On the other hand, during geotropic and heliotropic curvature, the convex side grows more rapidly than normally in spite of the general retardation of growth. It is, however, possible that organs may exist in which stimulation produces a retardation of growth on all sides, the convex side being merely that in which growth is least retarded.

Hofmeister[1] attached both ends of a straight piece of stem to the under side of a horizontal sheet of glass. The resultant geotropic curvature caused the concave side to be raised away from the glass, showing that elongation had taken place on both sides. The same applies to heliotropic curvature. Another method is to cover the surface with indian ink, the cracks which appear showing that the geotropic curvature of some stems involves an elongation of both sides, whereas in a grass-node only the convex side elongates[2].

Sachs[3] placed marks of indian ink 2 mm. apart on roots and grew them in various positions in loose earth behind glass plates. By means of protractor scales marked on mica-plates, the radius of curvature and the length of the marked segments of the concave and convex sides can be determined. In the case of a vertical radicle of *Vicia Faba* the terminal 8 mm. increased by 10·5 mm. in fourteen hours, and when placed horizontally the root curved through an arc of 135°, the concave side becoming 6·1 mm. longer, and the convex 10·8 mm., so that the growth of the middle lamella was 8·4 mm. The geotropic curvature hence involved an acceleration of growth of 0·3 on the convex side, and retardations of 4·4 and 2·1 mm. on the concave side and in the middle lamella respectively.

In the case of stems Sachs[4] measured the elongation by applying

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[1] Hofmeister, Jahrb. f. wiss. Bot., 1863, Bd. III, p. 86.

[2] Pfeffer, Druck- u. Arbeitsleistungen, 1893, p. 408.

[3] Sachs, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 463; Noll, ibid., 1888, Bd. III, p. 507; Macdougal, Botanical Gazette, 1897, Vol. XXIII, p. 361.

[4] Sachs, Flora, 1873, p. 324; Arb. d. bot. Inst. in Würzburg, 1872, Bd. II, p. 193. No measurements have been made of the curvature of unicellular organs.

paper measures, and observed in many cases only a slight retardation of the average rate of growth, while more especially in thick and slowly growing stems and peduncles a more or less pronounced shortening took place on the concave side. Similar results were obtained by Barth with nodes which show growth previously to geotropic excitation [1], whereas the nodes of grasses always shorten considerably on the concave side, which undergoes compression. Sachs [2] observed that the thick nodes of cinquantino Maize shortened from 4·3 to 2·5 mm. on the concave side during geotropic curvature, and lengthened from 4·1 to 9·0 mm. on the convex side. The more slender nodes of other grasses shorten but little on the concave side when the curvature is moderately pronounced, so that the neutral axis, which neither elongates nor contracts, lies near to the concave surface.

No cell-division accompanies the awakened growth of the nodes of grasses, the individual cells increasing in size by stretching growth [3]. The same is shown during the geotropic curvature of roots, so that, as Frank first observed, the cells are longer on the convex than on the concave side [4], and this holds good even when the curvature is accompanied by cell-division. When the concave side is compressed, as in pulvini and grass-nodes, the diameter of the cells will in general tend to increase, but not, or only to a slight degree, when growth is retarded without any compression. Kohl [5], however, observed that during the geotropic curvature of stems the cells of the concave side, and Noll that those of the convex side, attained a relatively greater diameter, so that individual peculiarities may occur. The varying growth of strips of equal length marked on straight and curving stems corresponds to what might be expected, that from the concave side being shorter and from the convex side longer than that from a stem in which growth was rectilinear [6]. According to Müller [7], the altered rates of growth in positively heliotropic stems and in negatively heliotropic aerial roots during curvature correspond to those observed during geotropic curvature, so that the same considerations may possibly apply to all forms of tropic curvature produced by growth.

Each lamella assumes during growth a rate of growth proportionate

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[1] Barth, Die geotropischen Wachsthumskrümmungen d. Knoten, 1894, p. 11.

[2] Sachs, Arb. d. bot. Inst. in Würzburg, 1872, Bd. I, p. 206; Pfeffer, Druck- u. Arbeitsleistungen, 1893, p. 393; Barth, l. c., p. 31. Pfeffer and Barth used microscopes with micrometer eyepieces.

[3] Sachs, l. c., p. 207.

[4] Frank, Beiträge z. Pflanzenphysiologie, 1868, p. 40; Cisielski, Cohn's Beiträge z. Biologie, 1872, Bd. I, Heft 4, p. 18; Sachs, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 466; Macdougal, Botanical Gazette, 1897, Vol. XXIII, p. 364.

[5] Kohl, Mechanik der Reizkrümmung, 1894, p. 50. Cf. also Sachs, l. c., pp. 462, 469; Cisielski, l. c., p. 18.

[6] Noll, Arb. d. bot. Inst. in Würzburg, 1888, Bd. III, p. 526.

[7] Sachs, Arb. d. bot. Inst. in Würzburg, 1872, Bd. I, p. 193; Experimentalphysiologie, 1865, p. 507. Cf. also Frank, l. c., p. 67.

to its relative position, as is especially well shown when a stimulated node of grass is cut into a series of parallel horizontal slices, and the growth of each followed. In this case the splitting releases no disturbing tissue-strains[1], but even when these come into play positive results may be obtained. Thus Sachs[2] found that when a root, split into two equal longitudinal halves which remained in contact, performed a positive geotropic curvature, the upper half elongated more than the lower. When an erect stem is split, the two halves curve apart owing to the released tissue-strains, and as the result of their changed position each performs a negatively geotropic curvature during which the under side of each half grows more rapidly than the upper inner one[3]. Similar experiments have been performed by Hofmeister[4] with the stalks of Agaricineae and by Copeland[5] with the stems of seedlings. The latter found that a horizontally placed segment in which a negatively geotropic curvature was produced grew more rapidly than a vertical one when the cut surface was upwards, and less rapidly when it faced downwards. Further investigation appears, however, to be needed in this direction.

In any case longitudinal halves of stem and roots are capable of geotropic curvature when placed horizontally, and the curvatures always take place in the same direction independently of which side is placed downwards, so that the curvature may either take place towards or away from the cut surface. It follows, therefore, that in the intact organ as in unicellular ones, correlative relationships determine the relative rate of growth of the different parts, and these must even influence the growth of the collenchyma strands in the nodes of grasses, since the tensions brought into play are incapable of directly stretching them[6].

The conditions are naturally rendered more complicated by the fact that the cells in a tissue are not all equally active and responsive, and that inactive elements may be present which, when comparatively rigid, may partially arrest or completely prevent an attempted curvature. Even a realized curvature may involve the compression of cells which strive to expand, as well as the regulation of the growth of some and the plastic or elastic stretching of others. Actions of this character, although they may influence curvature, do not induce it. Kohl[7] supposed that geotropic curvature was due to an active contraction of the tissues on the concave side, but Rothert and Noll[8] have shown the incorrectness of this supposition,

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[1] H. Müller-Thurgau, Flora, 1876, pp. 69, 92.

[2] De Vries, Landw. Jahrb., 1880, Bd. IX, p. 483; Pfeffer, Druck- und Arbeitsleistungen, 1893, pp. 394, 408; Sachs, Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 470.

[3] Sachs, Flora, 1873, p. 330.

[4] Hofmeister, Jahrb. f. wiss. Bot., 1863, Bd. III, p. 93.

[5] Copeland, Botanical Gazette, 1900, Vol. XXIX, p. 189.

[6] Pfeffer, l. c., pp. 401, 426.

[7] Kohl, Mechanik der Reizkrümmungen, 1894, pp. 4, 40, 87.

[8] Rothert, Biol. Centralbl., 1895, Bd. 15, p. 593; Noll, Flora, 1895, Ergzbd., p. 44.

which in any case could not apply to the curvatures of unicellular organs. Kohl supposed that the shortening of the cells was due to a rise of turgor in them, of which we have no positive evidence, although certain growth movements are actually produced by active contraction. The activity of the convex side of a curving node of a grass-haulm is well shown by the thickening and bulging it undergoes when curvature is mechanically prevented[1]. Indeed, if the haulm is closely fitted in a glass tube the growth of the under side may be so active in spite of the rectilinear direction enforced upon it as to tear the upper side of the node[2].

In the case of the nodes of *Triticum*, *Secale*, and many other Grasses, only the sheathing-leaf portion responds geotropically, the central portion being passively bent, whereas in *Zea Mays, Saccharum officinarum*, both the leaf and stem portions of the node are capable of perceiving and reacting to geotropic stimuli[3]. In Polygonaceae and Commelinaceae, however, the irritability of the leaf-sheath is either slight or absent, so that it is passively bent during curvature. Such cases make clear the fact that the different tissues may not all be equally excitable and responsive, but experiments with isolated tissues leave it uncertain whether the result observed represents the actual part played by the given tissue in the intact organ. Not only may the operation alter or inhibit the irritability of the tissue, but also the removal of the correlating influence of the neighbouring parts may produce a pronounced change of tone. In addition, tissues capable of reaction but not of perception must always appear irresponsive when isolated.

The removal of the epidermis or of the cells bordering upon it, as well as the removal of the pith and even of the ring of vascular bundles, does not suspend the power of geotropic reaction, whereas the isolated pith is in many cases incapable of any geotropic response[4]. According to Sachs[5], the pith taken from geotropically curving stems straightens itself, so that the permanent curvature ultimately assumed by the pith may be passively impressed upon it. There is, however, no certain proof in a single case that the pith is incapable of perception, but is able to actively respond to geotropic stimuli transmitted to it[6]. In many cases, however, the cortex of stems and stem-nodes, or portions of it, appears to be especially per-

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[1] Cf. Pfeffer, Druck- u. Arbeitsleistungen, 1893, p. 396; Noll, Arb. d. bot. Inst. in Würzburg, 1888, Bd. III, p. 509; de Vries, Landw. Jahrb., 1880, Bd. IX, p. 482.

[2] Pfeffer, Ber. d. Sächs. Ges. d. Wiss., 1891, p. 642.

[3] Barth, Die geotropischen Wachsthumskrümmungen der Knoten, 1894; Pfeffer, l. c., pp. 390, 409.

[4] Sachs, Flora, 1873, p. 330; Barth, l. c., p. 36; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 248; Haberlandt, Ber. d. bot. Ges., 1901, p. 269; Němec, ibid., 1902, p. 339.

[5] Sachs, Experimentalphysiol., 1865, p. 567. Cf. also Frank, Beiträge zur Pflanzenphysiol., 1868, p. 73.

[6] Cf. Haberlandt, l. c., p. 269.

ceptive and responsive. Similarly the geotropic stimuli perceived by the apex of the root appear to produce the most active response in the cortical tissues[1], and these, owing to their peripheral position, are more readily capable of producing curvature than centrally placed ones.

Sachs[2] found that the middle lamella cut out of a stem performed a negatively geotropic curvature when placed horizontally with the cut surface perpendicular, whereas when the cut surfaces face downwards or upwards the results obtained vary and are often negative. The absence of any curvature might possibly be due to the insufficient leverage exerted by the thin slice of the cortex. Czapek found, however, that a horizontal slice of the middle lamella of the hypocotyl of *Helianthus annuus* performed a negatively geotropic curvature when the section was prepared after an hour's previous geotropic excitation. This isolated observation does not necessarily prove that the horizontally placed lamella is always able to perform a geotropic response, but not to perceive geotropic stimuli.

Both irritability and the power of response change during development, and all tissues which have lost the power of growth can only experience a passive curvature. In addition, the less active tissues may be compressed or stretched in accordance with their position in regard to the more active ones. The latter applies to the nodes of grasses in which the originally active parenchyma tissue on the convex side is ultimately ruptured by the continued growth of the collenchyma strands[3]. In this way the previously compressed parenchyma is stretched, while the stretched collenchyma becomes subject to compression. Evidently, therefore, the strains in the tissues do not afford direct evidence as to the part each tissue plays in curvature. In addition, every nutation curvature, and the tissue-strains to which it gives rise, may co-operate in modifying the original growth-tendencies.

Even when the pith has no active power of curvature, its compression may aid in producing curvature when this is once initiated, but apart from this mechanical action the detailed changes of the tissue-strains during the progress of heliotropic and geotropic curvatures fail to reveal the mechanism of curvature[4]. The anatomical differences between negatively and positively tropic organs postulated by Dutrochet[5] were shown long ago by Mohl[6] to be non-existent. Dutrochet also erroneously supposed that

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[1] Macdougal, Annals of Botany, 1897, Vol. XXIII, pp. 346, 364.

[2] Sachs, Flora, 1873, p. 330; Arb. d. bot. Inst. in Würzburg, 1873, Bd. I, p. 470; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 250; Noll, Jahrb. f. wiss. Bot., 1900, Bd. XXXIV, p. 467; Haberlandt, Ber. d. bot. Ges., 1901, p. 270; Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 470; Němec, Ber. d. bot. Ges., 1902, p. 353.

[3] Cf. Pfeffer, Druck- u. Arbeitsleistungen, 1893, p. 407.

[4] Sachs, l. c.; Frank, l. c.; Hofmeister, Pflanzenzelle, p. 293; Kraus, Bot. Ztg., 1867, p. 129; Ratschinsky, Ann. sci. nat., 1858, 3^e sér., T. IX, p. 172; Johnson, ibid., 1835, 2^e sér., T. IV, p. 327; Pollock, Bot. Gazette, 1900, Vol. XXIX, pp. 25, 48.

[5] Dutrochet, Mémoires, etc., Bruxelles, 1837, pp. 322, 327.

[6] Mohl, Vegetabilische Zelle, 1851, p. 141.

heliotropic response was due solely to a tendency to curvature of the concave side, and the same objection applies to Kohl's view that geotropic curvature is due to active contraction of the concave side.

SECTION 54. **The Internal Causes of Movement.**

Neither the mode in which the changes of turgor responsible for variation movements, nor that in which the altered growth of nutation curvatures is produced, is precisely known. It is, however, certain that the changed rates of growth are not due to alterations of turgor, as de Vries[1] supposed, for, apart from the fact that no curvature could be produced in this manner in unicellular organs, plasmolytic researches have shown that no rise of turgor takes place during geotropic curvature[2]. Beit's unfounded supposition that positive heliotropism is the result of the decomposition of sugar on the illuminated side requires no discussion. In the case of rapidly curving organs, a slight fall of turgor may actually take place in the cells of the concave side, which apparently results from the rapid increase of volume, water being absorbed in greater amount than the self-regulatory production of osmotic materials is able to compensate for immediately.

Even when a general or unilateral rise of turgor accompanies a tropic reaction, its relationship to the induced irregularity of growth is accessory and not causal. Kohl's observations[3] do not prove that a rise of turgor takes place in the cells of the concave side during geotropic response, and Noll[4] has shown that a rise of turgor will not cause the cells of the concave side to shorten. The turgor of the nodal parenchyma of *Hordeum vulgare* rises by the equivalent of about 1 to 2 per cent. of potassium nitrate when the stem is fixed in a horizontal position[5], but this is not in itself sufficient to directly cause the growth of the cells, while no such rise is shown by the nodal cells of *Triticum vulgare* and *T. spelta*, which are capable of as ready and rapid geotropic response as those of *Hordeum vulgare*. In the same way a rise of turgor is shown by some plants, but not by all, when working against external resistance; and although such rises act as an aid to growth they do not directly induce it.

Although the mechanism of growth need not always be the same, the required expansion is usually produced by a plastic stretching of the cell-wall. Evidence of this is afforded by the fact that during curvature

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[1] De Vries, Landw. Jahrb., 1880, Bd. IX, p. 502.

[2] Wortmann, Ber. d. bot. Ges., 1887, p. 961; Bot. Ztg., 1889, p. 456; Noll, Arb. d. bot. Inst. in Würzburg, 1888, Bd. III, p. 511; Flora, 1895, Ergzbd., p. 36.

[3] Kohl, Mechanik der Reizkrümmungen, 1894, p. 59.

[4] Noll, Flora, 1895, Ergzbd., pp. 48, 54.

[5] Pfeffer, Druck- und Arbeitsleistungen, 1893, pp. 399, 405.

the thickness of the walls of the epidermal and collenchyma cells decreases[1], and often to a considerable extent, while the walls of the same cells on the concave side frequently become distinctly thicker. According to Wortmann[2], the cell-walls become very much thicker on the upper sides of shoots placed horizontally, and prevented from curving upwards by an attached weight. Elfving[3] found that a similar thickening was produced in the cells of the convex side when a shoot was strongly bent and fixed in this position. Since the same result is produced on a klinostat, it must be the direct result of the altered strains, whereas in Wortmann's experiment it probably results from the inductive action of gravity. Evenly distributed longitudinal strains do not appear to produce any increased thickening of the cell-walls[4], but where the strains are always unevenly distributed, as in the curved hooks of many tropical climbers, a pronounced effect may be produced[5].

The fact that the changes in the thickness of the cell-wall only appear during the curvature shows that they are the result and not the cause of it, as Wortmann supposes[6]. Since normally the distension of the walls lies within their limit of elasticity, the plastic growth of the cell-wall must be preceded by a physiological diminution of the cohesion of the component cellulose micellae. At the same time, the elasticity of the cell-walls on the convex side appears to be so modified as to allow of an elastic lengthening of the cells without any rise of turgor. The curvature produced in this way is reversible by plasmolysis until it has been followed up and fixed by growth. A combination of growth and variation movement is also shown by the young growing pulvini of *Phaseolus*, which, when adult, still remain capable of variation movements. A few days after a plant has been inverted, and the pulvini have performed a geotropic variation curvature, a certain amount of growth takes place in the inverted and unusually elongated dorsal sides of the pulvini[7]. The result depends to some extent, therefore, upon the nature and duration of the stimulus ; and, according to Möbius[8], the heliotropic curvature of the pulvinus of Marantaceae is rapidly rendered permanent by growth.

Frank[9] showed that the persistence of a completed curvature when turgor was

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[1] Noll, Arb. d. bot. Inst. in Würzburg, 1888, Bd. III, p. 526; Flora, Ergzbd., 1895, p. 73; Wortmann, Ber. d. bot. Ges., 1887, p. 463; Bot. Ztg., 1887, p. 808; 1888, p. 469; Kohl, l. c., p. 36; Macdougal, Botanical Gazette, 1897, Vol. XXIII, p. 364.

[2] Wortmann, Bot. Ztg., 1837, p. 824.

[3] Elfving, Zur Kenntniss d. Krümmungserscheinungen, 1888 (Öfvertryck af Finska Vet. Soc. Förhandlingar, Bd. XXX).

[4] Ball, Jahrb. f. wiss. Bot., 1903, Bd. XXXIX, p. 305.

[5] Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, Vol. XV, p. 190 seq.

[6] Cf. Noll, Flora, Ergzbd., 1895, p. 38.

[7] Pfeffer, Periodische Bewegungen, 1875, p. 139.

[8] Möbius, Festschrift für Schwendener, 1899, p. 60.

[9] Frank, Beiträge z. Pflanzenphysiol., 1868, p. 97.

removed by plasmolysing solutions was a sure indication that the heliotropic and geotropic curvatures were produced by unequal growth. De Vries[1] then found that curvatures which had just begun could be partially removed by the action of 20 per cent. solutions of salt, so that the primary curvature is due to elastic stretching, which is rapidly followed up by growth. De Vries, however, erroneously assumed that this was due to a rise of turgor on the convex side, whereas direct observation affords no evidence of any such rise. According to Noll[2], the primary curvature is due to an increased extensibility of the cells of the convex side, but at the same time it is possible that the thickening of the wall on the concave side may render this part less capable of extension although the energy of turgor may be the same throughout. In parts which had undergone positively heliotropic curvature, Weinzierl[3] found that the epidermis of the concave side possessed a higher breaking strain and limit of elasticity than the epidermis on the convex side, but it is uncertain whether this is due to changes in the properties or to unequal thickening of the respective cell-walls. Wiesner[4] supposed that positive heliotropism is due to a rise of elasticity on the shaded side, and to an increase of ductility in the cell-walls, and of turgor in the cells of the illuminated side. Hofmeister[5] also seems to have considered that changes of elastic extensibility took part in the production of heliotropic and geotropic curvature, but his conclusions are vitiated by physical errors and by his inability to discriminate between the results of growth and of strain.

In some cases no straightening of the curvature can be produced in young organs, and it is not known whether the same effect is given by suddenly killing the geotropically or heliotropically curving organs as by plasmolysis. To produce the latter often requires a considerable time, during which readjustment may occur[6]. Slowly curving hooks or tendrils, when suddenly killed during curvature, show no perceptible straightening[7]. Both plasmolysis and death by heat or the action of alcohol may cause a withdrawal of water from the cell-wall, and so produce contraction or compression which does not exist in the intact organ. Correns[8] found, in fact, that when curving tendrils were dropped into alcohol the curvature increased, whereas straightening was shown when the dead dehydrated tendril was returned to water.

Noll[9] found that the same force produced a greater bending when applied to a stem in the direction of an incipient geotropic curvature than when opposed to it,

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[1] De Vries, Landw. Jahrb., 1880, Bd. IX, p. 302. Cf. also Wiesner, Die heliotropischen Erscheinungen, 1880, Bd. II, p. 3; Noll, Arb. d. bot. Inst. in Würzburg, 1888, Bd. III, p. 516; Flora, 1895, Ergzbd., p. 82; Barth, Die geotropischen Wachsthumskrümmungen der Knoten, 1894, p. 12; Kohl, Mechanik der Reizkrümmungen, 1894, p. 67.

[2] Noll, l. c., 1888 and 1895.

[3] Weinzierl, Sitzungsb. d. Wien. Akad., 1877, Bd. LXXVI, Abth. i, p. 434.

[4] Wiesner (l. c., 1880, Bd. II, p. 20).

[5] Hofmeister, Jahrb. f. wiss. Bot., 1860, Bd. II, p. 265; 1863, Bd. III, p. 88; Pflanzenzelle, 1867, p. 287.

[6] Cf. Fitting, Ber. d. bot. Ges., 1902, p. 380.

[7] Cf. Ewart, Ann. du Jard. bot. de Buitenzorg, 1898, Vol. XV, pp. 210, 221.

[8] Cf. Ewart, l. c., p. 221.

[9] Noll, l. c., 1888, p. 514; 1825, p. 56. Cf. also Pfeffer, Druck- u. Arbeitsleistungen, 1893, p. 417; Kohl, l. c., p. 73.

but this does not necessarily afford positive proof of an increase of extensibility in the cell-walls of the convex side. In addition, it has still to be shown why a plasmolysing solution often produces at first a slight increase of curvature[1], and subsequently a decrease. Possibly this result may be due to the continuance of the tropic induction, but it might also be due to the more rapid penetration on the concave side or to other factors.

The special Metabolism connected with tropic reactions has been investigated by Kraus[2]. Kraus observed a rise in the percentage of reducing sugar and a diminution of acidity, especially in the under-surface of an ageotropic shoot when placed horizontally, even before the upward curvature had begun. During the curvature the total amount of sugar, and often also of free acid, decreased on the convex side. Thus in an etiolated bean-shoot, two hours after being placed horizontally, the upper half contained 0·2358 of a gram, the lower 0·2404 of a gram of reducing sugar, an excess of 0·0046 of a gram. Three-quarters of an hour later, other similarly-treated shoots of the same plant contained 0·2095 of a gram of reducing sugar in the upper half of the stem, and 0·2074 of a gram in the lower half, a deficiency of 0·0021. These changes are not produced in the absence of oxygen.

During and before the commencement of the geotropic curvature the percentage of water in the lower half of the shoot increases, so that the density of the expressed sap decreases. Kraus[3] found, for instance, that in a stem of *Anthriscus sylvestris*, which had been kept in a horizontal position for twenty-four hours, but had only slightly curved, the specific gravity of the expressed sap from the upper side was 1·0240, and that from the lower 1·0226, a difference of 0·0014. This coincides with the fact that during curvature the turgor of the cells on the convex side decreases, as measured by plasmolysis. At the same time, we have an interesting instance of the fact that the distribution of the denser nutrient sap in the tissues is not directly determined by gravity.

According to Kraus, the above changes begin before the commencement of curvature, and are also shown in stems which are no longer capable of curvature. Hence they do not appear to result from the performance of the bending, and, like the latter, represent reactions due to the stimulating action of gravity. Whether any causal relationship exists is, however, as uncertain as in the case of the increase of silver-reducing substances due to the inductive action of gravity, and taking place before the commencement of curvature. It is also uncertain whether changes in the respiratory activity accompany tropic curvature, and whether the phenomena observed are associated with all forms of tropic curvature, although Kraus[4] found similar differences

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[1] Noll, Arb. d. bot. Inst. in Würzburg, 1888, p. 517; 1895, p. 84. Cf. also Pfeffer, Studien zur Energetik, 1892, p. 247.

[2] G. Kraus, Ueber die Wasservertheilung in d. Pflanze, Bd. II, 1880, p. 38, and Bd. I, 1879, p. 23 (reprint from Abhandl. d. Naturforsch. Ges. in Halle). See also Bot. Ztg., 1877, p. 596; Ueber die Wasservertheilung, Bd. IV, 1884, p. 59. [The reducing sugars were estimated in the expressed sap by Fehling's method, which gives, of course, merely the total percentage of reducing substances. The differences observed are small and almost within the limit of experimental error.]

[3] Kraus, l. c., Bd. II, p. 42; Wiesner (Die heliotropischen Erscheinungen, 1878, p. 65) and Thate (Jahrb. f. wiss. Bot., 1882, Bd. XIII, p. 718) were, however, unable to detect any such differences, possibly owing to less exact experimentation.

[4] Kraus, l. c., Bd. II, p. 41.

as the result of heliotropic stimulation. In the case of geotropically stimulated roots, Kraus[1] found an increase in the percentage of water as usual on the convex side, which is here the upper one, while in old non-curving roots geotropic induction produces the same rise in the percentage of water on the upper side, as is shown in the lower side of non-curving old stems.

Similar changes are very rapidly produced by shaking, for Kraus[2] found that after shaking a growing defoliated shoot of *Alliaria officinalis* the amount of sugar rose from 0·1463 to 0·1618 of a gram, while the side kept convex during shaking contained sap of higher density and with a higher percentage of sugar.

PART V

SECTION 55. **Special Cases.**

Although the usual loss of the power of tropic curvature in adult organs may involve a certain disadvantage, nevertheless it would need too great an expenditure of energy and material to render the older parts of a tree not only capable of supporting the other organs but also of performing tropic movements. Hence the plant strives to adjust itself by means of the new shoots, and allows the older organs to remain in positions forced upon them.

ROOTS. The primary geotropic curvature of the main root may be more or less modified by hydrotropic, rheotropic, heliotropic, traumatropic, and aerotropic stimuli. In addition, obstacles may cause the plastic apex to diverge temporarily from its attempted line of growth, but the influence of all these factors upon the growth and shape of the root-system does not require detailed discussion[3]. The avoidance of obstacles does not appear to be the result of any contact stimulation but may in extreme cases partly result from traumatropic excitation. Roots can exercise a considerable downward pressure when lateral displacement is prevented, and the pointed growing apex has a high power of lateral expansion, as have also the older parts of the root during secondary growth. The weight of the seed, or of a thin covering of soil, gives usually a sufficient fulcrum for the downward pressure exercised by the radicle in penetrating an ordinary soil. In many cases the formation of mucilage or the early production of root-hairs aid in fixing the seed[4], while an increased leverage may be assured by the curvature assumed by the hypocotyl.

RHIZOMES are usually diageotropic, but certain forms may temporarily

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[1] Kraus, Ueber die Wasservertheilung, &c., 1880, Bd. II, p. 26.

[2] Kraus, l. c., p. 69.

[3] Freidenfelt, Flora, 1902, Ergzbd., p. 115.

[4] Pfeffer, Druck- u. Arbeitsleistungen, 1893, pp. 362, 365, 369; and for the literature concerning the escape of shoots from the soil, p. 383; also Areschoug, Beitr. z. Biol. d. geophilen Pflanzen, 1896.

become positively geotropic, owing to an aitiogenic or autogenic change of tone. The rhizomes of *Adoxa* and *Circaea* are, for instance, positively geotropic when illuminated, but become diageotropic as soon as their downward curvature below the surface of the soil brings them into darkness. It is, however, not known whether differences in the distribution of oxygen, carbon dioxide, water, and temperature may produce changes of tone or tropic reactions regulating the depth of the rhizome, or whether the distance between the rhizome and the subaerial parts influences the geotropic tone. The latter is, in fact, strongly affected in certain rhizomes by the partial or complete removal of the subaerial organs. Correlative reactions of this kind are often of predominant importance, according to Rimbach[1], although rhizomes of the same plant under similar conditions may vary in depth within wide limits. Müller[2], in fact, concludes that the depth of rhizomes is due solely to extraneous circumstances such as the action of earth-worms and the like. That such factors may influence the depth is certain, but it is hardly possible in this way to explain all the phenomena observed[3]. An instance of correlation is afforded by those cereals in which, according to Schellenberg, the illumination of the leaves influences the development at the nodes to which they are attached[4]. The development of contractile roots which draw bulbs and corms deeper into the soil is possibly also the result of correlative influences, as would also be the cessation of the formation of these roots when an appropriate depth is reached. Naturally other factors may also come into play in determining the position assumed, among which the peculiar downward transference of the corms of young seedlings of *Crocus* is included.

AERIAL STEMS. Owing to the tonic and orienting actions of light, and to the influence of such agencies as wind and moisture, the relationships are here more complicated, while in addition the mere weight of the organ may cause it to diverge more or less from the position which it strives to assume. The erect position of the main axis is largely due to its negative geotropism, while the lateral shoots either assume a plagiotropic position in virtue of their autotropism or are led into particular positions by various aitiogenic influences. The latter applies more especially to the leaves, and here the orienting action of light is naturally of primary importance, although heliotropic stimuli may also influence stems to a pronounced degree.

RUNNERS AND CREEPING SHOOTS[5]. The horizontal or obliquely

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[1] Rimbach, Beiträge z. wiss. Bot. von Fünfstück, 1899, Bd. III, p. 177.

[2] P. E. Müller, Bot. Centralbl., 1896, Bd. LXVI, p. 22.

[3] Areschoug, Beitr. z. Biol. d. geophilen Pflanzen, 1896; Goebel, Organography, 1900, p. 224.

[4] Schellenberg, Unters. über d. Lage d. Bestockungsknoten beim Getreide, 1902, p. 21 (reprint from Forschungen a. d. Gebiete d. Landw.).

[5] Frank, Die natürl. wagerechte Richtung, etc., 1870, p. 17; Bot. Ztg., 1873, p. 36; Czapek,

ascending position is in many cases due to diageotropism, which may either persist unaltered in light and darkness, as in *Fragaria vesca* and *F. grandiflora*, or may change more or less completely into negative geotropism in darkness, as in *Lysimachia nummularia*, *Polygonum aviculare*, *Rubus caesius*, *Vinca major*, and *Stachys sylvatica*, so that the shoots are nearly erect in darkness or when growing in thick grass and obliquely ascending when illuminated. Hence in sunny situations the shoots of these plants are pressed against the ground even when this necessitates a downward curvature.

The power of changing the geotropic tone varies according to the degree of development and morphological rank of the organs, although a day or two is sufficient under favourable conditions to produce a reversal in the active growing zone. Thus in *Glechoma hederacea* the runners formed in spring show a pronounced geotropic erection in darkness, whereas those formed later in the season show none at all[1]. It was owing to this fact that Czapek could detect no change of position in the runners of this plant and also of *Potentilla reptans* in darkness, whereas Maige[2] found that the last-named plant also became negatively geotropic in darkness.

In certain plants the geotropic tone may be modified by changes of temperature, and it is for this reason that the ascending shoots of *Veronica chamaedrys* and *Lamium purpureum* sink to a more or less horizontal position when the temperature is kept low. The photic and thermal changes of geotropic tone will be opposed when doubly responsive plants are subjected to simultaneous rises of temperature and of illumination.

Frank was the first to recognize that permanently diatropic positions were due to diageotropism, but supposed that the changes of position according to the illumination were due to negative geotropism and variable negative heliotropism. Czapek[3], however, showed that the same changes of position took place in homogeneous diffuse light, but not when the plants were rotated on a klinostat. When the action of gravity is eliminated in this way the shoots of *Lysimachia nummularia* and other plants are able to show feeble positive heliotropism[4], whereas the creeping shoots of a few other plants are feebly negatively heliotropic[5].

The runners and creeping shoots of most of these plants are originally physiologically radial, and only acquire a temporary dorsiventrality after

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Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, Abth. i, pp. 1234, 1249; Oltmanns, Flora, 1897, p. 24; Maige, Ann. d. sci. nat., 1900, 7ᵉ sér., T. XI, p. 334; Massart, L'irritabilité d. plantes supérieures, 1902, p. 13.

[1] Maige, l. c.; Oltmanns, l. c., p. 25; Klebs, Willkürliche Entwickelungsänderungen bei Pflanzen, 1903. On the influence of external and internal conditions on the formation of runners cf. Maige, l. c.; Goebel, Organography, 1905, p. 459.

[2] Maige, l. c., p. 340.

[3] Czapek, l. c., p. 1235. Cf. also Oltmanns and Maige, l. c.

[4] Czapek, l. c., p. 1236.

[5] Maige, l. c., p. 358.

remaining for some time in a plagiotropic position. If this acquired dorsiventrality induces a certain tendency to epinastic curvature[1], the latter must play some part in the orientation, as must also the primitive positive or negative heliotropism. Short shoots can raise themselves in spite of the action of gravity, whereas long ones unavoidably droop downwards more or less from their attempted position.

All plagiotropic orientation is not necessarily produced in this way, for many foliage-leaves and other objects are klino-heliotropic and assume their positions mainly in response to the incidence of the light rays. Similarly, under natural conditions negative geotropism and heliotropism may often co-operate in producing a plagiotropic orientation, as for instance when a parallelo-geotropic organ is caused to perform a positively heliotropic curvature by lateral illumination.

Marchantia[2]. As soon as a permanent dorsiventrality has been induced by the action of light, the subsequent growths take up positions like those assumed by dorsiventral leaves. Thus in strong light the thallus becomes approximately perpendicular to the incident rays, and hence usually assumes a plagiotropic position. This orientation is produced by light independently of the action of gravity, so that illumination from beneath may cause the thallus to become inverted. Hence if the apex is illuminated from the front the thallus tends to bend downwards, but rises up when the light comes from behind the apex[3]. In addition the plagio-phototropic position is assumed when the plants are rotated on a klinostat. Nevertheless the thallus reacts geotropically, and becomes erect in darkness, but more and more horizontal as the illumination increases and the predominant action of light comes into play. It is, however, uncertain whether the thallus is permanently weakly negatively geotropic or whether, as Czapek supposes, illumination affects the geotropic tone as it does that of many runners so that in light the thallus is plagio-geotropic as well as plagio-heliotropic.

Sachs found that the thallus of *Marchantia* under ordinary illumination grew at right angles to the direction of a centrifugal force of 3½ g., but was inclined at an angle near the centre of the wheel where the force was less. The exact causation of this result remains, however, uncertain until the action of gravity upon a thallus illuminated equally on all sides is known. Czapek[4] supposed that the radial lobes of the thallus developed on the klinostat were diageotropic, but his experiments are not conclusive. Since the upper side of the thallus may become either concave or convex in assuming a plagiotropic position, the latter is evidently not the result

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[1] Maige, Ann. d. sci. nat., 1900, 7e sér., T. XI, p. 340; Czapek, l. c., p. 1235; de Vries, Arb. d. bot. Inst. in Würzburg, 1872, Bd. I, p. 271.

[2] Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 229; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 260; Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, i, p. 1238.

[3] Sachs, l. c., p. 232.

[4] Czapek, l. c., 1898, p. 263.

of dorsiventral epinasty or hyponasty. It is not yet, however, certain whether a thallus grown in darkness may not perform a photo-epinastic curvature when exposed to light, the curvature increasing as the light becomes more intense.

As was first observed by Mirbel[1], illumination of the under side causes this to become concave until the upper surface is exposed to the light, the curvature being at first towards the light and then away from it. Sachs[2] considered the plagiotropism of *Marchantia* to be due to the interaction of negative geotropism with a positive heliotropism of the lower side, and epinasty in the upper one, whereas Czapek[3] supposed it to result from the co-operation of diaphototropism, photo-epinasty, and a diageotropism varying according to the illumination. The stalks of the fructifications of *Marchantia* are parallo-geotropic and parallelo-heliotropic, and owing to their high heliotropic irritability Sachs (l. c.) found that they assume a position nearly parallel to the incident rays when obliquely illuminated.

THE PROTHALLUS OF FERNS is also oriented mainly by its plagio-heliotropism, and reacts in the same way as does *Marchantia* when illuminated from beneath[4]. Since the induced dorsiventrality is labile, however, the new growths soon have their dorsiventrality reversed, and the orienting movement ceases or may never be shown if it is delayed too long.

HEDERA HELIX[5]. Unilateral illumination induces labile dorsiventrality in the stems of this plant, and so produces the plagiotropic position of the shoot. Hence the ascending stems press themselves against a vertical wall and curve over the top of it away from the light until the free ends bend downwards by their own weight. The hypocotyl as well as the inflorescence axes are, however, radial and ortho-geotropic[6].

When illuminated equally on all sides by rotation on a klinostat the shoots remain radial, while the dorsiventrality may be reversed by illuminating the under-surface. Owing to the slowness of curvature and the relatively rapid reversal of the dorsiventrality, an ivy-shoot when illuminated from beneath curves only slightly towards the light and then curves away from it[7]. It is not known, however, whether geotropic stimuli play any part in the orientation. The shoots of *Hedera* do actually react geotropically, but according to Sachs[8] they are negatively geotropic, whereas according to Czapek[9] they are diageotropic. Sachs states, however, that in a horizontal

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[1] Mirbel, Rech. anat. et physiol. sur le *Marchantia*, 1835 (reprint from Nouvell. Ann. du Muséum d'Histoire nat., T. I). Cf. also Czapek, 1898, l. c., p. 262.

[2] L. c., p. 239.

[3] L. c., 1898.

[4] Leitgeb, Flora, 1877, p. 174; 1879, p. 317.

[5] Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 257; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 258; Sitzungsb. d. Wien. Akad., 1895, Bd. CIV, i, p. 1236; Oltmanns, Flora, 1897, p. 26.

[6] Czapek, l. c., 1895, p. 1236.

[7] Sachs, l. c., p. 267.

[8] Id., p. 269.

[9] Czapek, l. c., 1898, p. 358.

position only slight epinastic curvature takes place, whereas vertical shoots curve until they assume a horizontal position both in light and in darkness. This certainly points to the existence of a diageotropic irritability which is not modified by illumination; but in any case the diageotropism is bound up with the induced dorsiventrality, since the radial shoots appear to be ortho-geotropic. It is possible that unilateral illumination may be capable unaided of producing a diaphototropic orientation, although Sachs[1] considered the plagiotropism to be due to negative heliotropism and geotropism, whereas Czapek[2] supposes it to result from phototropism, diageotropism, and photonasty.

THE PLAGIOTROPIC BRANCHES OF HERBS AND TREES. These appear in the case of *Cucurbita Pepo*[3], *Linaria cymbalaria*[4], and *Tropaeolum majus*[5] to resemble the ivy, in that unilateral illumination induces dorsiventrality. The latter is, however, so feeble in *Tropaeolum* that we may equally well suppose the plagiotropic position to result from the opposed action of diaheliotropism and negative geotropism. Permanently dorsiventral plagiotropic organs are, like radial and temporarily dorsiventral ones, unequally responsive to light and gravity. Naturally the action of light becomes of predominant importance in the case of photosynthetic organs or surfaces, as well as in the stem when the position of the latter is mainly responsible for that of the leaves. This applies to the plagiotropic shoots of *Atropa Belladonna*, *Pilea*, *Pellionia*, *Goldfussia anisophylla*, and *Selaginella*[6], although in part the influence of gravity which is exercised even upon foliage-leaves may predominate. Considerable uncertainty exists, however, in many cases. Thus it is not known whether the dorsiventrality and plagiotropism of *Polygonatum multiflorum*[7] is due to light, to gravity, or to both.

Obliquely ascending radial or dorsiventral branches which bear leaves[8] capable of self-orientation usually show only feeble phototropic reactions, lateral illumination producing little or no heliotropic curvature. The geotropic irritability may, on the other hand, be mainly responsible for the direction of growth assumed, this being always at a definite angle to the perpendicular. The primary and secondary branches of many herbaceous and woody plants may, however, show but feeble geotropic reactions, and have little or no power of plagiotropic orientation. In such cases the branches spread in all directions, and continue any direction of growth

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[1] Sachs, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 266.

[2] L. c., p. 258.

[3] Czapek, Flora, 1898, p. 427; Noll, Landw. Jahrb., 1901, Ergzbd., p. 425.

[4] Oltmanns, Flora, 1897, p. 26.

[5] Sachs, l. c., p. 271.

[6] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 265. Cf. also Wiesner, Ber. d. bot. Ges., 1902, p. 321; Sitzungsb. d. Wien. Akad., 1902, Abth. i, Bd. CXI, p. 733.

[7] Cf. Vöchting, Bewegungen d. Blüthen u. Früchte, 1882, p. 148; Frank, Die natürl. wagerechte Richtung von Pflanzentheilen, 1870, p. 21.

[8] Cf. de Vries, Arb. d. bot. Inst. in Würzburg, 1872, Bd. I, p. 271; Frank, l. c.

impressed upon them. According to Baranetzsky[1], however, these branches are negatively geotropic, but show no geotropic curvature because at the same time an equal and opposed epinastic curvature is excited.

Baranetzsky found that the apices of the branches of *Prunus*, *Fraxinus*, *Tilia*, *Ulmus*, *Philadelphus*, and other woody plants always performed a curvature when directed vertically upwards or downwards or when rotated on a klinostat, the original upper side becoming convex. This epinasty is induced by the action of gravity in whichever side happens to be uppermost. The induction is transitory and reversible, the curvature being automatically straightened again, while the shoots on a klinostat continue to grow in any direction in which they may be placed. Since the epinastic curvature is not shown in the normal plagiotropic position, it must be balanced by an opposed tendency to negatively geotropic curvature[2]. The latter actually appears according to Baranetzsky when a branch is laid flat, which was previously erect or had been rotated on a klinostat for a long time. Hence the epinasty is apparently more slowly induced, but persists longer when the exciting agency is removed than does the hyponastic geotropic induction. Since the epinastic tendency is shown by straight branches, it cannot result, as Baranetzsky supposed, from any realized curvature, although the latter does actually awaken reactions directed towards its removal.

This suppressal of the geotropic reaction is only possible when the epinastic and hyponastic tendencies alter correspondingly as the inclination varies. An autogenic epinasty may aid in balancing the negative geotropism, but it is impossible to follow de Vries in ascribing all plagiotropism to the antagonism of autogenic epinasty and negative geotropism[3]. Wiesner considers that changes of position are due to variations of epinasty, the negatively geotropic action remaining constant. He also concludes that the autogenic epinasty attains its maximal value with a medium rate of growth, so that either a diminution or increase of the average rate of growth increases the geotropic erection. Many of the objects in which Baranetzsky could detect no autogenic epinasty appear to possess this power[4], but it does not follow that relationships of the kind described exist in all cases, nor does their discovery reveal the causes producing them.

Whatever its origin may be, we are dealing with a positively geotropic reaction when a lateral shoot takes the place of the decapitated apex of a Pine, or when without injury the shoots of certain other plants, as occasionally happens, assume an erect position. The distribution of the buds and the factors which affect their development naturally exercise a considerable influence on the type of branching[5]. In addition, all long slender branches droop downwards more or less as the result of

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[1] Baranetzsky, Flora, 1901, Ergzbd., p. 138; Frank, l. c.; de Vries, l. c.; Vöchting, Organbildung im Pflanzenreich, 1884, Bd. II, pp. 4, 93; Wiesner, Ber. d. bot. Ges., 1902, p. 321; Sitzungsb. d. Wien. Akad., 1902, Bd. CXI, Abth. i, p. 733.

[2] [If this is so, the growth of the under side should presumably be more rapid in the normal position than it is on a klinostat.]

[3] Cf. Baranetzsky, l. c., p. 141.

[4] Wiesner, Sitzungsb. d. Wien. Akad., 1902, Bd. CXI, Abth. i, p. 733.

[5] Cf. Goebel, Organography, 1900; Wiesner, l. c., p. 326.

their own weight. The growing apices are, however, usually not only strong enough to bear their own weight, but also to curve vigorously upwards. In some cases the parts which have become woody and ceased to elongate may perform an upward curvature and so counteract the mechanical drooping of the branch. The young shoots of the *Pinus* are at first more erect and then spread horizontally, but this is not due to the influence of their own weight, as Baranetzsky supposed, for Wiesner has shown[1] that to produce such a curvature a load of fifteen to thirty times the weight of the branch is required in the case of *Pinus Laricio*. Vöchting and Baranetzsky have shown, however, that in certain weeping varieties the branches droop owing to their own weight, and the apices continue to grow in the same direction without attempting to curve upwards.

Frank found that the branches of various trees returned to their original position in both light and darkness after forcible displacement, whereas Baranetzsky observed no such return. Further researches must determine whether the apparent contradiction is due to the existence of varying powers of reaction. Frank[2] also observed orienting torsions in twigs of *Abies* in which dorsiventrality had been previously induced, and these can hardly be mechanical in origin as Baranetzsky[3] suggests.

SECTION 56. **The Orientation of Foliage-leaves**[4].

The leaves of such plants as *Erica*, *Dracophyllum*, and *Viscum* orient themselves in regard to the stem alone, and so may stand out at various angles with the perpendicular. Dorsiventral photometric leaves, however, strive usually to place their surfaces at right angles to the direction of the strongest diffuse light, whereas certain other leaves place themselves parallel to it. Other leaves, again, place themselves parallel to the light only when it is so intense that protection against it is needed[5].

Many responsive leaves when displaced in darkness return approximately to their original position, and if necessary by the aid of torsion, so that gravity as well as light may act as an orienting stimulus, and Dutrochet[6]

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[1] Vöchting, Organbildung im Pflanzenreiche, 1884, Bd. II, p. 90; Bot. Ztg., 1880, p. 595; Baranetzsky, l. c., p. 216.

[2] Frank, l. c., p. 22. See also Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 267.

[3] L. c., p. 203.

[4] Bonnet, Unters. über d. Nutzen d. Blätter, 1762, p. 45; Dutrochet, Rech. anat. et physiol., 1824, p. 126; Frank, Die natürl. wagerechte Richtung von Pflanzentheilen, 1870; Bot. Ztg., 1873, p. 72; de Vries, Arb. d. bot. Inst. in Würzburg, 1872, Bd. I, p. 223; Wiesner, Die heliotropischen Erscheinungen, 1880, Bd. II, p. 39; Biol. Centralbl., 1899, Bd. XIX, p. 1; Darwin, The Power of Movement in Plants, 1880; F. Darwin, Linnean Society Journal, 1881, Vol. XVIII, p. 420; Schmidt, Das Zustandekommen d. fixen Lichtlage blattartiger Organe, 1883; Noll, Arb. d. bot. Inst. in Würzburg, 1885-7, Bd. III, pp. 189, 315; Flora, 1892, Ergzbd., p. 265; Vöchting, Bot. Ztg., 1888, p. 501; Krabbe, Jahrb. f. wiss. Bot., 1889, Bd. XX, p. 211; Schwendener und Krabbe, 1892 (Gesammelte Abhandl. von Schwendener, Bd. II, p. 255); Oltmanns, Flora, 1892, p. 231; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 269; Flora, 1898, p. 429; Wiesner, Biol. Centralbl., 1903, Bd. XXIII, p. 209; Ber. d. bot. Ges., 1902, Generalvers. (p. 84).

[5] Cf. Ewart, Annals of Botany, 1897, Vol. XI, p. 447; Wiesner, Biol. Centralbl., 1899, Bd. XIX, p. 1.

[6] Dutrochet, Mémoires, etc., Bruxelles, 1837, p. 312; Vöchting, Bot. Ztg., 1888, p. 549.

showed that centrifugal force acted in the same way as gravity upon leaves. Under normal conditions, however, the influence of light preponderates, so that dorsiventral leaves when illuminated from beneath may bend so as to face downwards. These movements take place independently of the epinastic tendency, which the stimulus of light is in fact able to overcome. The plagio-geotropism of the leaf is also able to overcome its epinasty, so that a leaf which has attained its plagio-geotropic position usually needs only to move slightly in order to become plagio-heliotropically oriented.

Fig. 47. *Coleus* sp. *A*. Plant in normal position. *B*. After a day's rotation on a klinostat.

In addition, the curvature of the stem is usually such as to aid in the assumption of the proper position by the leaves. The movements of the latter are usually performed by the petiole or in sessile leaves by the lamina, and in most cases the power of movement is lost when growth ceases. The latter, however, often persists for a long time in certain regions of the leaf, so that a leaf may remain capable of orienting movements long after it is fully adult. Leaves which possess motile pulvini usually retain this power until death.

De Vries and also Wiesner have assumed that the plagiotropic orientation of leaves is due to negative geotropism and autogenic epinasty, whereas Frank, Darwin, Vöchting, and Krabbe have shown that leaves are not only plagio-heliotropic but also plagio-geotropic. Naturally other factors may influence the position assumed, and among these autogenic epinasty is included, which is often extremely pronounced. Evidence of its existence is afforded by the fact that the leaves often curve strongly backwards when the action of gravity is eliminated on the klinostat (Fig. 47)[1]. When such a plant is inverted, plagio-geotropism and epinasty co-operate so that a very rapid curvature ensues, but if a stronger curvature is produced than in Fig. 47 *B*, on placing the plant on a klinostat a certain hyponastic lessening of the curvature ensues, in place of the original epinasty. The epinasty of certain leaves appears to be increased by a rise of the intensity of diffuse illumination, and possibly a photonastic action of this kind may be responsible for the rising up of leaves in weak light or in darkness. Further evidence is, however, required, for many leaves curve downwards instead of upwards in darkness. The 'radical' leaves of many plants which become more or less erect in darkness press themselves against the soil in strong light, and may even curve downwards when the plant is raised above the level of the soil[2].

The leaf in many cases droops more or less owing to its own weight, but nevertheless the plagiotropic orientation will take place under water, in which an upthrust is exercised on the leaf[3]. In many cases complicated bending or actual torsion is required to return the leaf to its proper position, but since this also is produced under water, it cannot be due to the mechanical action of the weight of the leaf, as de Vries supposed to be the case[4]. Any lateral curvature of the leaf may tend to produce torsion, but nevertheless the energy of movement is sufficient to overcome this action not only in the case of leaves but also of flower-stalks[5]. It is also certain that some of the torsions shown by branches are not mechanical in origin, as Baranetzsky[6] supposed them all to be.

Orienting torsions are produced in darkness by gravity, but are still better shown as the result of suitable lateral illumination[7], although in many cases only under the conjoint action of a gravitational stimulus. Thus, on a klinostat the leaves of *Viola* and *Dahlia* no longer react to lateral illumination, while those of *Phaseolus*, *Soja*, and *Acacia* orient themselves to the light by pronounced curvature without torsion[8]. The flowers of *Viola* orient themselves by torsion on a klinostat to lateral illumination, so that the co-operation of gravity is not always required for the production of torsion[9]. It is, however, uncertain whether the orientation of the leaves of *Malva*

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[1] F. Darwin, Linn. Soc. Journ., 1881, Vol. XVIII, p. 426; Vöchting, l. c., 1888, p. 534; Krabbe, l. c., 1889, p. 248; Schwendener und Krabbe, l. c., 1892, p. 340.

[2] Frank, Die natürl. wagerechte Richtung von Pflanzentheilen, 1870, p. 45; Darwin, Insectivorous Plants, 1876, p. 343; Wiesner, l. c., 1880, p. 43; F. Darwin, l. c., 1881, p. 430; Vöchting, Bewegungen d. Blüthen u. Früchte, 1882, p. 179; Neger, Flora, 1903, p. 371.

[3] Bonnet, l. c., 1762, p. 61; Frank, Bot. Ztg., 1873, p. 55; Noll, l. c., p. 222.

[4] De Vries, l. c., 1872, p. 266; Wiesner, l. c., 1882; O. Schmidt, l. c., 1883.

[5] Vöchting, l. c., 1888, p. 552; Noll, l. c., 1885-7, pp. 220, 337.

[6] Baranetzsky, Flora, Ergzbd., 1901, pp. 211, 194.

[7] [The suggested terms 'geotortism' or 'geostrophism' and 'heliotortism' or 'heliostrophism' are as unnecessary as would be 'helioturgotropism' or 'geoheterauxecism.']

[8] Krabbe, l. c., 1889, p. 244; Schwendener u. Krabbe, l. c., 1892, p. 339.

[9] Schwendener u. Krabbe, l. c., 1892, pp. 327, 335, 348.

neglecta[1] on a klinostat, and the similar instances observed by Darwin[2], afford true cases of torsion. No orientation by torsion is produced by the action of light upon most dorsiventral flowers, whereas gravity exercises this effect upon the flowers of *Aconitum*, *Delphinium*, and *Scrophularia*[3].

Tropic orientation to a single agency may be performed by torsion as well as by curvature, and since the former only requires the existence of a physiological dorsiventrality, it is not surprising that Schwendener and Krabbe[4] should fail to detect in the peduncle of *Aconitum* any visible signs of morphological dorsiventrality. On the other hand, Vöchting[5] found that the small flowers, which *Impatiens* develops in darkness, act like radial organs. Noll[6] assumed that the supporting axis radiated an 'exotropic' influence upon the orientation of dorsiventral flowers and leaves, but there is no evidence of any such action in the case of leaves, while the stalks of the dorsiventral flowers of *Aconitum* place themselves at a definite angle with the perpendicular, and hence with the axis of the inflorescence, owing to their geotropic irritability. According to Czapek[7] the pedicel of *Aconitum* performs its orienting torsion when the flower is removed, but according to Meissner this is not the case[8].

It is probably owing to correlative influences that after the severance of the inflorescence of *Orchis* the flower-buds near to the injury perform simple geotropic curvatures in assuming their proper position instead of the normal torsion movements[9]. In addition, a realized torsion excites a counter-action, which is sufficient to remove the torsion of a pulvinus of *Phaseolus* when the agency inducing it is removed. Autogenic torsions may also occur, as, for instance, when the leaves of *Allium ursinum* and *Alstromeria* change from the inverted position to the normal one as they expand from the bud. These leaves are also capable of aitiogenic torsion[10].

Although the detailed mode of production of torsion is unknown it certainly is not necessarily always the result of growth movements, although these usually accompany it. Noll[11] assumes that torsion is due to the co-operation of dissimilar tendencies to curvature, which may possibly apply in certain cases in spite of Schwendener and Krabbe's dictum to the contrary[12]. The fact that certain torsions cease when the stimulating action of gravity is eliminated shows that the combined action of more than one stimulus may be necessary to produce them.

If a plant of *Chenopodium*, *Coleus*, or *Helianthus* is inverted and the curvature of the main axis prevented, the leaves at first sink slightly owing to their own weight. An upward curvature then begins, due to the co-operation of epinasty and geotropism or heliotropism, which continues in active leaves until the dorsal side again faces upwards. In many cases this curvature is not completed, owing to the early or late

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[1] Vöchting, Bot. Ztg., 1888, p. 534.

[2] F. Darwin, l. c., 1881, p. 426.

[3] Noll, Arb. d. bot. Inst. in Würzburg, 1885–7; Schwendener u. Krabbe, l. c., 1892.

[4] L. c., p. 317.

[5] Vöchting, Jahrb. f. wiss. Bot., 1893, Bd. XXV, p. 179.

[6] Noll, l. c., 1885–7, Bd. III, p. 367; Flora, 1892, Ergzbd., p. 273; Schwendener u. Krabbe, 1892, Gesammelte Abhandl., Bd. II, p. 255.

[7] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 279.

[8] Meissner, Bot. Centralbl., 1894, p. 12.

[9] Noll, l. c., p. 329.

[10] Czapek, Flora, 1898, p. 249. Cf. Goebel, Organography, 1900, p. 250.

[11] Noll, l. c., 1885–7 and 1892. Cf. also Meissner, Bot. Centralbl., 1894, Bd. LX, p. 1.

[12] Schwendener u. Krabbe, l. c., 1892.

commencement of an orienting torsion in the petiole. It is by a torsion of this kind that the young leaves on hanging branches of *Fraxinus*, *Caragana*, *Salix*, and *Betula* assume their proper positions.

If the stem is placed in a horizontal position the lateral leaves perform an epinastic backward curvature, and then by torsion and a forward movement come to face upwards with the lamina parallel or obliquely inclined to the stem. The leaves on the upper side may attain a suitable position by the primary epinastic and geotropic backward curvature, but frequently they do not reach or retain this position, lateral curvatures coupled with torsion bringing them into positions similar to those assumed by the lateral leaves. The same applies to the leaves on the under side.

It is in this way that the leaves on plagiotropic shoots of *Vinca*, *Glechoma*, *Lysimachia nummularia*, *Buxus*, *Acer*, and *Taxus* assume a more or less complete dorsiventral arrangement, whereas on erect shoots they are radially arranged[1] (Fig. 48). The decussate leaves of *Deutzia*, *Lonicera* and *Philadelphus*, as well as the spirally-arranged ones of *Spiraea salicifolia* and *Kerria japonica*, are caused to assume an exact two-rowed arrangement in sloping and horizontal shoots by the twisting of the internodes, so that the individual leaves need only twist slightly to place themselves in a horizontal position. This torsion only begins in each internode when that in the precedent one is completed, so that unnecessary torsion is avoided[2]. The torsion is not only produced by gravity, but also in erect shoots by unilateral illumination[3], and since the leaves then exercise no torsion moment on the stem, it is

FIG. 48. ***Euonymus radicans.*** ***A***, **a vertical shoot with decussatel eaves.** ***B***, **a horizontal shoot.**

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[1] Frank, Die natürl. wagerechte Richtung von Pflanzentheilen, 1870, pp. 14, 37, 57, 64. See also the figures in Kerner's Natural History of Plants, 1894, Vol. 1, pp. 417–23.

[2] Frank, l. c., p. 16.

[3] Schwendener u. Krabbe, l. c., p. 320.

evident that de Vries[1] was incorrect in supposing that the twisting of the internodes was due to the mechanical action exercised by the weight of the leaves. The absence of torsion in the internode when the pair of leaves are removed may be due to a change of tone, or to the cessation of the directive influences radiating from the leaf. According to de Vries, the torsion of the internode of *Philadelphus* is inhibited by the removal of the upper but not by that of the lower leaf. This requires further investigation, however, as does also the absence of torsion in the defoliated branches of *Ulmus* and *Celtis*[2], since Czapek[3] found that similarly treated branches of *Taxus* and *Picea* do undergo torsion[4].

INTENSE LIGHT or direct sunlight causes many photometric leaves to rise, sink, or twist in such fashion as to place their laminas or those of the leaflets more or less parallel to the incident rays. This is especially well shown by the compound leaves of *Mimosa pudica* in which the primary pulvini set the plane of the leaf during the daytime in a plagiotropic position which is the resultant of the diageotropic and diaheliotropic irritability. The pulvini of the leaflets are, however, able to perform one movement only, and this is photonastic in character. In ordinary light the leaflets are expanded, in darkness and in intense light they close. The latter movement depends

FIG. 49. A horizontal shoot of *Diervilla lonicera*. From the edges of the stem it can be seen that the torsion is completed in the internodes 1, 2, and 3, while internode 4 is still straight.

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[1] See Noll, Arb. d. bot. Inst. in Würzburg, 1885–7, Bd. III, p. 358; Schwendener u. Krabbe, l. c., p. 320.

[2] De Vries, l. c., p. 272.

[3] Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 288.

[4] On the orientation of Mosses and their protonomata see Coesfeld, Bot. Ztg., 1892, p. 192; Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 265; Correns, Festschrift f. Schwendener, 1899, p. 385. A summary of the orienting movements of flowers is given by Noll, Arb. d. bot. Inst. in Würzburg, 1885–7, Bd. III, pp. 189, 315. See also Wiesner, Biol. Centralbl., 1901, Bd. XXI, p. 801; the quoted works of Schwendener u. Krabbe, Oltmanns, Czapek, as well as Vöchting, Jahrb. f. wiss. Bot., 1886, Bd. XVII, p. 297; 1893, Bd. XXV, p. 179; Schaffner, Bot. Centralbl., 1898, Bd. LXXVI, p. 22 (*Helianthus*); Meissner, Bot. Centralbl., 1894, Bd. LX, p. 1.

solely upon the intensity of the light rays independently of their direction or heating effect, and hence the leaflets fold together when the sunlight is reflected upon the pulvini from beneath, but expand when the pulvini are shaded and the laminas fully exposed[1]. When the leaf is strongly illuminated from the side the main pulvinus twists into a more or less diaheliotropic position and the leaflets perform the same closure as before in response to the intense light. We have, therefore, here an instance in which the irritability in the pulvini of the same leaf varies according to their position and the task they have to perform. All leaves provided with pulvini seem able to respond to intense illumination, although it is not in all cases certain whether the response is photonastic or heliotropic in character.

Photometric leaves which respond by growth-curvatures may, however, also place themselves at varying angles with the direction of intense illumination. It is, however, only rarely that they attain a profile position as in *Lactuca virosa*, *Silphium laciniatum*, and a few other plants, in which the position is assumed by a torsion at the base of the leaf. Since this orientation is mainly due to the intense midday sun, the leaves of these so-called compass-plants set their laminas in exposed localities, mainly in a perpendicular plane running north and south, whereas in shady situations the leaves show neither this orientation nor do they assume the profile position[2].

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[1] Cf. Ewart, Annals of Botany, 1897, Vol. XI, p. 448.

[2] Stahl, Ueber sogenannte Compasspflanzen, 1881 (reprint from the Zeitschr. f. Naturwiss., Bd. XV); Oltmanns, Flora, 1892, p. 248; Bay, Botanical Gazette, 1894, Vol. XIX, p. 251. On the branching system of *Biota* see Czapek, Jahrb. f. wiss. Bot., 1898, Bd. XXXII, p. 268.

CHAPTER IV

LOCOMOTORY AND PROTOPLASMIC MOVEMENTS

PART I

THE CHARACTER AND MECHANISM OF MOVEMENT

SECTION 57. **General.**

APART from the spermatozoids of vascular cryptogams and a few Gymnosperms, no power of independent locomotion is shown by any vascular plant. Many Fungi, and an even larger number of Algae, produce motile zoospores, and in the case of many Volvocineae, Flagellatae, Bacteria, Diatomaceae, and Myxomycetes the power of active locomotion is only interrupted by certain resting stages, or during reproduction.

Motile organisms are usually free-swimming and possess special locomotory organs such as cilia or flagellae; but others creep or glide over the substratum, and others again show amoeboid movements over moist surfaces or even under water. No plant or part of a plant is, however, able to propel itself through the air, although spores and winged seeds may float in it for some time. The different types of movement are not always sharply distinguished, and the zoospores of Myxomycetes may perform alternately amoeboid and ciliary locomotion. Indeed, transitions occur between transitory pseudopodia and typical cilia, while certain Infusoria may either swim freely or run over the substratum by the aid of their cilia. A swimming movement will always become a gliding one when an organism is fixed to the substratum by a mucilaginous layer, which is viscous enough to prevent the upward escape of the organism but not its lateral movement.

Transitions also occur between the active movements of rooted plants and of free-swimming organisms. Thus a swarm-spore attached at one end performs nodding and bending movements like a rooted plant. In addition, the movement of certain Desmids due to the excretion of a gelatinous stalk may be compared with the movement of a growing apex produced by the elongation of the zones beneath. Growth curvatures cause locomotory movements in the free threads of *Spirogyra*, and may also cause them to group together in bunches.

Dermatoplasts may remain capable of swimming and gliding movements, whereas the production of a rigid cell-wall renders external amoeboid movement impossible so long as no extra-cellular protoplasm is present.

Various internal amoeboid movements are still possible, as well as streaming, and slow changes in the shape and position of the organs. Visible movements are never entirely absent, though often extremely slow, so that a slight change of position can be seen only after a considerable time. Slow movements necessarily accompany the growth of the cell and the conversion of a solid protoplast into a vacuolated one, while cellular and nuclear division involve special grouping and separating movements. Active growth does not, however, involve active movement, and protoplasmic streaming is, for instance, absent from the cells of the primary meristem. Streaming persists in many adult cells so long as they remain living, whereas in other cells it is not aroused during the most active respiration and metabolism.

The ejection of seeds may be regarded as a passive movement even when due to tensions created by vital activity. The same applies to the rise of algal filaments owing to the adherence of bubbles of gas to them. If the gas is oxygen produced by photosynthesis, the movement is indirectly due to vital activity, just as when the air-spaces formed in shoots cause them to ascend as soon as they have developed from the resting buds, which sank the previous autumn owing to their higher specific gravity[1]. Certain lower organisms possess gas vacuoles within the protoplasm, and these may be used like the air-bladders of fishes to produce ascent and descent in the water[2]. It it, however, uncertain to what extent modifications in the specific gravity of the protoplasm and cell-sap may take part in flotation[3].

For such movements not only the specific gravity but also the shape and relative amount of surface are of importance. This is evidenced by hairy and winged seeds, and by the transport of dried bacteria and other micro-organisms, as dust particles in the air[4]. In the same way slow currents of water suffice to prevent the settling of minute particles denser than the water, although in the case of plankton organisms active movements may aid in producing the same result[5].

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[1] Cf. Goebel, Pflanzenbiol. Schilderungen, 1893, T. ii, p. 356. On the work done in forming intercellular spaces cf. Pfeffer, Energetik, 1892, p. 232.

[2] On gas vacuoles see Engelmann, Pflüger's Archiv f. Physiol., 1869, Bd. II, p. 307; Klebahn, Flora, 1895, p. 241; Strodtmann, Biol. Centralbl., 1895, Bd. XV, p. 113; Celakovsky, Ueber den Einfluss des Sauerstoffmangels auf die Bewegung einiger aëroben Organismen, 1898, p. 21 (reprint from Bull. internationale de l'Académie de Bohême); Wille, Biol. Centralbl., 1902, Bd. XXII, pp. 207, 257; Molisch, Bot. Ztg., 1903, p. 47; Hinze, Ber. d. bot. Ges., 1903, p. 394.

[3] Cf. Brandt, Biol. Centralbl., 1895, Bd. XV, p. 855; Schütt, Jahrb. f. wiss. Bot., 1899, Bd. XXXIII, p. 680.

[4] Nägeli, Sitzungsb. d. Bayerisch. Akademie, 1879, p. 389; Ostwald, Biol. Centralbl., 1902, Bd. XXII, p. 596.

[5] On Brownian or 'molecular' movements see Exner, Ann. d. Physik, 1901, II, 4, p. 843; Lehmann, Molekularphysik, 1889, Bd. I, p. 264; Bd. II, p. 7. Seeds and spores which are not wetted by water may be supported on the surface-tension film, and appear to float. Cf. Nägeli, Beiträge z. wiss. Bot., 1860, Heft ii, p. 105; Nägeli u. Schwendener, Mikroskop, 1877, 2. Aufl., p. 377.

Mechanical factors of this kind are of the greatest biological importance[1], for they aid in the dispersal of seeds, pollen-grains, spores, and bacteria by wind and water. The same applies to many freely motile organisms, which are only able to cover comparatively small distances by the aid of their own activity, since their absolute velocity of movement is small. Within these limits, however, the organisms are able to seek out the regions where the best conditions for their nutrition and development prevail.

SECTION 58. **Ciliary Movement.**

Most motile vegetable organisms possess fine hair-like protoplasmic projections, which are termed cilia when small and numerous, flagellae when long and few in numbers, although naturally transition forms occur. In some cases the cilia are uniformly distributed, but in others are grouped in one or more bundles, while the flagellae are usually restricted to a definite point on the body[2].

Many of the gametes and zoospores of Algae, as well as the cells of *Chlamydomonas*, have two flagellae attached at the germinal spot, while the zoospores of *Oedogonium* have a group of large flagellae arranged around the anterior hyaline end[3]. In these radial objects the flagellae are placed at the anterior end of the oval body, whereas in the dorsiventral Peridineae and in the zoospores of Phaeophyceae they are laterally inserted. The zoospores of *Vaucheria* have cilia over their whole surface[4], and the same applies to the coenobia of *Pandorina* and *Volvox*, although the individual cells have each a pair of cilia only. In another member of the Volvocineae, *Gonium*, the individual cells are arranged to form a flat plate-like expansion covered with cilia on one side.

Among Bacteria the cilia may either be distributed all over the body or a tuft or a single cilium may be present at one or both ends. The latter applies usually to *Spirillum*, which is spirally twisted like the sperms of Ferns, although these have only the anterior end covered with a diffuse tuft of cilia. The sperms of Mosses are rod-like in shape, and have only a pair of cilia at the anterior end.

A few of the zoospores mentioned have cilia of unequal size, and in many Flagellatae and Peridineae one of the flagellae is pointed in the

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[1] Cf. Ludwig, Biologie der Pflanzen, 1895.

[2] Cf. Hertwig, Die Zelle und die Gewebe, 1893, p. 64.

[3] See Hofmeister, Pflanzenzelle, 1867, p. 28; Falkenberg in Schenck's Handbuch d. Botanik, 1882, Bd. II, p. 194 (Algae); Zopf, Die Pilze, 1890, p. 61 seq.; A. Fischer, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 84 (Bacteria); Migula, System d. Bacterien, 1897, Bd. I, p. 97; Ellis, Centralbl. f. Bact., 2. Abth., 1902, Bd. IX, p. 546. On animal organisms and certain lower Algae cf. Bütschli, Die Protozoen, 1880–9. On Flagellatae and Peridineae cf. also A. Fischer, Jahrb. f. wiss. Bot., 1894, Bd. XXVI, p. 230; Schütt, Die Peridineen d. Planktonexpedition, 1895, p. 111.

[4] Cf. Strasburger, Histologische Beiträge, 1900, Heft vi, p. 187.

direction of locomotion, while the other trails behind like a rudder. Many animals possess in addition to large motile cilia others which function as organs of taste or touch, while the ciliated epithelium of Vertebrata no longer serves for bodily locomotory but for other purposes.

All free-swimming forms possess cilia as locomotory organs, and these either vibrate to and fro or, when large, perform a corkscrew-like action through the water, drawing the organism after them. If the cilia or flagellae are removed or thrown off, the movement of the organism ceases[1]. In the case of minute bacteria, however, the movement of the cilia cannot be directly followed. Even in the case of the swarm-spores of Myxomycetes the free-swimming is due to the cilium and not to any amoeboid movement, although this may be shown at the same time[2]. Most zoospores, however, even when naked, have no power of amoeboid movement, and there seems to be no free-swimming organism devoid of cilia. The latter were recognized as locomotory organs by Unger[3], and Nägeli's assumption that they were only passively moved like the oars of a boat was shown by Siebold to be incorrect[4]. The supposition that bacteria moved without the aid of cilia was disproved by the detection of these organs by special methods of fixing and staining[5]. Berthold[6], however, assumes that the swarm-cells of *Erythrotrichia* move without the aid of cilia, and it is not impossible that locomotion might be produced by the backward ejection of water absorbed laterally or anteriorly. That certain zoospores such as those of *Chromophyton rosanoffii*[7] should be able to creep on the surface of the water is not surprising, since the surface-tension film is capable of affording the required resistance.

The forward movement is usually accompanied by one of rotation around the organism's own axis, and the ciliated end is usually first[8]. Under these circumstances the cilia must draw the body onwards, whereas when they are at the hinder end they must push it forwards. The latter is the case in *Chytridium vorax*[9] and *Polyphagus euglenae*[10], and possibly it may be

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[1] Strong shaking often causes the cilia to be thrown off. Cf. Strasburger, Wirkung des Lichtes u. d. Wärme auf Schwärmsporen, 1878, p. 6. If a zoospore is nipped in two during its escape from the zoosporangium, only the ciliated portion shows any free-swimming movement. Cf. Hofmeister, l. c., p. 29.

[2] For instances see Plenge, Verhandl. d. naturh.-med. Vereins in Heidelberg, 1899, N. F., Bd. VI, p. 216; Kolkwitz, Bot. Centralbl., 1897, Bd. LXX, p. 186. On the mechanical distortions of antherozoids cf. Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 394.

[3] Die Pflanze im Momente der Thierwerdung, 1843, p. 93.

[4] Nägeli, Gattungen einzelliger Algen, 1849, p. 22; Siebold, Zeitschr. f. wiss. Zoologie, 1849, I, p. 287.

[5] Cf. A. Fischer, l. c.; also Migula, l. c.

[6] Berthold, Protoplasmamechanik, 1886, p. 125.

[7] Woronin, Bot. Ztg., 1880, p. 630.

[8] Nägeli, Beiträge z. wiss. Bot., 1880, Heft 2, p. 96.

[9] Strasburger, Die Wirkung des Lichtes u. d. Wärme auf Schwärmsporen, 1878, p. 13.

[10] Nowakowski, Cohn's Beiträge z. Biologie, 1877, Bd. II, p. 208.

of common occurrence, since this mode of progression is usually adopted by the spermatozoa of animals[1]. In general, there is a definite relation between the direction of movement and the direction of the main axis. Thus in *Volvox*[2] the vegetative or trophic pole goes first, while in the ellipsoid zoospores of *Vaucheria*, as well as in equipolar ellipsoid individuals of *Pandorina*[3], the long axis is parallel to the direction of movement and in the same line. In all these cases the continually active cilia must work in harmony, since if they all acted in different directions, no definite locomotion could be produced.

The same applies to the diffusely ciliated as well as to the bipolar bacteria. Among the latter *Spirillum undula* is included, and it moves alternately with one end first, and then with the other after a period of rest[4]. Intermittent movement is in fact shown by many motile organisms[5]. In the case of *Spirillum* it is not known whether the cilia at each end undergo a periodic reversal in their mode of action, or whether only one set acts at a time, and whether the two groups produce movement in opposed directions. The organism may either follow a spiral path around an ideal axis or may move along a straight or curved line parallel to the long axis of the body. In the former case the ideal axis may either be parallel or inclined to the long axis of the body[6].

The movements of the cilia are autogenic in character and either pursue the same rhythm under constant external conditions or may be subject to self-regulatory periodic inhibition or reversal[7]. As in the case of other forms of movement, the external conditions may modify the ciliary activity, and may under special circumstances produce a reversal of the movement. The same result may on occasion be caused by an autogenic or aitiogenic modification of the orientation of the cilia in regard to the body. Possibly it is in this way that *Paramaecium* is induced to move in the opposite direction to the normal one when placed in 0·4 to 0·7 per cent. solutions of sodium chloride[8]. According to Pütter the backward direction of movement continues until the organisms have accommodated themselves to the salt solution.

In many cases the impact against a foreign body causes the organism

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[1] Hertwig, Zelle u. Gewebe, 1893, p. 65.

[2] Overton, Bot. Centralbl., 1889, Bd. XXXIX, p. 68.

[3] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 443. The same applies to *Gonium*, in which the long axis of the body is the shorter axis of the colony. On *Stephanosphaera* see Cohn, Zeitschr. f. wiss. Zoologie, 1853, Bd. IV, p. 84.

[4] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. II, p. 591; Migula, System d. Bacterien, 1897, Bd. I, p. 108.

[5] Bütschli, Die Protozoen, 1880–9, p. 850.

[6] Nägeli, l. c. Cf. also Bütschli, l. c., p. 850. On the importance of the rotation of the body in asymmetric organisms cf. Jennings, The American Naturalist, 1901, Vol. XXXV, p. 369.

[7] Loeb, Pflüger's Archiv f. Physiologie, 1897, Bd. LXVI, p. 533.

[8] Pütter, Arch. f. Anat. u. Physiol., physiol. Abth., Supplementband, 1900, p. 297.

to withdraw somewhat while the rotation around its own axis is reversed. The normal rotation and forward movement is then resumed and may again produce an impact against an obstructing plate of glass[1]. At the same time, the orientation is usually somewhat altered, so that on the next forward movement the organism has a better chance of avoiding the obstacle. In other cases the organism continues the normal rotation around its own axis when the glass plate prevents any forward movement. According to Nägeli, organisms which normally move in a straight line remain pressed against the same point of the glass, but perform circles on the surface of the glass when they have a natural tendency to eccentric or spiral movement. In other cases, as for instance when the organism glides or creeps over a solid substratum, the former locomotion continues, while the rotary movement ceases[2]. The boat shape of the free-swimming *Bodo saltans* causes the twisting movement of the cilia to produce a rocking movement but no rotation[3].

Since both locomotion and rotation are due to ciliary activity, it is not surprising that the same type of rotation should be retained so long as the direction of movement is unaltered. The ciliary activity might, however, easily be so modified as to reverse the rotation without producing any change in the direction of locomotion, but observations pointing to this conclusion must be accepted with caution[4]. A reversal of this kind does, however, appear to be satisfactorily established in the case of *Gonium pectorale*[5].

The rapidity and duration of the movement are naturally very dependent upon the external conditions. Antherozoids, as well as the asexual zoospores of Algae and Fungi, come to rest after a definite period of activity, which may be comparatively short. It is, however, possible under special nutrient conditions to keep bacteria, the swarm-spores of Myxomycetes, and possibly also many Flagellatae and Volvocineae, permanently motile, and to prevent the recurrence of any resting stage[6].

Even under favourable conditions the most active plant zoospores do not attain the speed of movement of Infusoria, and progress but slowly in absolute measure. The highest velocity does not appear to exceed 1 mm. per second, and is often not above 0·05 mm. per second[7]. A zoo-

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[1] Cf. Nägeli, Beiträge zur wiss. Bot., 1880, Heft 2; Bütschli, l. c., p. 854; Jennings, Centralbl. f. Physiol., 1900, Bd. XIV, p. 106.

[2] See Nägeli, l. c., p. 101; Bütschli, l. c., p. 853; Schütt, Die Peridineen d. Planktonexpedition, 1895, p. 117; Jennings, American Naturalist, 1901, Vol. XXXV, p. 372.

[3] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. II, p. 594.

[4] Cf. also Bütschli, l. c., p. 853.

[5] Migula, Bot. Centralbl., 1890, Bd. XLIV, p. 104; Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 443. Cf. also Nägeli, l. c., p. 97.

[6] On the zoospores of Myxomycetes cf. Klebs, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 196.

[7] According to Hofmeister, Pflanzenzelle, 1867, p. 30, the zoospores of *Aethalium septicum* cover per second 0·7–0·9 mm., and those of *Gonium pectorale* 0·046 mm. See also Nägeli, l. c.;

spore which moves at a speed of 0·2 mm. per second appears to move very rapidly under a magnification of 300 diameters, since in one second it appears to cover a distance of 60 mm., although it actually only traverses 720 mm. in the course of an hour. Relatively to their size, however, these motile organisms are very active, for they may travel two or three times their length in a second, whereas a man while walking may cover about the half of his length in a second, an express-train may travel about one-third of its length in a second, and the earth moves through a space of about $\frac{1}{420}$ of its diameter per second as it rotates around the sun[1]. A swallow may, however, cover 100 times, and a bee more than 1,000 times its length in a second, but here the movement is in a less resistant medium. Many active fishes may cover their own length or several times their length in a second, so that the zoospore is in this respect inferior as a locomotory organism. Owing to the small size and relatively large surface of the zoospore, it needs a greater expenditure of energy per unit mass to give it the same velocity as a larger organism[2]. Zoospores may indeed drag with them adhering bodies greater than themselves.

Such forms as *Chlamydomonas* and *Euglena* respond at first by a negatively geotropic movement when exposed to increasing centrifugal action, and are only overcome by its mechanical action when its intensity is eight times that of gravity. It follows that these organisms are able to lift about eight times their own weight in water[3], and according to Jensen *Paramaecium* may raise nine times its own weight. Owing to the smallness of the organism, however, about 600 would be required to raise one milligram[4]. To do this the two cilia of *Chlamydomonas* or the single one of *Euglena* must develop as much energy as the cilia of ciliated epithelium[5]. The strength of these organisms, is, therefore, greater than that of a horse, which is able to lift a load about its own weight, whereas an insect can raise a load about sixty-seven times greater than its own weight[6]. In any case it is only to be expected that the movements of cilia and of

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Bütschli, l. c.; and Bd. II, § 143. On Bacteria see Lehmann, Centralbl. f. Bact., 1903, 2. Abth., Bd. X, p. 545.

[1] Nägeli, Beiträge zur wiss. Bot., 1880, p. 30.

[2] Cf. Pfeffer, Studien zur Energetik, 1892, p. 255.

[3] Schwarz, Ber. d. bot. Ges., 1884, p. 60.

[4] Jensen, Centralbl. f. Physiol., 1893, Bd. VII, p. 568.

[5] Cf. Engelmann in Hermann's Handbuch der Physiologie, Bd. I, p. 392.

[6] See Jensen, l. c. [These comparisons are without value, since in the one case the weight lifted is in water, but in the other in air. The experiments on centrifugal action can only yield accurate results when the relative densities of the *Paramaecium* and of the liquid are known. A living *Paramaecium* is evidently not much denser than the liquid in which it lies, so that but little more work is done when swimming upwards than when swimming downwards, and in any case the actual lifting power is relatively trifling. A *Paramaecium* having a diameter of 0·2 mm. when spherical would have a volume of $\frac{1}{250}$ cub. mm., so that thirty living ones would be needed to lift a mass of one cubic millimetre of inactive *Paramaecia* in water; but the actual power of work cannot be given.]

zoospores should be considerably retarded in viscous media, and should cease in moderately firm gelatine[1].

Cilia are living plasmatic organs which in some cases may protrude through an investing cell-wall[2]. They arise, therefore, in the same way as pseudopodia, and like these may be retracted in certain cases[3]. When highly specialized, however, they are usually thrown off when injured, but undergo the deformations characteristic of living protoplasm throughout their whole substance. Whether cilia are connected with the nucleus or with centrosomes or with special blepharoplasts (cilium formers, or prominences bearing cilia), they possess a certain degree of autonomy like other plasmatic organs. Hence ciliary movement may continue for a time on separate non-nucleated fragments of a cell, or even on isolated cilia[4]. Nevertheless attached cilia must be partially governed by the cell to produce harmonious movement, although it is not certain whether each cilium is isochronous or may vary its phases of movement within certain limits. It is not necessary that the cilia should all be exactly isochronous to produce the even harmony of movement in a colony of *Volvox*[5] or *Eudorina*. According to Migula the cilia of the cells of *Gonium* do not work as harmoniously and regularly as those of *Volvox*. Interprotoplasmic communications occur between the cells of *Volvox*[6], but have not been detected in the case of *Gonium*, and the existence of a disharmonic ciliary movement affords no proof of their absence. In ciliated epithelium and in ciliated infusoria waves of action run over the cells or body, each cilium bending over a little later than the one behind it, but all retaining the same rhythm. The undulatory rhythm is maintained by non-nucleated fragments of Infusoria, so that the regulation is due to the ectoplasm[7].

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[1] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 391.

[2] On the formation of cilia cf. Zimmermann, Beihefte z. bot. Centralbl., 1894, Bd. IV, p. 169; A. Fischer, Jahrb. f. wiss. Bot., 1894, Bd. XXVI, p. 207; 1895, Bd. XXVII, pp. 34, 126; Strasburger, Histologische Beiträge, 1900, Heft 6, p. 188; Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 520; Plenge, Verhandl. d. naturh.-med. Vereins in Heidelberg, 1899, N. F., Bd. VI, p. 218; R. Hertwig, Archiv f. Protistenkunde, 1902, Bd. I, p. 22; Maier, Archiv f. Protistenkunde, 1903, Bd. II, p. 73.

[3] For instances see Strasburger, 1901, l. c., p. 521. According to Rothert (Ber. d. bot. Ges., 1894, p. 277), the zoospores of *Saprolegnia* retract their cilia at the end of the first swarm-stage, but not at the close of the second period of activity. On pseudopodia cf. Plenge, l. c.; Hertwig, Zelle u. Gewebe, 1893, pp. 26, &c.; Verworn, Allgem. Physiologie, 1901, 3. Aufl., p. 248. On the pseudopodia of *Amoeba radiosa*, which vibrate like cilia, cf. Bütschli, l. c., p. 856.

[4] See A. Fischer, 1895, l. c., p. 73; Plenge, l. c., p. 261. On Infusoria cf. Verworn, Psycho-physiol. Protistenstudien, 1889, p. 169; A. Fischer, l. c.; Jennings and Jamieson, Biological Bulletin, 1902, Vol. III, p. 225.

[5] On *Volvox* cf. Klein, Jahrb. f. wiss. Bot., 1889, Bd. XX, p. 162; Migula, Bot. Centralbl., 1890, Bd. XLIV, p. 104.

[6] Kohl, Beihefte z. bot. Centralbl., 1902, Bd. XII, p. 345; Klein, l. c.; Migula, l. c.; Goebel, Organography, 1900, Vol. I, p. 28.

[7] Verworn, Psycho-physiol. Protistenstudien, 1889, p. 183. On ciliate epithelium cf. also Engelmann in Hermann's Handbuch d. Physiologie, 1879, Bd. I, p. 385.

The mode of movement of cilia. In the case of typical ciliated epithelium the cilia bend sharply over in one plane and then more slowly return to their original position[1]. Naturally rotation will in such cases only result when the free-swimming body is appropriately shaped or the cilia specially distributed. It is, however, not known to what extent this type of movement occurs in the zoospores of plants. In most cases at least each flagellum appears to curve in successive zones along its length in cork-screw fashion, like a piece of string rotated at one end[2]. Under the microscope the movement appears to be more in one plane, and is carried out either at the apical end or along the whole length of the flagellum. If the movement is slowed by low temperatures or by the viscosity of the medium, the spiral nature of the movement is more prominent, and the photographs of the movement taken under high magnification by Marey[3] seem likely to be of great value. In some cases a flagellum may retain a transitory or permanent spiral curvature, while others may describe cone-like revolutions with or without a spiral curving along their lengths. Among the Peridineae, according to Schütt, one flagellum appears to perform mainly cone-like revolutions, and the other to be thrown into spiral waves. In some cases the character of movement is strongly affected by the external conditions, but in what way the motor mechanism is affected is uncertain.

When a flagellum is thrown into spiral waves the action is the same as that of a screw fixed in the bow of a boat, a forward movement being produced and the other component of the resolved force tending to produce an axial twisting movement. In both cases, by reversing the motion, the motile organ may push or draw the body onwards, just as in the case of an ordinary screw-steamer, in which, however, the tendency to a rotary movement is negligible. A slight contraction or spiral curvature of the flagellum will not suffice to produce a forward movement, but will produce a lateral one, especially if the flagellum is in contact with a solid body. In this way a jerky locomotion may be produced in many swarm-spores.

SECTION 59. **Gliding Movements.**

These are shown by most Diatoms and Oscillarias and also by certain Desmids, which possess no cilia and have no power of amoeboid movement.

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[1] Cf. Engelmann, and also Verworn, l. c.; Bergel, Centralbl. f. Physiol., 1900, Bd. XIV, p. 34. On the spermatozoa of animals cf. Hensen in Hermann's Handbuch d. Physiologie, 1881, Bd. VI, Abth. ii, p. 90.

[2] For details see Bütschli, Die Protozoen, 1880–9, p. 850; Schütt, Die Peridineen d. Plankton-expedition, 1895, p. 119; Kolkwitz, Bot. Centralbl., 1897, Bd. LXX, p. 185. Cf. also Pfeffer, Studien zur Energetik, 1892, p. 255.

[3] Marey, Compt. rend., 1892, T. CXIV, p. 989.

Diatoms and Oscillarias glide slowly over solid substrata or over moist surfaces which serve as a fulcrum for movement. After a time the direction of movement is usually reversed, the posterior end becoming anterior. Since, however, the motion is usually along a more or less curved path, the organism does not always regain its original position. If owing to tropic stimulation the movement towards the light is more energetic and lasts longer than that away from it, progression will on the whole be made in a definite direction.

Usually Diatoms and Oscillarias glide along with one of their longer surfaces lying mainly or entirely on the substratum, but they may sometimes raise themselves so far as to balance on one end. Except in the case of *Cylindrotheca* and *Nitzschiella*[1] Diatoms do not revolve during the forward movement, whereas all Oscillarias show a rotation round the longitudinal axis, which is genetically connected with the mode of locomotion, and which is reversed when the direction of motion changes. Both in the case of the rigid Diatoms and the flexible Oscillarias the movement takes place without any appreciable bending of the body, although mechanical curvatures are readily produced when a flexible Oscillaria comes into contact with an obstacle or temporarily adheres to some fixed body. It is in this way that the nodding, snaky, or jerky movements are produced which are very pronouncedly shown by certain species[2]. Some forms may, however, be found to perform active autonomic curvatures due to heterauxesis, as do various species of Algae.

The locomotory energy can be shown to be developed on the outer surface by the streaming movement of external protoplasm, which undergoes a periodic reversal of direction. This is shown by the fact that particles of sand or indigo adhering to the upper valve side of a fixed Diatom are moved alternately backwards and forwards from one pole to the other. We owe this observation to Siebold, and its confirmation to Schultze[3]. Although the detailed mode of locomotion of *Oscillaria* is uncertain, here also adhering particles move on the outer wall, but in correspondence with the rotation shown by filaments free to move, the streaming protoplasm, as evidenced by the adhering particles, travels to and fro in a spiral path around the filament.

Diatoms. Several authors[4] have considered the movement to be due to

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[1] Borscow, Die Süsswasser-Bacillariaceen des südwestlichen Russlands, 1873, p. 35.

[2] Nägeli, Beiträge z. wiss. Bot., 1860, Heft ii, p. 89; Correns, Ber. d. bot. Ges., 1897, p. 141; Kolkwitz, ibid., 1897, p. 460.

[3] Siebold, Zeitschr. f. wiss. Zool., 1849, Heft i, p. 284; Schultze, Archiv f. mikr. Anat., 1865, Bd. 1, p. 386.

[4] Nägeli, Gattungen einzelliger Algen, 1849, p. 20; Siebold, l.c.; Dippel, Beiträge z. Kenntniss der in den Soolwässern von Kreuznach lebenden Diatomeen, 1870, p. 332; Borscow, l.c.; Mereschkowsky, Bot. Ztg., 1880, p. 529.

the backward ejection of water, whereas Schultze, Pfitzer, and Engelmann[1] concluded that it was the result of the movement of extracellular masses of protoplasm, which by friction against the surrounding media produced a forward movement in the opposite direction. The existence and mode of action of the extracellular protoplasm was, however, first determined by O. Müller[2], who showed that the protoplasm exudes through the polar furrow on each of the valve sides, streams along the crevice of the raphe to its termination at the median nodule, where each stream returns to the interior, and travels back internally. Although most Diatoms usually lie on one of the valve sides, some forms frequently lie on the girdle side where the edges of the valves overlap, but even here sufficient energy is developed to move the Diatoms along by the friction of the protoplasm against the surrounding water[3]. It is, however, only on the valve sides that any movement of adhering particles by the streaming protoplasm can be seen, and Schultze has shown that they are only moved as far as the end of the valve and not around its edge[4].

The extracellular protoplasmic layer is extremely thin, but this does not affect its frictional surface, and Müller[5] has shown that the rate of streaming need not exceed 3 mm. per minute to produce a velocity of movement of about 1 mm. per minute, which is approximately the maximal speed shown by any Diatom. These values correspond very well with the rates of streaming shown in large plant-cells, and Ewart has shown that whereas the streaming protoplasm of a Diatom may perform 0·5 to 0·8 erg of work per minute per gram of moving plasma, the streaming protoplasm of large plant-cells only performs 0·18 to 0·22 erg per minute per gram of streaming protoplasm[6].

Although Diatoms may adhere to a surface-tension film and creep along it, the exceptional cases of free-swimming observed by Pfitzer have been denied existence by Müller[7]. It is, however, impossible to doubt that a slowly-sinking Diatom would show lateral progression if its long axis was more or less horizontal, and if the protoplasm was streaming in the usual manner along the raphe. Under such circumstances a tendency

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Schultze, Archiv f. mikr. Anat. 1865, p. 388; Pfitzer, Unters. über Bau u. Entwickelung d. Diatomeen, 1871, p. 176 (in Hanstein's Bot. Abhandl., Bd. 1); Engelmann, Bot. Ztg., 1879, p. 54.

[2] O. Müller, Ber. d. bot. Ges., 1899, p. 445; 1897, p. 70; 1889, p. 169. Summaries are given by Karsten, Die Diatomeen d. Kieler Bucht, 1899, p. 163; Klebhahn, Archiv f. Protistenkunde, 1902, Bd. 1, p. 429. Lauterborn (Unters. über Diatomeen, 1896, p. 113) has recently adopted Müller's views.

[3] O. Müller, Ber. d. bot. Ges., 1894, p. 143; Karsten, l. c., p. 165; Benecke, Jahrb. f. wiss. Bot., 1900, Bd. xxxv, p. 551.

[4] O. Müller, l. c., 1894, p. 143; M. Schultze, l. c.

[5] O. Müller, l. c., 1897, p. 75. Müller (l. c., 1896, p. 121) observed velocities of 0·007 to 0·017 mm. per second. The colourless forms move most rapidly, according to Benecke (l. c.).

[6] Ewart, Protoplasmic Streaming in Plants, 1903, p. 31.

[7] Pfitzer, l. c., p. 176. Cf. O. Müller, Ber. d. bot. Ges., 1896, p. 128.

to a waltzing movement would be shown when, as frequently happens, the protoplasm streams in opposite directions on the two valve sides. The moment of the couple is not, however, great enough to produce rotation around the short axis in forms lying on the substratum, the opposed forces mutually antagonizing so that the movement ceases[1]. All Diatoms do not possess an investing layer of mucilage, which is, therefore, not essential to movement[2]. When present it is either set in motion by the streaming protoplasm or the latter by friction against it gives the organism an onward movement. In both cases a trail of mucilage is often left behind, and this has in some cases given rise to the idea that Diatoms possessed a motory flagellum, while the same appearance probably gave rise to the theory of propulsion by a backwardly directed water-jet. In any case the resulting trail, as in the case of Oscillarias, serves to indicate the path of movement[3], but whether the movement may also be induced or aided by the extrusion of masses of mucilage must remain at present an open question[4]. The existence of attached Diatoms serves to indicate that all the members of this group do not necessarily behave similarly or develop the power of independent locomotion.

Oscillariaceae. The existence of a power of movement in these plants has been known since the time of Adanson (1767)[5], and the threads are usually covered by a gelatinous sheath in which or with which they move[6]. Continual secretion keeps the apex covered with the mucilage, in spite of that which is left behind along the path of movement. The locomotion is not connected with any power of curving, since it is also shown when the filaments remain perfectly straight, but no sure proof has as yet been brought forward of the existence of extracellular protoplasm[7]. It is in fact uncertain whether the locomotion results from the exudation and swelling of mucilage or from an appropriate development and utilization of surface-tension energy. Hansgirg supposed that the ejection of water produced the movement, but all the weight of evidence is against this assumption, for if such action existed perceptible signs of it would be detected upon minute neighbouring suspended particles. Cilia do not appear

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[1] M. Schultze, Archiv f. mikr. Anat., 1865, Bd. I, p. 386. Cf. Benecke, l.c., p. 553.

[2] O. Müller, l.c., 1897, p. 81.

[3] M. Schultze, l. c., p. 399; O. Müller, l. c.; Lauterborn, l. c., &c.

[4] Cf. Schütt, Jahrb. f. wiss. Bot., 1899, Bd. XXXIII, pp. 645, 656; Ber. d. bot. Ges., 1902, p. 202; O. Müller, Ber. d. bot. Ges., 1899, p. 445; 1900, p. 481; 1901, p. 195.

[5] Meyen, Pflanzenphysiol., 1839, Bd. III, p. 563; Mohl, Vegetabilische Zelle, 1851, p. 136; Nägeli, Beiträge z. wiss. Bot., 1860, Heft 2, p. 89; Correns, Ber. d. bot. Ges., 1897, p. 141; Kolkwitz, Ber. d. bot. Ges., 1897, p. 460; Hansgirg, Bot. Ztg., 1883, p. 831; Physiol. u. Phycophytol. Unters., 1893, p. 207; Brand, Beihefte z. bot. Centralbl., 1903, Bd. XV, p. 53.

[6] Cf. Hunger, Biol. Centralbl., 1899, Bd. XIX, p. 385; Schröder, Verhandl. d. naturh.-medic. Vereins zu Heidelberg, 1902, Bd. VII, Heft 2, p. 187.

[7] Cf. Engelmann, Bot. Ztg., 1879, p. 54.

to be present, although certain observers appear to have mistaken adhering flagellate bacteria for them.

Although foreign particles adhering to or embedded in the mucilaginous sheath may be moved along spiral lines around the filament, this is not shown over the whole length of the filament, and according to Correns a portion of the filament always adheres to the substratum during locomotion. The latter never exceeds 0·004 of a mm. per second, a velocity which does not suffice for free-swimming movement. Nägeli[1] and Kolkwitz[2] state, however, that free-swimming is shown on rare occasions, and Kolkwitz also observed a creeping locomotion on the surface of the water.

The radiating arrangement of *Oscillaria* colonies when growing on moist substrata[3] probably results from the realized movements along the path of least resistance. Similar groupings may be shown by the threads of *Spirogyra* and by Diatoms[4]. Hansgirg concludes that stimulatory reactions also come into play, but without bringing forward any definite proof[5].

Desmidiaceae. The slow movements of Desmids are due, according to Klebs, to the excretion of mucilage, and it is in fact easy to see that certain forms are actually raised to a certain height in water by the formation of a gelatinous stalk[6]. Progression would also be possible over a substratum by the continued forcible excretion of mucilage from the hinder end. Many Desmids progress with one end only resting on the substratum, the body being inclined obliquely upwards, while the attached end may change from time to time. This applies to *Closterium moniliferum*, which shows a phototactic progression to light by turning repeatedly over so that first one end and then the other is attached to the substratum as it moves towards the light[7].

It does, however, seem probable that the locomotion is due to the regulation of the excretion of mucilage, although it does not follow that the same means of locomotion is used in all cases, and in fact many Diatoms and a few Desmids adhere very firmly to stones and rocks. In any case it is worthy of note that if a snake were reduced to the size of

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[1] Nägeli, Beiträge z. wiss. Bot., 1860, Heft ii, p. 90.

[2] L. c., p. 466.

[3] Nägeli, l. c., p. 91.

[4] Schultze, Archiv f. mikr. Anat., 1865, Bd. I, p. 396.

[5] Hansgirg, l. c., 1893, p. 207.

[6] Klebs, Biol. Centralbl., 1885, Bd. V, p. 353; Unters. a. d. bot. Inst. zu Tübingen, 1886, Bd. II, p. 383; Stahl, Bot. Zeit., 1880, p. 397; Verhandl. d. phys.-med. Ges. in Würzburg, 1879, Bd. XIV; Aderhold, Jenaische Zeitschrift f. Naturw., 1888, N. F., Bd. XV, p. 323. On the excretion of mucilage by Desmids cf. Schütt, Jahrb. f. wiss. Bot., 1899, Bd. XXXIII, p. 676; Schröder, Verhandl. d. naturh.-med. Vereins in Heidelberg, 1902, N. F., Bd. VII, p. 139; Lütkemüller, Cohn's Beiträge z. Biol., 1902, Bd. VIII, p. 347.

[7] Stahl, l. c.

a Desmid, it would be extremely difficult, even under the highest powers of the microscope, to detect its mode of progression by moving the ventral scales attached to the ribs.

SECTION 60. **Amoeboid Movement.**

Pronounced amoeboid movements are only shown among plants by the plasmodia and swarm-spores of Myxomycetes, as well as by the zoospores of a few Fungi, and the zoospores and tetraspores of a limited number of Algae[1]. All other gymnoplasts (zoospores, ova, &c.) and also plasmolysed protoplasts show no power of amoeboid movement, although slow internal amoeboid movements may be possible, and do often in fact cause alterations in the shape of the vacuoles. In addition, the reproductive nuclei of the pollen-tubes of Phanerogams appear to be capable of slow amoeboïd change of shape. The same applies to the nuclei in the epidermal hairs of *Tradescantia* and in the leaf-cells of *Elodea canadensis*, and the movement appears to become more active under the action of asparagin[2].

The protrusion of the pseudopodia is often followed by retraction, but progression is possible in a definite direction when a pseudopodium steadily enlarges until the whole body has flowed into it[3]. The pseudopodia of Rhizopoda are extremely fine and slender, whereas Myxomycetes, in addition to forming short fine pseudopodia, also produce broader-lobed, fan-like or netted expansions. In plasmodia the amoeboid activity appears to undergo an autonomic alternation from one side to the other, which causes a to-and-fro streaming of the fluid contents. The latter is always directed towards the developing pseudopodia, but it is not shown in all cases[4], as for instance in the zoospores of Myxomycetes. These are also provided with cilia, and when swimming freely often perform leaping or backward movements when the cilia collide with a resistant body[5].

Amoeboid locomotion is a form of vital activity which is not explained by saying that it is due to the expansion and contraction of the protoplasm. To speak of the rounding off under strong excitation as being due to a spherogenic activity, and the re-expansion as being due to

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[1] Berthold, Protoplasmamechanik, 1886, p. 94; de Bary, Morphologie u. Biologie d. Pilze, 1884, p. 174; Zopf, die Pilze, 1890, p. 102. On the amoeboid movements of Protozoa cf. Hertwig, Die Zelle u. d. Gewebe, 1893, p. 55; Verworn, Allgemeine Physiologie, 1901, 3. Aufl., p. 244.

[2] Kohl, Bot. Centralbl., 1897, Bd. LXXII, p. 168. Cf. also Mottier, Fecundation in Plants, 1904. Amoeboid movements are often shown by the nuclei of animals.

[3] De Bary, Morphologie u. Biologie d. Pilze, 1884, p. 453; Zopf, in Schenk's Handb. d. Botanik, 1887, Bd. III, 2. Hälfte, p. 1; Pfeffer, Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, p. 256. On *Amoeba* and other animals cf. Rhumbler, Archiv f. Entwicklungsmechanik, 1898, Bd. VIII, p. 114; Jensen, Die Protoplasmabewegung, 1902, Sep. a. Ergebnisse der Physiol., 1. Jahrg.

[4] Cf. Berthold, l. c., p. 109; Jensen, 1902, l. c., p. 14.

[5] De Bary, l. c., p. 954; Fayod, Bot. Ztg., 1883, p. 171.

a cylindrogenic activity[1] is merely to play with useless terms. The adherence of the body to the substratum which permits of the extrusion of a pseudopodium does not necessarily require the extrusion of mucilage[2], and the retraction of the hinder pseudopodia during onward movement merely involves the overcoming of the adhesion of the pseudopodium to the substratum. It is, however, not impossible that the degree of adhesion is capable of autogenic modification and that a mode of progression somewhat resembling that of the foot of a snail is involved.

The movement is about as rapid as that of Diatoms and Oscillarias, since under favourable circumstances it does not exceed 0·006 mm. per second. Hofmeister[3] gives a velocity of 0·4 mm. per minute for *Didymium serpula*, and one of 0·15 of a millimetre per minute for *Stemonitis fusca*. In certain animals, however, the pseudopodia are rapidly protruded and retracted. The fact that plasmodia may creep upwards over moist substrata in air shows that the energy of movement is sufficient to support the weight of the organism and even to raise a somewhat greater load. The latter cannot, however, be very great owing to the feeble cohesion of the protoplasm. Hence in soft gelatine locomotion is arrested, although periodic attempts at amoeboid movement may be recognized[4]. Small amoebae as well as leucocytes may, however, be able in virtue of their plasticity to worm their way through minute pores, which they either find at their disposal, or which they produce by a solvent action like that of parasitic Fungi[5].

SECTION 61. **The Mechanics of Amoeboid Movement.**

It was assumed by Mohl and Nägeli that protoplasm has the properties of a viscous fluid, and no doubt now exists that this is true in the great majority of cases. The views of certain authors that protoplasm is a colloidal solid are incorrect, although naturally no hard and fast boundary exists between such solids and viscous liquids[6]. Evidence of the liquid nature of protoplasm is afforded by the spherical shape assumed by isolated portions of protoplasm when suspended in a liquid of the same density, as well as by the rounded shape of the vacuoles. The existence of streaming movement[7], the drawing out of the protoplasm

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[1] Jensen, Die Protoplasmabewegung, 1902, p. 7.

[2] De Bary, l. c., p. 458; Rhumbler, l. c., p. 158; Jensen, l. c., p. 36.

[3] Hofmeister, Pflanzenzelle, 1867, p. 23. Cf. also Jensen, l. c., p. 15.

[4] Pfeffer, l. c., p. 277. On the work done by the pseudopodia of animals cf. Jensen, l. c., p. 14.

[5] On *Plasmodiophora* see Nawaschin, Flora, 1899, p. 404.

[6] Hofmeister, Pflanzenzelle, 1867, p. 1; Berthold, Protoplasmamechanik, 1886, p. 85; Pfeffer, Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, p. 267; Bütschli, Unters. über mikroskop. Schäume, 1902; Rhumbler, Archiv f. Entwickelungsmechanik, 1898, Bd. VII, p. 172; Zeitschrift f. allgem. Physiologie, 1902, Bd. I, p. 279; 1903, Bd. II, p. 183.

[7] Ewart, Protoplasmic Streaming in Plants, 1903, p. 16.

into threads, and its general lack of resistance to mechanical agencies including surface-tension all afford evidence of its liquid consistency. The viscosity of the protoplasm, varies, however, apart from the direct physical action of temperature upon it[1], but it is usually viscous enough to prevent the vibratory molecular movement of small particles embedded in it[2], and to stop the locomotion of ingested bacteria and Volvocineae[3], whereas both these movements continue in the cell-sap. The viscous nature of the protoplasm renders the removal of protoplasmic aggregations slow in the absence of streaming movement, or even in its presence[4], and also results in the plasmolysed protoplasts of elongated cells breaking up less readily into fragments as compared with similar threads of water. External agencies may, however, increase or decrease the viscosity of the protoplasm either by a direct or indirect action[5]. It may ultimately be possible to determine the actual viscosity of the protoplasm in streaming cells, by measuring the amount of slip of minute oil particles of known density under the action of gravity[6].

The same physical factors which regulate the spread of liquids over solid surfaces, and the creeping movements in emulsions of oil and soap-solution, are also involved in determining the shape and movement of the more or less viscous protoplasm[7]. Thus the spherical shape assumed by a plasmolysed protoplast floating in a liquid of the same density is due to its homogenous surface-tension. If the protoplast is very small it will assume an approximately spherical shape even when resting on a solid substratum just as do sufficiently small drops of mercury, and also drops of water while in the spheroidal condition on a white-hot plate. A local decrease of surface-tension will cause a prominence to appear at that point, and this will continue until the lesser radius of the protrusion enables it to exercise the same centrally directed pressure, as does the larger sphere with a higher surface-tension. The same applies when a distended balloon bulges out at a weak point. If the position of equilibrium is passed and the difference of surface-tension is maintained, the entire mass will be pressed towards the side of least surface-tension, and the impelling force will automatically increase as the radius of curvature of the original body lessens. Drops of a non-miscible fluid lying in a medium or on a substratum may be caused to assume all varieties of form by appropriate local modifications of surface-tension. The spreading movements of a drop of oil upon an alkaline

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[1] Ewart, Protoplasmic Streaming in Plants, 1903, pp. 20, 59.

[2] Vellen, Flora, 1873, p. 120.

[3] Celakovsky, Flora, 1892, Ergzbd., p. 223.

[4] Ewart, l. c., p. 9.

[5] Ewart, l. c., pp. 10–20, 36, 38.

[6] Id., p. 23.

[7] For details see textbooks of Physics, and Lehmann, Molecularphysik, 1888, Bd. I, p. 251. Also Berthold, l. c.; Bütschli, l. c.; Rhumbler, l. c.; Jensen, Pflüger's Archiv f. Physiologie, 1901, Bd. LXXXVII, p. 366, and the works of Quincke here quoted.

solution do in fact resemble the amoeboid movements of certain organisms[1].

Locomotion is possible in a definite direction without any pronounced amoeboid changes of shape, as for instance when a drop of olive-oil, or of paraffin-oil, lying in water is in contact with a soap-solution on one side. The local diminution of surface-tension produced on this side causes the drop to bulge towards the soap-solution, while the peripheral layer of oil is drawn by the surface-tension film from the region of low to that of high tension. In this way a definite circulation is maintained in the oil-drop, and also in the neighbouring soap-solution, for as the film is drawn over the drop the adhering soap-solution is diluted and the surface-tension raised[2]. At the same time the drop of oil progresses towards the soap-solution, that is to the side of least surface-tension[3]. In the same way drops of castor-oil floating in dilute alcohol move towards chloroform, or potassium hydrate[4], and according to Bernstein[5] drops of mercury move towards potassium bicromate.

Similar effects are shown when a drop of a mixture of olive-oil and potassium carbonate is placed in pure water, the lowering of surface-tension being in this case produced by the soap, which rises to the surface of the drop and spreads over its exterior[6]. The protoplast can, therefore, always create the physical conditions for a change of shape or for streaming by appropriate metabolic activity. In the same way by the activity of the nucleus, of the chloroplastids, or of the surrounding protoplasm, internal changes of surface-tension may be produced capable of causing changes of shape or internal streaming. The cytoplasm of streaming cells does in fact appear to behave like an emulsion in which the surface-tension changes on the individual drops are responsible for the movement, and in which the whole energy of movement is liberated internally[7].

Changes of surface-tension inducing movement may also be produced by electrical means. Thus Ermann observed in 1809 that if the positive terminal of an electrical battery was connected with a drop of mercury lying in dilute sulphuric acid, and the negative terminal was placed in the acid, the mercury moved away from the positive pole. The principle is in fact the same as that of Lippmann's capillary electrometer, and a feeble current will produce relatively considerable movement.

The amoeboid movements of fluid masses of protoplasm can only be

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[1] Cf. Berthold, Protoplasmamechanik, 1886, p. 96.

[2] Bütschli, l. c., p. 43. Additional instances are given by Berthold and Rhumbler.

[3] Bütschli, l. c., p. 44.

[4] Rhumbler, Physikalische Zeitschrift, 1899, Nr. 3.

[5] Bernstein, Pflüger's Archiv f. Physiologie, 1900, Bd. LXXX, p. 628.

[6] Cf. Bütschli, l. c., p. 33.

[7] Cf. Ewart, Protoplasmic Streaming in Plants, 1903, pp. 113, 116.

due to changes of surface-tension when the protoplast is freely suspended in a liquid, but in other cases the cohesion of the peripheral layers may more or less counteract the direct action of surface-tension. In Myxomycetes, for instance, the ectoplasm appears to be more solid in consistency than the central endoplasm, and it forms a layer of variable thickness and properties. Changes of consistency may often play an important part in amoeboid movement, as well as in the formation of cilia, and many protoplasts appear able to raise their consistency when necessary[1], or to render themselves solid like gelatine by forming a slender framework of solid substance in which the more fluid materials are embedded. The cell-wall is in fact a peripheral skeletal structure formed either by external secretion or by protoplasmic metamorphosis. All stages of transition may be shown between a viscous liquid and a colloidal solid, just as during the solidification of melted gelatine.

Since the protoplast is able to dissolve away its cellulose investment in case of need, it is not surprising that the increased consistency of the protoplasm should be capable of decrease, as appears to be the case in Myxomycetes. When this occurs, surface-tension again becomes of predominant importance, and may be able to produce the retraction of prominences formed in the more solid condition. In case the expansion and contraction are produced by an antagonism of this kind, a pseudopodium may be produced without any change of surface-tension, whereas otherwise a very strong depression of surface-tension would be required. No definite conclusions can be made as yet, for the cohesion and viscosity of the protoplasm cannot at present be accurately determined, and in addition it is not known to what extent the protoplast may raise or lower its general surface-tension.

Even when a particular mechanical action has been proved to be due to surface-tension energy or some other agency, it still remains to be determined how the supplies of energy are controlled and utilized, and how the conditions for their action are produced. Apart from its physical action surface-tension energy and like forces may act as stimuli and induce special responses. It is easy to see how the firmer ectoplasm of the plasmodia of *Chondrioderma*, *Aethalium*, and other Myxomycetes is produced from fluid endoplasm, and may be reconverted into the latter[2]. The ectoplasm may be 0·01 mm. thick, and is, therefore, more than a mere surface-tension film, and is much thicker than the ectoplasmic membrane. Its production is the direct result of its peripheral position, and similarly the cell-wall and the ectoplasmic membrane are only formed on the surface

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[1] Cf. Pfeffer, Zur Kenntniss der Plasmahaut u. d. Vacuolen, 1890, p. 255; Rhumbler, Zeitschrift f. allgem. Physiologie, 1902, Bd. I, p. 281.

[2] Pfeffer, Zur Kenntniss der Plasmahaut u. d. Vacuolen, 1890, p. 256.

of the protoplasm. The ectoplasm may not only include the somewhat thinner layer of hyaloplasm, but also a little of the neighbouring layers of granuloplasm.

By using plasmodial threads of about 0·3 mm. in thickness, in which the surface-tension effect is small, Pfeffer[1] was able to determine that the consistency was about that of a jelly, and the same is shown by the way in which moving particles are repelled from the surface layers without producing any perceptible deformation or inducing any streaming movement. Similarly oil-drops and vacuoles passing through a tube of ectoplasm are compressed and distorted without producing any bulging in the tube. The appearance closely resembles that shown when fluid gelatine containing suspended particles is passed through a fine glass tube kept lined with a layer of solidified gelatine[2]. The existence of such a condition of cohesion in the peripheral layers renders it impossible that amoeboid movement can be directly and solely due to a modification of surface-tension. In addition, the increased surface involves an increase of the total amount of ectoplasm, and this is probably the result of the same vital activity which yields the energy for movement. It is, however, uncertain whether the retraction of a pseudopodium is due to an active change of shape or to a softening of the ectoplasm allowing surface-tension to come into play. Possibly both factors may co-operate. The streaming movement of the endoplasm is probably the direct result of the successive contractions and expansions, the direction of movement being towards the region of expansion. Hence but little endoplasm escapes when a plasmodial thread is severed[3], whereas when an internodal cell of *Chara* is cut open a large quantity of the streaming endoplasm may escape[4]. When the streaming is reversed in a thread the return movement begins at the end nearest to where the expansion or contraction is most active[5].

It is always possible that the amoeboid movements of certain organisms may be solely due to surface-tension[6], although the arguments of the different authors supporting this view are mainly based upon the assumption that the whole of the protoplasm is fluid. In many Amoebae, however, the temporary presence of a firm ectoplasm has been

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[1] Pfeffer, Zur Kenntniss der Plasmahaut u. d. Vacuolen, 1890, p. 264.

[2] Id., p. 263.

[3] De Bary, Mycetozoen, 1864, p. 48.

[4] See Corti, Meyen, Pflanzenphysiologie, 1838, Bd. II, p. 218. [The shock always causes a temporary stoppage of streaming, and the phenomenon is only shown properly if streaming is resumed again before death ensues, which is not always the case.]

[5] Cf. de Bary, l. c., p. 48; Bütschli, l. c., p. 175.

[6] Berthold, Protoplasmamechanik, 1886, p. 85; Bütschli, Unters. über mikroskopische Schäume, 1892, p. 172; Verworn, Die Bewegungen der lebendigen Substanz, 1892, p. 36; Rhumbler, Archiv f. Entwickelungsmechanik, 1898, Bd VIII, p. 172; Zeitschr. f. allgem. Physiologie, 1902, Bd. I, p. 279; 1903, Bd. II, p. 183; Jensen, Pflüger's Archiv f. Physiologie, 1901, Bd LXXXVII, p. 361.

proved[1], and the long and slender pseudopodia of many animals appear always to have an axial rod of firmer material[2], which acts as a skeletal framework and appears to be capable of apical growth by the reversible solidification of protoplasm streaming on the surface by the aid of surface-tension energy. Even rapid amoeboid movements may involve changes of cohesion, and the fact that all strong stimuli cause a tendency to the assumption of a spherical shape may point either way. The fact that most cilia are incapable of retraction indicates that they have differentiated into solid organs, and are not liquid protrusions maintained by special conditions of surface-tension. The contractible myoid fibres in the stalk and protoplasm of a *Vorticella* are also solid structures[3].

Rhumbler[4] now adopts the view that amoeboid movements may be aided by changes in the consistency of the ectoplasm, but the possible complexity of the conditions in motile organisms is indicated by the fact that Blochmann[5] found the rapid locomotion of *Pelomyxa* produced streaming in the surrounding water in the opposite direction to that caused by the movement of a drop of oil towards a soap-solution. According to Blochmann, this is due to the fact that a special streaming movement takes place on the surface of the organism.

Whether surface-tension or other sources of energy are employed or not, the causes which determine the changes of cohesion still remain to be determined. In addition, surface-tension energy may be brought into play in the interior of the protoplasmic emulsion wherever non-miscible substances are in contact, and in this way much greater total manifestations of energy are possible than when only the external surface-tension comes into play[6]. It is of course always possible that the special surface conditions may directly induce or affect the changes of cohesion in the peripheral layers, and Quincke has shown that surface-tension does affect the formation of precipitation membranes[7].

The foam structure which appears to be characteristic of protoplasm[8] produces for physical reasons a maximum consistency with a minimum of material[9], but does not cause the endoplasm to lose its fluid character. The solidity of the mass increases as the emulsion becomes finer, but the rise of cohesion in Myxomycetes does not appear to be produced in this

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[1] Rhumbler, Zeitschr. f. allgem. Physiol., 1898, p. 195.

[2] Id., p. 114.

[3] Cf. Verworn, Allgem. Physiologie, 1901, 3. Aufl., p. 252.

[4] Rhumbler, l. c., 1903, Bd. II, p. 315.

[5] Blochmann, Biol. Centralbl., 1894, Bd. XIV, p. 82.

[6] Cf. Ewart, Protoplasmic Streaming in Plants, 1903, p. 112 seq.

[7] Quincke, Annalen der Physik, 1902, Bd. VII, pp. 631, 701.

[8] Cf. Bütschli, Archiv f. Entwickelungsmechanik, 1901, Bd. XI, p. 499; Rhumbler, l. c., 1903, Bd. II, p. 326.

[9] Lehmann, Molecularphysik, 1884, Bd. I, p. 257; Quincke, Ann. d. Physik, 1894, Bd. LIII, p. 616; 1902, Bd. XVII, p. 639.

way, and can only be due to an actual increase of cohesion in the walls of the films or in their contents. In the more solid portions of the protoplasm of *Aethalium*, for instance, the reticulum is as thick in relation to the meshes between as in the fluid endoplasm. The altered cohesion might either result from chemical or physical changes in the actual substance of the reticulum, or might be due to modifications of the surface-tension between the walls of the meshes and their contents. In any case, however probable the foam structure may seem, it is not necessarily essential, and the facts collected by Rhumbler[1] fail to afford absolute proof of its universal existence. The properties of colloids may in part be due to their reticulate structure[2], although surface-tension forces are less prominent than in a froth of soap bubbles or in an emulsion of two non-miscible substances.

Active changes in the shape of the walls of the chambers will naturally produce corresponding alterations in the shape of the mass of protoplasm. In addition, the contents of the chambers might be capable of expanding and contracting by imbibing and extruding water. Internal osmotic actions can, however, only come into play when the walls of the chambers are semi-permeable, as are those of small vacuoles. Pulsating vacuoles afford striking instances of rapid expansion and contraction, and when the vacuoles are small the expansion takes place against a strong tendency to contraction due to surface-tension. In the filaments of Cynareae the individual cells are the actively contractile elements, and although the energy of movement is here due to changes of turgor, it might also be produced by changes of tension in the walls of the cells, or of the protoplasmic meshes. It is indeed not impossible that the mechanism of movement in the stamens of Cynareae may resemble that of cilia, although the latter has still to be determined.

The power of movement of protoplasm was ascribed to its general power of contractility[3], until Hofmeister[4] attempted to show that it was due to changes of imbibition or swelling. Engelmann[5] also concluded that owing to imbibition changes of shape occurred in the molecular aggregations termed inotagmas by him. The importance of the surface-tension of the superficial layer of protoplasm was first put forward by Berthold, while Bütschli showed that the surface-tension actions in an emulsion were even more important. In finely divided emulsions enormous amounts of surface-tension energy may be brought into play, which far more than suffice for the ordinary protoplasmic movements[6], and may even be able to produce the whole of the energy

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[1] Rhumbler, Zeitschr. f. allgem. Physiol., 1903, Bd. II, p. 327.

[2] Cf. Posternak, Ann. de l'Institut Pasteur, 1901, T. XV, p. 85; Pauli, Naturw. Rundschau, 1902, Bd. XVII, Nr. 25.

[3] Cf. Bütschli, Unters. über mikroskopische Schäume, 1892, p. 173.

[4] Hofmeister, Flora, 1865, p. 7; Pflanzenzelle, 1867, p. 63.

[5] Engelmann, Handbuch d. Physiologie von Hermann, 1879, Bd. I, p. 374.

[6] Cf. Ewart, Protoplasmic Streaming in Plants, 1903, pp. 26, 114, 116.

of contraction in muscle[1]. The exact part played by this internal surface-tension energy in ciliary, amoeboid, and muscular movement is not yet fully established, but in any case the minute subdivision into fibrillar chambers containing liquid sarcoplasm gives muscle the properties of a soft solid, and not of a liquid, as Jensen supposes[2].

In the present uncertainty it is impossible to say whether the changes of surface-tension are produced by the excretion of metabolic products or in other ways. Verworn[3] assumed that amoeboid movements were due to the combination of oxygen with the superficial biogens lowering the surface-tension, and that the use or dissociation of the oxygen caused the surface-tension to be raised again. Jensen[4] supposed that the increase in the size of the superficial molecules produced by assimilation lowered the surface-tension, while the diminution in the size of the molecules produced by dissimilation raised it. Neither hypothesis is, however, capable of proof, although the fact that amoeboid movement and protoplasmic streaming often continue for a long time in the absence of oxygen, and the existence of motile ciliate anaerobic bacteria show that Verworn's hypothesis cannot possibly be of general application. These theories also assume the predominant importance of surface-tension and neglect the part often played by changes of consistency and cohesion. The fact that external agencies when intense usually produce retraction affords no conclusive evidence, and merely shows that under these circumstances the conditions for expansion are suppressed.

SECTION 62. **Protoplasmic Streaming.**

The protoplasm of many dermatoplasts exhibits streaming movements, which may either be confined to the layer enclosing the central vacuole (rotation), or may also follow more or less irregular paths up and down the bridles of protoplasm crossing the latter (circulation). These two types are, however, merely the direct result of the protoplasmic configuration, for no cell in which protoplasmic strands cross the vacuole shows regular rotation. In addition, when the application of external stimuli causes the protoplasmic strands to be retracted so that a single uninterrupted central vacuole is present, the previous circulatory streaming passes into rotation[5]. At the same time the velocity of streaming increases owing to the diminished internal friction, possibly aided by an increased liberation of propulsive energy[6]. In the adult leaf-cells of *Vallisneria* and *Elodea* and in the internodal cells of *Chara* and *Nitella* the direction of streaming

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[1] Cf. Bernstein, Pflüger's Archiv für Physiol., 1901, Bd. LXXXV, p. 305; Naturwiss. Rundschau, 1901, Bd. XVI, Nos. 33–5.

[2] Jensen, Pflüger's Archiv für Physiol., 1900, Bd. LXXX, p. 227.

[3] Verworn, Allgem. Physiol., 1901, 3. ed., p. 595.

[4] Jensen, Die Protoplasmabewegung, 1902, p. 29. (Reprint from Ergebnisse d. Physiologie, Vol. I.)

[5] Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 193.

[6] Ewart, Protoplasmic Streaming in Plants, 1903, pp. 29, 35.

is constant, and is such as to be in opposite directions on the two sides of the dividing-wall between each pair of contiguous cells. Occasionally, however, as the result of injury or death to neighbouring cells, the direction of streaming may be altered or reversed [1], and during circulatory streaming reversals or changes of direction may occur at longer or shorter periodic intervals [2].

In comparison with the movement of zoospores, protoplasmic streaming is slow, for the maximum rate observed in the plasmodium of *Didymium serpula* is 10 mm. per minute, while in the cells of *Vallisneria* and of *Elodea* the streaming protoplasm usually does not cover more than 1·5 mm. per minute [3], and in the internodal cells of *Chara* and *Nitella* rarely exceeds 2 to 3 mm. per minute [4]. Arthur [5] observed a velocity of 3·3 mm. per minute in the hyphae of *Rhizopus nigricans*. In the case of *Chara* and *Nitella*, where the streaming endoplasm is comparatively thick, the velocity varies in different parts, being most rapid in the layers just outside the median line of the endoplasm, falling thence abruptly to *nil* against the ectoplasm, and diminishing gradually towards the cell-sap, the outer layers of which move with the protoplasm. In addition, gravity affects to a very slight extent the speed of floating particles of varying density, accelerating or retarding their velocity according to whether the streaming is upwards or downwards [6]. In regard to the size of the cell, however, the movement is comparatively rapid, for four to six rotations may be performed per minute by the streaming protoplasm in the cells of *Elodea* and *Vallisneria*.

Although the protoplasm is never absolutely at rest, numerous cells do not show any perceptible streaming, nor can any be awakened in them. Frequently, however, rapid streaming can be excited in inactive cells by injury or by treatment with various chemical substances. This applies to the leaf-cells of *Vallisneria* and to the leaf-parenchyma cells of *Elodea*, whereas in the leaf-hairs of *Cucurbita* and *Urtica* and in the staminal hairs of *Tradescantia* as well as usually along the midrib of *Elodea* streaming appears under normal conditions. Hauptfleisch attempts to distinguish between the streaming normally present and that excited by stimuli as 'primary' and 'secondary' streaming, but the distinction is a purely artificial one and cannot be applied in all cases [7]. In any case

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[1] Ewart, Protoplasmic Streaming in Plants, 1903, p. 34.

[2] On the distribution and special peculiarities of streaming cf. Hofmeister, Pflanzenzelle, 1867, p. 48; Velten, Bot. Ztg., 1872, p. 672; Wigand, Bot. Hefte, 1885, Heft i, p. 169; Berthold, Protoplasmamechanik, 1886, p. 119; Janse, Jahrb. f. wiss. Bot., 1890, Bd. XXI, p. 198 (*Caulerpa*); Ternetz, ibid., 1900, Bd. XXXV, p. 273 (*Ascobolus*).

[3] Hofmeister, l. c., p. 48.

[4] Cf. Ewart, l. c., pp. 24, 25, 63, 65.

[5] Arthur, Annals of Botany, 1897, Bd. XI, p. 493.

[6] Cf. Ewart, l. c., pp. 23, 113.

[7] Cf. Ewart, pp. 4, 75; Hauptfleisch, Jahrb. f. wiss. Bot., 1892, XXIV, pp. 190-200.

streaming is not shown by the cells of the primary meristem, irregular sliding movements appearing as the cells enlarge and vacuoles begin to appear, and circulatory streaming being then established, which passes into rotation if the protoplasm is restricted to the peripheral membrane. The streaming, after attaining a maximum at a certain period of development, then often persists until death[1], and in the case of *Chara* and *Nitella* cannot be stopped for any length of time without killing the cells. In the cells of *Elodea* and *Vallisneria* the newly-awakened streaming may die away again, and it is even possible by prolonged culture in strong sugar-solution to render the protoplasm of *Elodea* permanently immotile[2]. That streaming is possible in the absence of well-defined vacuoles is shown by the plasmodia of Myxomycetes, although here the streaming is presumably the direct result of the amoeboid expansion and contraction of the peripheral layers. The non-vacuolated protoplasm of certain cells of the primary meristem may also show slight sliding movements under special conditions[3], and the existence of streaming in the threads crossing the cells of *Spirogyra* shows that well-defined streaming may be shown by embryonic cells containing a large vacuole.

Although distinct streaming movement does not appear to be a general necessity of protoplasmic existence, there can be no doubt that it has in most cases a definite purpose. Usually it appears to have as its function the rapid transport of material from one part to another, and it is largely for this reason that it only appears when the developing cells reach a certain size, and becomes inextricably connected with vitality in the extremely large internodal cells of *Chara* and *Nitella*. In the latter the protoplasm is able to stream several times around the cell in the time required by most dissolved substances for complete diffusion across its length, whereas in small cells diffusion is more rapid than streaming[4]. The absence of streaming from very small cells is, however, also partly due to the relatively high internal resistance to flow[5]. It is, in any case, always possible that the streaming movement may be an accessory but unavoidable accompaniment of some other form of vital activity. A certain advantage is probably gained by the absence of streaming from the meristem cells in so far as the grouping and arrangements preceding cell-division are undisturbed. Cell-division in *Amoeba* and *Spirogyra* and nuclear division in Myxomycetes

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[1] Cf. Wigand, Bot. Hefte, 1885, Heft i, p. 186; also Nägeli, Beiträge z. wiss. Bot., 1860, Heft ii, p. 61 seq.; Vesque-Püttlingen, Bot. Ztg., 1876, p. 574; Braun, Ber. über die Verhandl. der Berl. Akad., 1852, p. 214.

[2] Ewart, Protoplasmic Streaming in Plants, 1903, pp. 15, 58.

[3] Cf. Bütschli, Archiv f. Entwickelungsmechanik, 1900, Bd. x, p. 52.

[4] This is owing to the fact that the time required for complete diffusion is proportional to the square of the distance across which diffusion occurs. Cf. Ewart, On the Ascent of Water in Trees, Phil. Trans., 1905, p. 40 (reprint).

[5] Ewart, Protoplasmic Streaming in Plants, 1903, pp. 26-30.

are, however, not affected injuriously by the existence of streaming movement. Although streaming may favour nutrition and metabolism, it does not necessarily make them especially pronounced; and, on the other hand, streaming may be inhibited by treatment with chloroform, which does not stop and may even accelerate respiration, and it may continue under partial pressures of oxygen which do not suffice for the formation of chlorophyll in etiolated chloroplastids[1].

With the exception of the peripheral layer, all the rest of the protoplasm shows streaming or is capable of it. In the case of *Chara* and *Nitella* the non-motile peripheral layer is thick and contains almost all the chloroplastids embedded in it, whereas in *Elodea* and *Vallisneria* when streaming is active all the chloroplastids are carried with the stream and only the extremely thin ectoplasmic membrane adhering to the cell-wall is at rest. Hanstein was, however, incorrect in supposing that the entire protoplast turned round within the cell[2]. When the protoplast is plasmolysed streaming may continue, but particles adhering to the ectoplasmic membrane remain at rest. Hence the absence of movement in the peripheral layer is not due to its contact with or adherence to the cell-wall. In certain cases, however, plasmolysed portions connected by a thread appear to show a slight rolling movement, but this does not appear to be directly connected with the streaming movement, and is possibly the result of the action of surface-tension or gravitational forces[3]. In the case of *Chara* and *Nitella* it is easy to see that the peripheral, well-defined, and permanent layer of ectoplasm acts like a gelatinous solid which is incapable of being set in motion by the friction of the moving layers. Similarly the cohesion of the protoplasm of streaming cells of *Elodea* and *Vallisneria* probably increases towards the periphery, so that when the rapidity of streaming rises, more of the ectoplasm is brought into motion until only the extreme peripheral layer which has the properties of a fixed membrane remains at rest. The fact that the vacuolar membrane moves with the plasma and sets the cell-sap in motion shows that either the ectoplasmic membrane is more solid in character or that it is thickened by the attachment of more highly cohesive layers of ectoplasm[4]. In the case of many pseudopodia and in that of the external plasma of Diatoms, the water and peripheral layers of protoplasm appear to move in the same direction, so that it is possible that cells may exist in which the ectoplasmic membrane of dermatoplasts may be capable of streaming movement. Apart from the

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[1] Ewart, Journ. of Linn. Soc., 1897, Vol. XXXI, p. 566.

[2] Hanstein, Bot. Abhdlg., 1880, Bd. IV, Heft ii, p. 15. Cf. Velten, Flora, 1873, p. 97; Hofmeister, Pflanzenzelle, 1867, pp. 35, 45; Pfeffer, Plasmahaut u. Vacuolen, 1890, p. 269; Wigand, l. c., p. 194; Hörmann, Studien über die Protoplasmaströmung bei d. Characeen, 1898, p. 24; Ewart, Protoplasmic Streaming in Plants, 1903, p. 6 seq.

[3] Ewart, l. c., p. 9.

[4] Velten, l. c., p. 98; Hofmeister, l. c., p. 43; Berthold, l. c., p. 122; Rhumbler, Zeitschr. f. allgem. Physiologie, 1902, Bd. I, p. 304.

fact that the thickness of the non-streaming ectoplasmic layer is variable and that it is often extremely thin, its immotility is only relative, for it undergoes changes of shape during plasmolysis and amoeboid movement.

In addition to the non-moving external layer, large or smaller portions of the general protoplasm may be temporarily or permanently in relative rest. A transitory period of quiescence occurs between each rhythmic reversal of circulatory streaming, and in some cases streaming may be shown only along isolated bands. Even when streaming is general, a narrow or even a broad indifferent line of rest is interposed between the ascending and descending streams, and this line is characterized in *Chara* and *Nitella* by the absence of chloroplastids. The dividing line between neighbouring streams may, however, be of merely theoretical dimensions without any signs of mutual disturbance, obliquely moving chloroplastids being repelled from the neutral line as though an invisible elastic limiting membrane separated the two moving layers[1].

Local streaming or gliding movements will naturally be produced whenever the motory energy is localized, or is insufficient in amount to produce complete streaming. Temporary local sliding movements are in fact shown when young cells are acquiring the full power of streaming, and also when streaming is recommencing in anaesthetized or partially disorganized cells[2]. These movements have been termed digression movements by Wigand[3], and they often consist merely of to-and-fro movements of individual particles of protoplasm.

The streaming endoplasm may carry with it various inactive suspended bodies such as crystals, starch-grains, oil-drops, and vacuoles, and even the nucleus or nuclei and chloroplastids may be passively carried with the stream. At the same time the latter may possess a feeble tendency to slow locomotion, which is, however, imperceptible when they are rapidly carried round the cell, but which becomes perceptible when they are embedded in resting protoplasm. Apart from their slow amoeboid changes of shape, it is doubtful whether the nucleus and chloroplastids possess any well-defined powers of locomotion. Naturally when a non-motile body is in contact with a stationary layer on one side it will move more slowly and tend to acquire a rotary movement or may even temporarily move in the opposite direction as compared with particles surrounded on all sides by streaming protoplasm[4]. Hörmann[5] has suggested that the chloroplastids

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[1] Ewart, Protoplasmic Streaming in Plants, 1903, p. 108.

[2] Cf. Nägeli, Pflanzenphysiol. Unters., 1855, Heft i, p. 49; Beiträge z. wiss. Bot., 1860, Heft ii, pp. 10, 84; Velten, Bot. Ztg., 1872, p. 651.

[3] Bot. Hefte 1885, Heft i, p. 180.

[4] Göppert und Cohn, Bot. Ztg., 1849, p. 698; Nägeli, Beitr. z. wiss. Bot., 1860, Heft ii, p. 66; Velten, Activ oder passiv? Oesterr. Bot. Zeitschrift, 1876, Nr. 3; Berthold, l. c., pp. 118, 150; Wigand, l. c., p. 195.

[5] Hörmann, Studien über die Protoplasmaströmung bei d. Characeen, 1898, p. 24.

of Characeae in passing into the endoplasm become covered with a layer of the motory protoplasm which he supposes to bound the endoplasm externally, and so acquire a power of independent locomotion. All the phenomena described may, however, be shown by dead bleached chloroplastids, and isolated chloroplastids never show any power of independent locomotion or of orientation, however long they may remain living and functionally active[1].

Frequently the starch-grains or chloroplastids may ball together and form an obstruction round which the protoplasm flows until it is swept away[2]. In this way and also by partial plasmolysis, variations in the contour of the vacuolar membrane may be produced, while as the result of exposure to high temperatures partial coagulation may influence the direction and manner of streaming[3], and by exposure to localized intense light streaming may be restricted to the two unaffected ends of a cell of *Chara*[4].

The Physics of Streaming Movement[5]. In spite of the fluid character of the endoplasm, gravity exercises relatively little action upon the speed of ascent and descent of particles of varying density[6]. Whatever the motor mechanism may be, it is such that no backward reaction is exercised upon either the cell-wall or cell-sap. The total resistance to flow depends upon the viscosity of the moving liquids and upon the diameter and length of the cell. Any factor which decreases the viscosity, such as a rise of temperature or an increase in the percentage of water, will decrease the resistance to flow and hence will tend to increase the velocity of flow. The relative resistance to flow is proportional to the square of the radius of the moving portion of the cell, so that in very small cells the resistance to flow becomes disproportionately great, and in the case of the minute interprotoplasmic connexions between contiguous parenchyma cells flow in mass becomes practically impossible. The amount of energy actually consumed in the production of the streaming cannot be determined, but the theoretical consumption based upon the assumption that the protoplast is a perfect machine is exceedingly small. Thus the energy used by a streaming cell of *Nitella* represents only a theoretical consumption of $\frac{1}{200000}$ of a gram of cane-sugar per annum per gram of plasma moving at a rate of 2 mm. per minute in a cell of 0·4 mm. radius. In the smaller cells of ordinary plants less than a tenth of a per cent. of the energy of respiration appears to be consumed in the production of streaming movement. In the large cells of *Chara* and *Nitella* the normal rate of streaming is more rapid than in the smaller cells of *Vallisneria* and *Elodea* of lesser radius, but this is not necessarily the direct result of the relatively greater resistance, for it is hardly likely that in all cases the same proportion is

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[1] Ewart, Protoplasmic Streaming in Plants, 1903, pp. 107, 108.

[2] Meyen, Pflanzenphysiologie, 1838, Bd. II, p. 220; Nägeli, l. c., p. 62; Hofmeister, Pflanzenzelle, 1867, p. 44; Rhumbler, Zeitschr. f. allgem. Physiol., 1902, Bd. I, p. 321.

[3] Ewart, l. c., p. 59.

[4] Pringsheim, Jahrb. f. wiss. Bot., 1882, Bd. XII, p. 326.

[5] For fuller details see Ewart, l. c., p. 6 seq.

[6] Cf. Ewart, l. c, p. 23.

maintained between the total energy of respiration and that used in streaming. In fact, streaming is usually more rapid, or at least as rapid in the narrow cells along the midrib of *Elodea*, as in the broader parenchyma cells.

Historical[1]. Streaming movements were first observed in the cells of plants by Corti in 1774[2]. These observations were amplified and extended by Fontana, Treviranus[3], Amici[4], Slack[5], Meyen[6], Dutrochet[7], Schleiden[8], and Hassal[9], but it was not until Von Mohl had established the fact that the protoplasm was the essential living substance of the plant-cell that Schacht[10] showed the seat of active movement to be in the protoplasm, and concluded that streaming was merely an outward and visible sign of the activity of the latter.

Velten assumed that streaming was a general and normal phenomenon, whereas Frank, Keller, and Hauptfleisch have shown that in many cases it is only awakened by external stimulation[11]. De Vries and also Janse considered that streaming was of primary importance for the rapid transport of food-materials, and the same conclusion has been made by Hörmann[12]. It is, however, only in very large cells that this applies, for in ordinary plant-cells transference by diffusion is more rapid than by streaming movement[13].

Theories of Streaming. Heidenhain and Kühne[14] considered that waves of contraction passed round the cell, producing streaming in the same way as when the finger is drawn round an india-rubber tube filled with water. A similar explanation was originally put forward by Corti[15], but de Bary and others have shown that the contour of the protoplasm towards the cell-sap does not alter in the way required by the theory[16]. In any case, the streaming in dermatoplasts can hardly be produced in the same way as in gymnoplasts, in which it is passively produced by the contractile activity of the peripheral layers. Yet another type of passive streaming has been shown by Arthur[17] to exist in the mycelial filaments of many Fungi when local variations of osmotic pressure coupled with the excretion or absorption of water

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[1] See Ewart, Protoplasmic Streaming in Plants, 1903, p. 1 seq.

[2] Osservazioni microscopiche sulla Tremella e sulla circolazione del fluido in una pianta acquaiola, Lucca, 1774, p. 127.

[3] Physiologia, 1807.

[4] Mem. della Soc. Ital. delle Scienze in Modena, 1818, T. XVIII, p. 182.

[5] Ann. sci. nat., 1834, 2e sér., T. I, pp. 193, 271.

[6] Id., 1835, 2e sér., T. IV, p. 257.

[7] Id., 1838, 2e sér., T. IX, pp. 5, 65.

[8] Principles of Botany (Eng. Trans.), 1849, p. 92.

[9] British Freshwater Algae, Vol. I, p. 85.

[10] Die Pflanzenzelle, 1852, p. 340.

[11] Velten, Bot. Ztg., 1872, p. 147; Flora, 1873, p. 82; Frank, Pringsh. Jahrb., 1872, Bd. VIII, p. 220; Keller, Ueber Protoplasmaströmung im Pflanzenreich, 1890, pp. 12, 40; Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV.

[12] De Vries, Bot. Ztg., 1885, Nos. 1 and 2, p. 1; Janse, Jahrb. f. wiss. Bot., 1890, Bd. XXI, p. 163.

[13] Ewart, The Ascent of Water in Trees, Phil. Trans., 1905, p. 80.

[14] Heidenhain, Studien d. physiol. Inst. in Breslau, 1863, Bd. II, p. 60; Kühne, Unters. über d. Protoplasma, 1864, pp. 73, 91.

[15] Quoted by Göppert and Cohn, Bot. Ztg., 1849, p. 666.

[16] De Bary, Flora, 1862, p. 250; Schultze, Das Protoplasma d. Rhizopoden u. d. Pflanzenzellen, 1863, p. 40; Nägeli und Schwendener, Mikroskop, 1877, 2. Aufl., p. 389.

[17] Arthur, Annals of Botany, 1897, Vol. XI, p. 491.

causes to-and-fro movements in mass of the protoplasm. Ternetz[1] has also shown that similar passive movements are produced in the filaments of *Ascobolus* (*Ascophanus*) *carneus* by the expansion and contraction of the vacuoles. Streaming movements may also be produced by pressure, and physical streaming of this kind is only secondarily dependent upon vital activity, whereas true circulatory streaming and rotation appear to be directly connected with the latter. There is, however, naturally more than one way in which streaming could be produced by vital activity[2].

Engelmann considered streaming to be due to changes of shape in his hypothetical inotagmas[3], while Hofmeister[4] and also Sachs[5] suggested that progressive changes of imbibition passing round the cell by causing the protoplasmic particles alternately to absorb and extrude water would cause them to move in a definite direction. This would, however, involve a movement of the water in the protoplasm in the opposite direction, and as a matter of fact this does not take place[6]. Similarly the supposition of Brücke, Hanstein, and Heidenhain that the movement is produced by the contractile activity of a system of tubes or fibrillar network hardly harmonizes with the fact that the whole of the endoplasm is in motion[7]. A forward movement might be produced by an oblique ejection or exudation of water, but if this took place internally it would involve a movement of the cell-sap in the opposite direction, while it could not take place externally in cuticularized hairs exhibiting streaming.

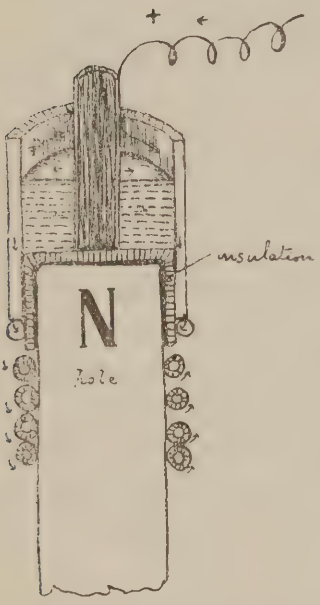

FIG. 50. Sectional diagram of electro-magnetic streaming. The small arrows show the direction of the electrical current and the large ones the movement of the mercury.

Amici[8] concluded that the chloroplastids electrically propelled the endoplasm, and a similar conclusion was made by Dutrochet and Becquerel[9]. Velten[10] also considered that the movement had a direct electrical origin, and was able to produce a circulation of dead floating particles in a cell which was reversed on reversing the direction of the strong electrical currents used. The same occurs when mercury placed over a strong electro-magnet is traversed by an electrical current, so that presumably the cell-wall is capable of acting as a magnetic membrane[11]. (Fig. 50.) Such action involves a corresponding backward reaction upon

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[1] Ternetz, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 273.

[2] See the literature quoted by Bütschli, Unters. über mikr. Schäume, 1892, p. 173.

[3] Engelmann, l. c., p. 373.

[4] Hofmeister, Pflanzenzelle, p. 63.

[5] Sachs, Physiologie, 1865, p. 451.

[6] Cf. Ewart, Protoplasmic Streaming in Plants, pp. 109, 110.

[7] Brücke, Unters. über das Protoplasma und die Contractilität; Sitzungsb. d. Wien. Akad., 1862, Bd. XLVI, Abth. ii, p. 36; Hanstein, Protoplasma, Heidelberg, 1880; Heidenhain, Einiges über die sog. Protoplasmaströmungen, 1897 (reprint from Sitzungsb. d. physik.-medic. Ges. zu Würzburg). Cf. Ewart, l. c., p. 108.

[8] Cf. Dutrochet, Ann. d. sci. nat., 1838, 2e sér., T. IX, p. 78.

[9] Dutrochet and Becquerel, l. c., pp. 85–7.

[10] Velten, Bot. Ztg., 1872, p. 147; Flora, 1873, p. 82; Sitzungsb. d. Wien. Akad., 1875, Bd. LXXIII, Abth. i, p. 343.

[11] On the paramagnetism of cellulose cf. Ewart, l. c., 1903, p. 47.

the cell-wall or magnet, and this does not appear to be exercised in the streaming cell[1]. In addition, the direction and velocity of streaming are not directly affected by the use of strong magnets[2], so that the motor mechanism in the living cell can hardly be of electro-magnetic origin, for the retarding effect produced after prolonged exposure to intense magnetic action is probably of secondary origin[3].

Berthold considered that amoeboid movement was directly due to changes of surface-tension, the movement always taking place towards the side of least surface-tension[4]. The latter statement does not, however, apply to all cases, for a piece of camphor floating on water moves towards the side where the surface-tension is greatest. Streaming he considers to be due to changes of surface-tension in the vacuolar membrane, and in support of this conclusion adduces the fact that the velocity of streaming decreases from the vacuolar membrane towards the ectoplasm[5]. In cells with a thick layer of endoplasm, by using minute floating particles of similar diameter

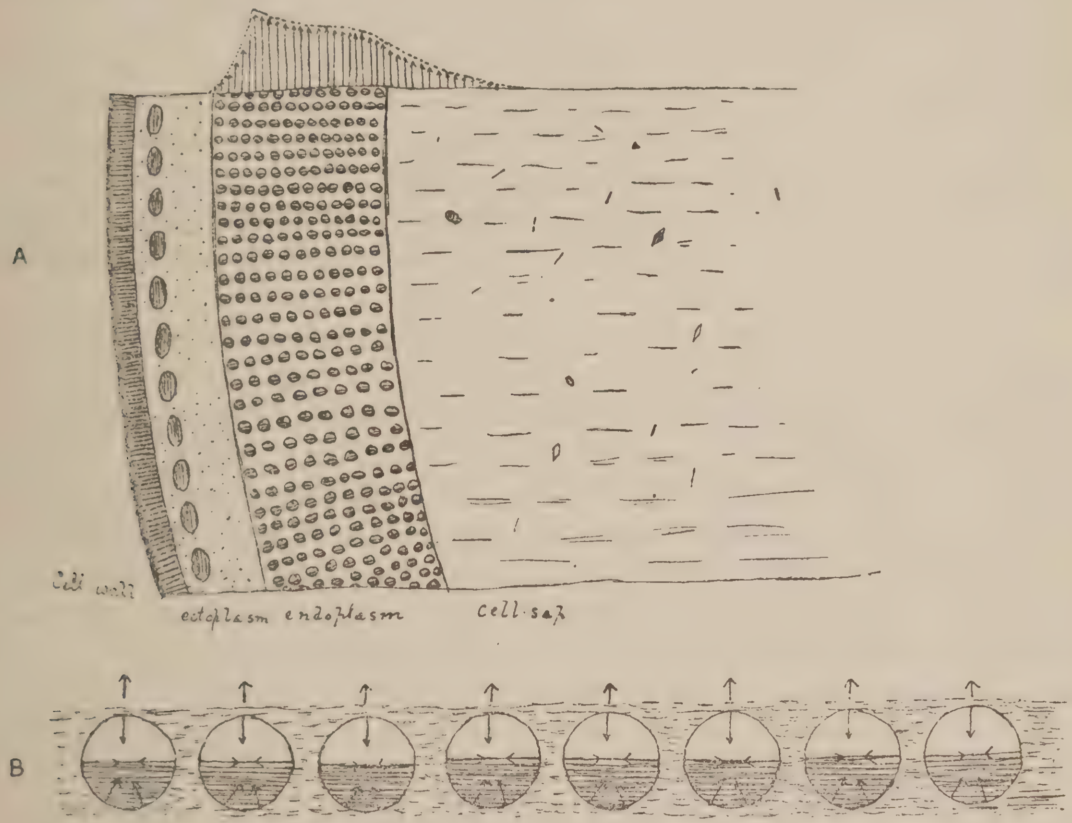

FIG. 51. A. Diagram of section of *Chara* cell, showing rows of emulsion globules in endoplasm. The row of arrows shows the relative velocities of different layers. B. Row of emulsion globules showing surface-tension forces and resultant movement. (After Ewart.)

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[1] Cf. Ewart, Protoplasmic Streaming in Plants, 1903, p. 110 seq.

[2] Becquerel, Compt. rend., 1837, T. V, p. 784; Dutrochet, Compt. rend., 1846, T. XXII, p. 619; Reinke, Pflüger's Archiv f. Physiol., 1882, Bd. XXVII, p. 140. [The orientation of suspended streaming cells in a strong magnetic field, due mainly to the magnetic properties of the cell-wall, would probably have led these observers to exactly the opposite conclusion had they not overlooked it. Cf. Ewart, l. c., p. 45 seq.]

[3] Ewart, l. c., p. 50.

[4] Berthold, Protoplasmamechanik, 1886, p. 115 seq. Cf. also Bütschli, l. c., p. 210.

[5] Berthold, l. c., p. 123; cf. also Wigand, l. c., p. 196.

as indicators, it can usually be distinctly seen that the velocity of streaming increases slightly from the vacuolar membrane to a point lying a variable distance beneath the ectoplasm, and thence rapidly decreases to *nil* outwardly[1]. (Cf. Fig. 51.) This distribution of velocity affords definite proof that the energy of movement is liberated not at the boundary of the cell-sap but throughout the substance of the streaming endoplasm. If we assume that the bipolar paramagnetic and diamagnetic particles of protoplasm in the endoplasmic emulsion are definitely arranged in regard to the paramagnetic cell-membrane, it is easy to see how continuous rotation might be brought about if electrical currents are produced by the differences of potential at the internal and external boundaries of the feebly-conducting protoplasm[2], and are maintained by the chemical actions in the latter. For these currents traversing the endoplasm and producing definite changes of surface-tension in the regularly-arranged particles of the emulsion might in this way cause a movement of the whole protoplasm[3]. Where the regular arrangement is not maintained, circulatory movements, or a cessation of streaming, may ensue.

Although this hypothesis coincides more exactly with the facts observed in dermatoplasts than that of Berthold, it may ultimately prove to be as far from the truth as Quincke's conclusion that the movement was due to surface-tension actions exercised by the non-moving ectoplasm[4].

The influence of the shape of the cell and of the union in tissues. The typical rotation in elongated cells takes place parallel to the long axis of the cell[5], the plane of rotation being parallel to the surface of the leaf in *Vallisneria* and at right angles to the surface in the cortical cells of *Chara*[6]. The plane of rotation can, however, be altered by injuries, by the death of neighbouring cells and by exposure to strong light after prolonged darkening[7]. According to Velten, in rotating around the longitudinal axis of the cell the plasma follows the path of least resistance[8]. In *Chara*, however, as was observed by Braun[9], spiral streaming appears when the internodes undergo torsion, and then Hörmann[10] considers the streaming to be along the path of absolutely greatest resistance, while, according to Rhumbler[11], the arrangement of the chloroplastids is due to the spiral streaming instead of inducing it. Neither Velten nor Hörmann brings forward any experimental evidence or theoretical calculation in support of his statements, and as a matter of fact the resistance to flow in cylindrical cells with rounded ends is not affected by the direction of flow. Naturally in cells showing circulation the total resistance to flow increases as the number of threads increases and their diameter decreases, but the path of least resistance is that in which the passage across a definite space requires the least expenditure of

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[1] Ewart, Protoplasmic Streaming in Plants, 1903, p. 113.

[2] Id., p. 123.

[3] Id., p. 116.

[4] Pfeffer, Plasmahaut und Vacuolen, 1896, p. 277.

[5] Nägeli, Beiträge zur wiss. Bot., 1860, Heft ii, p. 62. See also A. Braun, Ber. über d. Verhandlg. d. Berliner Akad., 1852, p. 214; Hofmeister, Pflanzenzelle, 1867, p. 36.

[6] Berthold, l. c., p. 122.

[7] Ewart, l. c., p. 34.

[8] Velten, Flora, 1873, p. 86; Berthold, l. c., p. 120.

[9] A. Braun, l. c., p. 225. See also Berthold, l. c., p. 121; Meyen, Pflanzenphysiol., 1838, Bd. II, p. 236; Velten, l. c., p. 85.

[10] Hörmann, Studien ü. d. Protoplasmaströmung b. d. Characeen, 1898, p. 16.

[11] Rhumbler, Zeitschrift f. allgem. Physiologie, 1902, Bd. I, p. 300.

energy. This will be along as straight or as uniformly curved a path as possible, so that the tendency to eddy currents with their increased resistance to flow is avoided. A spiral path around the long axis of the cell fulfils this condition best when the cell is an elongated cylinder as in *Chara* and *Nitella*. When the ends of the cell are rounded the direction of streaming may be parallel to the long axis of the cell[1].

The influence exercised by neighbouring cells is shown by the fact that a stimulus awakening or accelerating streaming may radiate to some distance from an injured region. In addition, the planes of streaming in the cortical and medullary cells of the internodes of *Chara*[2] show definite relationships, which may possibly be such as to favour translocation[3]. According to Berthold[4], there is no constant relationship between the direction of streaming in the cells of *Elodea* and *Vallisneria*, but as a matter of fact, almost without exception, the direction of streaming is opposed on the two sides of each dividing wall[5]. In the deeper leaf-cells, especially near the midrib, the planes of rotation may intersect at various angles owing to the oblique points of contact of the cells, while in other cases the direction of streaming appears to be primarily determined by the shape of the individual cell.

SECTION 63. **Pulsating Vacuoles.**

Vacuoles may show various changes of shape and volume, and frequently fuse as the living cell grows older. When vacuoles periodically diminish and re-enlarge, or disappear and reappear, we speak of contractile or pulsating vacuoles, such as are especially well shown by Infusoria[6] and by many other Protozoa. They also occur in various Thallophytes and Protophytes, such as most Volvociniae and Flagellatae[7], a few Palmellaceae[8], and also in the zoospores of *Stigeoclonium*, *Chaetophora*[9], *Ulothrix*[10], *Microspora*[11], and many other Algae, as well as in the zoospores of such Fungi as *Saprolegnia*[12] and *Cystopus*[13], and in the zoospores and plasmodia

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[1] Ewart, Protoplasmic Streaming in Plants, 1903, p. 35.

[2] A. Braun, l. c., p. 231. For other cases cf. Hofmeister, l. c., p. 40.

[3] Hörmann, l. c., 1898, p. 13; cf. also Ewart, l. c., p. 34; and The Ascent of Sap in Trees, Phil. Trans., 1905, p. 40.

[4] Berthold, l. c., p. 121.

[5] Ewart, l. c., 1903, p. 34.

[6] Bütschli, Protozoen, 1880–8, p. 1411.

[7] Bütschli, l. c., p. 708; O. Hertwig, Zelle u. Gewebe, 1893, p. 69, and the literature here quoted; Cohn, Beitr. z. Biol. d. Pflanzen, 1877, Bd. II, p. 117; Klebs, Unters. a. d. bot. Inst. zu Tübingen, 1883, Bd. I, p. 246; Senn, in Engler's Natürl. Pflanzenfamilien, 1900, T. I, Abth. i, p. 101.

[8] Cienkowski, Bot. Ztg., 1865, p. 22; 1876, p. 70.

[9] Id., 1876, p. 70.

[10] Strasburger, Zellbildung u. Zelltheilung, 1875, p. 157; Dodel, Bot. Ztg., 1876, p. 183.

[11] Maupas, Compt. rend., 1876, T. LXXXII, p. 1,451. See also Falkenberg in Schenk's Handbuch d. Botanik, 1882, Bd. II, p. 194; Hofmeister, Pflanzenzelle, 1867, p. 12; Woronin, Bot. Ztg., 1880, p. 628 (*Chromophyton*).

[12] Rothert, Cohn's Beitr. z. Biol., 1892, Bd. V, p. 323.

[13] De Bary, Ber. d. nat. Ges. zu Freiburg, 1860, p. 8.

of Myxomycetes[1]. No typical pulsating vacuoles have hitherto been detected in the cells of plants above the Thallophyta, but nevertheless transition forms occur between normal and pulsating vacuoles. All vacuoles are formed in the same way by the protoplasm, and many normal vacuoles undergo pronounced but slow changes of volume[2], which are in some cases mechanically produced by protoplasmic streaming or surface-tension action. In fact there is probably no vacuole whose size and shape are constant, while various external agencies may progressively reduce and ultimately inhibit the rhythmic activity of pulsating vacuoles. Periodic changes of concentration in the external medium involve corresponding periodic changes of volume in the vacuole, so that the normal progress of metabolism is bound to influence the size of the vacuole, although such purely mechanical actions may be controlled and regulated by the protoplast within certain limits. Thus a rise of concentration in the external medium will exercise no influence upon the size of the vacuole, if the osmotic concentration of the cell-sap is proportionately increased, and when the vacuole is very small, a fall of the surface-tension of the vacuolar membrane would be almost equally effective in balancing the increased external pressure.

In *Closterium*, and a few other Desmids, the vacuole occurring at each pole becomes smaller when the direction of streaming of the protoplasm is towards that end, and it regains its original size with the periodic reversal of the stream[3]. In the hyphae of *Ascobolus* and other Fungi, periodic alterations in the volume of the vacuoles produce to-and-fro streaming movements in the protoplasm, while the periodic movements of the leaves and leaflets of *Desmodium* and *Trifolium* and of other plants involve rhythmic contraction and dilation of the cells and hence also of the vacuoles. The same occurs during every stimulatory movement of the filaments of Cynareae and the pulvini of *Mimosa*, for this involves a considerable escape of water from the cell and its subsequent reabsorption.

Pulsating vacuoles are always small, they usually maintain the same locus and commonly not more than one to three are present in plant-cells[4]. The plasmodia of Myxomycetes have, however, numerous pulsating vacuoles which may be present not only in the ectoplasm but also in the streaming endoplasm. Most Volvocineae have two pulsating vacuoles, but *Volvox* has only one, and *Chlorogonium* has numerous contractile vacuoles[5]. According

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[1] De Bary, Mycetozoen, 1864, pp. 41, 81; Cienkowski, Jahrb. f. wiss. Bot., 1863, Bd. III, p. 329; Pfeffer, Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, pp. 192, 219, 336. On *Amoeba* cf. Bütschli, Protozoen, 1880–8, p. 105; Rhumbler, Archiv f. Entwickelungsmechanik, 1878, Bd. VII, p. 256.

[2] Pfeffer, l. c., p. 257; Bütschli, l. c., pp. 1412, 1435; Rhumbler, l. c.

[3] De Bary, Unters. ü. d. Familie d. Conjugaten; Schumann, Flora, 1875, p. 66; A. Fischer, Jahrb. f. wiss. Bot., 1884, Bd. XIV, p. 142.

[4] Bütschli, l. c., p. 708.

[5] Massart, Bull. de l'Acad. royale de Belgique, 1901, p. 100.

to Massart, *Paramaecium aurelia* forms numerous vacuoles when warmed to 30 or 35° C. Similar vacuolations in the protoplasm of various plant-cells were observed by Klemm[1] after the application of injurious agencies, so that the phenomenon is probably a general one.

In all cases the systolic contraction is very rapid, whereas the re-expansion or diastole takes place much more slowly. The vacuole may reappear at the same or another spot, and expands at first rapidly, but then more slowly until it regains its original size, when it suddenly collapses again. In the case of the plasmodia of *Aethalium septicum* and *Chondrioderma* the maximal diameter of the contractile vacuoles varies from 0·004 to 0·01 of a millimetre[2], but when the vacuoles are large the systole, though rapid, can be followed, and often does not lead to the entire disappearance of the vacuole.

The pulsatile frequency varies according to the external conditions, and attains a maximum at a somewhat variable optimal temperature. Under favourable circumstances 12 to 15 seconds may elapse from one systole to the next in the case of the zoospores of *Ulothrix*[3], and 26 to 60 seconds in the case of *Gonium*[4]. The duration of each period, is however, usually 60 to 90 seconds[5] in the case of the plasmodia of *Aethalium* and *Chondrioderma*, and the vacuoles of these organisms which do not completely empty often pulsate still more slowly[6]. In the case of the Infusorian *Spirostomum teres* the pulsatile frequency is given as 30 to 40 minutes[7], so that vacuoles may exist in plants which pulsate so slowly that hitherto their special character has not been detected.

Although the pulsation usually maintains the same frequency under constant external conditions there are naturally exceptions to this rule. Cienkowski[8] observed a very variable frequency in certain Palmellaceae, and the same applies to those vacuoles of plasmodia which undergo imperfect systole[9]. In addition neighbouring vacuoles of plasmodia may be in all stages of systole and diastole at the same moment, whereas when two vacuoles only are present one is usually expanding while the other collapses[10]. In many cases, as for instance in certain Palmellaceae, both vacuoles contract at the same time.

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[1] Klemm, Desorganisations-Erscheinungen in pflanzlichen Zellen, Jahrb. f. wiss. Bot., Bd. XXVIII, 1895, p. 685.

[2] Pfeffer, l. c., p. 192.

[3] Strasburger, l. c.; Dodel, l. c.

[4] Cohn, Nova Acta Acad. Caesar. Leopold., 1854, Bd. XXIV, i, p. 196; Bütschli, Protozoen, 1880–8, pp. 714, 1453, gives summaries of the pulsatile frequency in various Infusoria.

[5] Cienkowski, Jahrb. f. wiss. Bot., 1863, Bd. III, p. 329.

[6] Pfeffer, Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, p. 192.

[7] Bütschli, l. c., p. 1454.

[8] Cienkowski, Bot. Ztg., 1865, p. 22.

[9] In the individual cells of colonies of *Gonium* approximately the same rhythm may sometimes be maintained.

[10] See Bütschli, l. c., p. 713.

The systole of a pulsating vacuole may either drive out the contents into the surrounding water or merely into the surrounding protoplasm. The former is usually the case in such Infusoria as the Acinetarias and Vorticellidae, which have special exit channels leading from the vacuole to the exterior[1]. The latter appear, however, to be absent from all other animals, and from plants also if we except the Flagellatae. Transition forms occur, however, for in *Paramaecium* and other organisms the radiating channels from the vacuole do not always appear at the same point, and do not lead to the exterior. In many Amoebae, again, the peripheral vacuoles bulge out externally and rupture when the wall has become very thin, so that the escape of their contents may take place at any point on the surface[2]. The emptying of a number of the peripheral non-pulsating as well as of the pulsating vacuoles of Myxomycetes is effected in this way. The coalescence of small vacuoles with one another or with a large one also involves a gradual approach of the vacuoles and a thinning of the dividing membrane until the point of rupture is reached[3]. Deep-seated vacuoles, however, can only empty their contents into the surrounding protoplasm when they are not connected with any actual or potential channels to the exterior. The extruded fluid may, however, either be imbibed by the protoplasm or exude outwardly through it. In the latter case a corresponding diminution of the total volume must ensue. The existence of organisms with a single vacuole or with two synchronous ones shows that the vacuolar fluid is not always driven from one vacuole to another.

The escape from deep-seated vacuoles without special affluent channels takes place by filtration under pressure through the vacuolar membrane, since, owing to the plastic nature of the vacuolar membrane and of the surrounding protoplasm the former cannot be ruptured under the conditions existent in the cell. In all cases the centrally-directed pressure exercised by the vacuolar membrane partially antagonizes the internal osmotic pressure required for the maintenance of the vacuole, and any change in either of these factors is bound to influence the size of the vacuole. It is, however, only when the latter is very minute that the centrally-directed pressure attains relatively high values[4]. Under ordinary circumstances the diminution or collapse of the vacuole can only result from a decrease or removal of its internal osmotic pressure, produced either by the exosmosis of the dissolved materials or by their conversion into larger or insoluble molecules. According to Cohn, just before the systole of the vacuole of *Gonium pectorale* the vacuolar fluid becomes turbid, possibly owing to the precipitation of the dissolved materials[5], but it is also possible that the phenomenon may have a different origin and not be directly connected with the vacuolar contraction.

When the vacuole is small, very rapid filtration under pressure through its relatively large surface is possible, so that the vacuole may disappear instantaneously. If the protoplasm is not at once able to absorb all the extruded water, radiating channels

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[1] Cf. Bütschli, Protozoen, 1880–8; Hertwig, Zelle und Gewebe, 1893.

[2] See Rhumbler, Archiv f. Entwickelungsmechanik, 1898, Bd. VII, p. 257.

[3] Cf. Pfeffer, Aufnahme u. Ausgabe ungelöster Körper, 1890, p. 159.

[4] Pfeffer, Plasmahaut u. Vacuolen, 1890, p. 298.

[5] Cohn, Nova Acta Acad. Caesar. Leopold., 1854, Bd. XXIV, i, p. 194.

filled with sap may appear around it, or the vacuole may appear to have undergone fine fragmentation[1].

No increase of external pressure could produce a complete collapse of the vacuole so long as it retained its dissolved substances, for any diminution of size involves a corresponding increase of concentration and of osmotic pressure. For this reason moderate changes in the external pressure are readily balanced without appreciably affecting the size of the vacuoles, and the same applies to the protoplasm in general[2]. The fact that neighbouring vacuoles may expand and contract at different times, and that isolated fragments with single vacuoles may show pulsation for some time, afford sufficient evidence that the systole and diastole are not produced by local or general changes of pressure in the protoplasm. Nor can the pulsation be due to changes in the percentage of osmotic substances in the protoplasm.

It does not, however, follow that the mechanism is alike in all cases[3], and in fact the position of the vacuole in various Amoebae may determine whether it bursts on the surface or allows its contents to escape into the surrounding protoplasm by filtration under pressure[4]. The latter always occurs when only a diminution in size is shown, for an actual rupture of the vacuolar membrane would presumably involve an escape of the whole of its contents. Under special conditions the vacuoles of most organisms do not empty completely[5], but this does not necessarily show that the complete collapse is also merely due to filtration under pressure, however probable this assumption may be. Vacuoles of Myxomycetes which have absorbed aniline blue by passive secretion retain it during partial pulsations[6], whereas the selective permeability of the vacuolar membrane enables it to allow the diosmotic excretion of other dissolved materials. The addition of non-exosmosing dissolved substances to a vacuole must necessarily convert a previous total pulsation into a partial one, and possibly this is why the union of a pulsating vacuole with a non-pulsating one produces in the plasmodium of *Chondrioderma* only a feebly pulsating vacuole[7].

The continuance of rhythmic pulsation in isolated vacuoles shows that the thinnest protoplasmic layers may develop the required self-regulatory activity. Although the systole ensues when a definite size is reached, other inactive vacuoles may surpass this size without ever pulsating. Hence the pulsation is the result of some specific peculiarity, and this holds good even when pulsation may be induced under special circumstances in previously inactive vacuoles[8]. It is not easy to say whether a vacuole entirely disappears at the close of the systole or merely decreases to submicroscopic dimensions. In the former case the vacuolar membrane would be reconverted into ordinary protoplasm, but it is also possible that special factors might prevent this happening, in which case the potential walls at least of the new vacuole would be retained. The reproduction of a new contractile vacuole would,

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[1] See Rhumbler, Archiv f. Entwickelungsmechanik, 1878, Bd. VII, p. 289; Bütschli, l. c., &c.

[2] See Pfeffer, Plasmahaut u. Vacuolen, 1890, p. 337.

[3] A summary of the views of different authors is given by Bütschli, l. c., pp. 1433, 1458, 1452.

[4] Rhumbler, l. c., pp. 257, 271.

[5] See Bütschli, l. c., p. 1457; Cohn, l. c., p. 200.

[6] Pfeffer, l. c., 1890, pp. 219, 337.

[7] Pfeffer, l. c., 1890, p. 219.

[8] Cf. Rhumbler, l. c., p. 263.

however, be no more remarkable than the formation of a non-contractile one[1], and this might still occur even though the vacuole always reappeared at the same spot. A localization of the vacuole merely involves a localized production of the conditions for its formation. The latter may or may not involve the coalescence of preformed droplets, but in any case the degree of independence and of differentiation attained by pulsating vacuoles is not in all cases certain[2].

External influences. The frequency attains a maximum at a certain optimal temperature, and in general the responses resemble those for other forms of vital activity[3], although the vacuoles appear to have a higher resistant power. Thus, according to Klebs, mechanical agencies, high temperatures, and strychnine stop the general protoplasmic movements before the pulsation of the vacuoles ceases, and the latter is the first to begin on returning to normal conditions. Indeed, according to Klebs[4], irregular slow pulsations may continue for a time after the general mass of the cytoplasm has been killed by heat or disorganized by pressure. Evidently, therefore, the pulsation is independent of the nucleus, and it may also continue for a time in non-nucleated masses of living cytoplasm. Rossbach found that induction-shocks as well as certain alkaloids stopped the ciliary movement and locomotion of Infusoria before the pulsation of the vacuoles had ceased. Dodel[5], however, found that the vacuolar pulsation and ciliary movement of the zoospores of *Ulothrix* ceased simultaneously, and that in other zoospores the cilia continued to move after pulsation had ceased, so that specific differences appear to occur according to the organism examined[6].

Various agencies may cause an enlargement of the vacuole, and this change is in some cases reversible and extremely pronounced. When thus swollen the vacuoles may pulsate little or not at all. Klebs found that this effect was produced in the case of *Euglena* by various neutral salts which, however, appear to be less effective in their action upon Infusoria. Rossbach was indeed unable to detect any action at all upon them, but Massart has shown that it takes place at a particular concentration[7]. High concentrations naturally produce a plasmolytic contraction, and in some cases a complete collapse of the vacuoles[8]. Rossbach found that alkaloids and alkalies caused an enlargement of the vacuoles of Infusoria, but Klebs was unable to detect any distension when *Euglena* was exposed to the action of strychnine. Both Klebs and Massart have, however, observed a gradual accommodation of the vacuoles to concentrated solutions.

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[1] Pfeffer, Plasmahaut u. Vacuolen, 1890, p. 223. Bütschli and Rhumbler also consider that the vacuoles are formed anew after each complete pulsation.

[2] Cf. Pfeffer, l. c., 1890, p. 223.

[3] Bütschli, Protozoen, 1880–8, pp. 715, 1454; Klebs, Unters. a. d. bot. Inst. zu Tübingen, 1883, Bd. I, p. 248.

[4] Rossbach, Die rhythmischen Bewegungserscheinungen d. einfachsten Organismen, 1872, p. 56. See also Bütschli, l. c., p. 1455.

[5] Dodel, Bot. Ztg., 1876, p. 185.

[6] Cienkowski, Bot. Ztg., 1865, p. 23; Strasburger, Ueber Zellbildung u. Zelltheilung, 1875, p. 157.

[7] Massart, Archive de Biologie, 1889, T. IX, p. 550.

[8] Cohn, Nova Acta Acad. Caesar. Leopold., 1854, Bd. XXIV, i, p. 194; Klebs, l. c.; Massart, l. c.

Sudden changes presumably exercise the customary shock-effect upon pulsation, and it is possibly owing to some such action that only a few observers have been able to detect an increased frequency when oxygen is deficient or carbon dioxide abundant[1].

Functional importance. It is generally assumed that the contractile vacuoles aid in the absorption of oxygen and other food-materials as well as in the excretion of carbon dioxide and other waste products[2]. Maupas[3] has indeed calculated that Infusoria may expel and reabsorb their own volume of water in two to forty-six minutes. All Protozoa do not, however, possess pulsating vacuoles, nor do the cells of Fungi or of primary meristems which also possess very active powers of respiration and of metabolism. In tissues, however, the transit between the cell and the external world becomes of greater importance and is slower than the entry into or escape from particular cells. Hence the latter do not require special aids to absorption and excretion, and in fact the excretion of water in the tissues of aerial organs, as occurs when the filaments of Cynareae and irritable pulvini are stimulated, always involves a certain hindrance to gaseous exchange external to the cell. It is possible also that the contractile vacuoles may in some cases serve special purposes, and in the case of *Chilodon propellens* each ejection of water causes a jerky movement of the organism in the opposite direction[4].

SECTION 64. **Other Protoplasmic Movements.**

All these movements, including those involved in cell and nuclear division, are the direct or indirect results of vital activity, although their detailed origin is comparatively unknown. All parts possessing the properties of a viscous liquid must be subject to the physical laws already discussed which determine or modify their shape. The flattened character of many nuclei is, for instance, probably often due to the existence of lateral pressure upon it. Every active enlargement of the nucleus, as well as the growth of starch-grains, necessarily produce corresponding displacements in the protoplasm, and in fact the expansion and contraction of vacuoles may originate definite streaming movements in the protoplasm.

The rounding of the viscous protoplasm on plasmolysis is the direct result of the existence of a uniform surface-tension pressure at its external boundary, but a bulging will always be produced at any point where a lower surface-tension is maintained. An accumulation of the denser constituents at one end of a cell produced by centrifugal action may, however, take more than a week to be readjusted, whereas a rapid

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[1] Bütschli, Protozoen, 1880–8, p. 1452.

[2] Cohn, Beiträge z. Biologie, 1877, Bd. II, p. 118. For details see Bütschli, l. c., p. 1452.

[3] Quoted by Bütschli, l. c., p. 1455. According to Rhumbler (Archiv f. Entwickelungsmechanik, 1898, Bd. VII, p. 257), *Amoeba proteus* shows a pronounced contraction with every collapse of the vacuole.

[4] Engelmann, Zur Physiologie d. contractilen Vacuolen der Infusionsthiere, 1878.

redistribution takes place when the protoplasm exhibits streaming movement. Even in this case, however, a local accumulation of protoplasm or chloroplastids may pass several times around a cell before being broken up.

When displacements are only slowly readjusted, the protoplast may never reach a condition of stable equilibrium, owing to the continued production of new dispositions before the adjustment to the older ones is completed. It is, therefore, impossible to predict what the stationary condition of equilibrium would be, and in fact the protoplast might maintain permanently an unequal distribution of tension. In general, however, the shape and arrangement of the protoplast and of its organs correspond to what would be expected in a viscous emulsion.

Since the organs of the protoplast lie in an active living medium, local changes of surface-tension are likely to be of common occurrence, quite apart from the changes of imbibition and swelling produced in the interior of the organs affected. In addition, the various organs as well as portions of the cytoplasm or nucleoplasm may acquire temporarily or permanently a more solid consistency, and may then be capable of active changes of shape. The preservation of their shape by the chlorophyll-bands of *Spirogyra* demands the existence of a fair degree of consistency in them, and possibly changes of cohesion play a part in the changes of shape and configuration of the chromosomes during nuclear division. It is, however, uncertain in most cases how the various internal movements and changes of shape are produced. Even in the much studied case of protoplasmic streaming an element of doubt still attaches, for the evidence in favour of its surface-tension origin is for the most part indirect in character[1].

Although in certain cases the chloroplastids and nuclei are undoubtedly passively carried by the streaming protoplasm, they may also be capable of slow independent locomotion by amoeboid change of shape, or by the maintenance of appropriate differences of surface-tension. In the case of comparatively large plastids and nuclei embedded in viscous protoplasm only very slow movements could be produced in this way; but the smallest force will produce movement, since the resistance to flow is kinetic and proportional to the velocity. The total force available in such cases would not, however, suffice to overcome the static resistance offered even by a very attenuated colloid to an incipient movement. In any case, if the differences of surface-tension were only produced by the metabolic activity of the surrounding cytoplasm, it is doubtful whether we should be justified in speaking of an active locomotion of the nucleus, although the motory energy was actually liberated at the boundary of nucleus and cytoplasm. Similarly, when a drop of oil comes into contact with a soap-solution the

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[1] Cf. Ewart, Protoplasmic Streaming in Plants, 1903, pp. 108–19.

difference arises in the external medium, whereas a drop of a mixture of oil and potassium carbonate shows movement when surrounded on all sides by a homogeneous medium, water. Even if the locomotory energy is actually supplied by the cytoplasm the nucleus might easily exercise a directive influence upon it, and so determine the direction of movement.

It is, therefore, not surprising that doubt should exist as to whether the slow translocatory movements of nuclei and chloroplastids are always passive in character or not. The nucleus may be passively carried to any point where an accumulation of protoplasm is produced either by traumatic, chemical, or other agencies. Even without such accumulation a passive movement of the nucleus is as readily possible as an active one. Some authors assume the former to be the case, others the latter [1], but no critical experiments have as yet been performed. The occasional amoeboid or gradual changes of shape of the nucleus appear, however, to be active in character, but even here interaction with the surrounding cytoplasm may aid in their production [2]. The same applies to the chloroplastids, whose movements in response to illumination may either be active or produced by a directive utilization of the motile energy of the cytoplasm. In the same way it is impossible to say whether the movements of the chromosomes are active or passive, or are compounded of both.

The special elongated, lobed, twisted, or even spirally coiled shapes sometimes assumed by nuclei can often be seen to be independent of the shape of the cell, and not to be mechanically impressed upon the nucleus. The nuclei of animals more often show amoeboid movements than those of plants [3], but whether amoeboid activity plays a part in the passage of the reproductive nuclei from the pollen-tube to the ovum and embryo-sac is still uncertain [4]. The same applies when the nucleus passes from one cell to a neighbouring one during cases of vegetative fusion [5]. It is quite possible that the fibrillae appearing during cell-division, but which may also be produced in various ways, may be capable of producing internal movement by their supposed contractile activity. These structures are, however, transitory in character, and their tendency to shorten is of similar

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[1] Cf. Hanstein, Mittheil. ü. d. Bewegungserscheinungen des Zellkerns, 1870, p. 224 (reprint from Sitzungsb. d. Niederrh. Ges.); Berthold, Protoplasmamechanik, 1886, pp. 150, 164; Haberlandt, Function u. Lage d. Zellkerns, 1887, p. 103; Behrens, Bot. Ztg., 1890, p. 100.

[2] Cf. Molisch, Studien ü. d. Milchsaft u. Schleimsaft, 1901, pp. 87, 107; Bot. Ztg., 1899, p. 177; Haberlandt, l. c., p. 124; v. Wasielewski, Jahrb. f. wiss. Bot., 1902, Bd. XXXVIII, p. 415; Ewart, Journ. Linn. Soc., Vol. XXXI, 1896, p. 448.

[3] [The nuclei of such parasitic plants as *Cuscuta*, *Lathraea*, and *Orobanche* seem to show amoeboid movement more commonly and markedly than those of ordinary plants, but whether this is connected with the rich nitrogenous nutrition or the general activity of metabolism is uncertain.]

[4] Cf. Mottier, Fecundation in Plants, 1904, p. 176.

[5] Cf. Strasburger, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 551; Koernicke, Sitzungsb. d. Niederrh. Ges., March, 1901.

character to that of a thread drawn from a viscous liquid. Any secretion of mucilage in the interior of the protoplasm would also produce a certain amount of displacement reversible by the reabsorption of the mucilage.

Nuclear division may be accompanied or preceded by an increase in the total amount of nuclear material, and may take place independently of the cytoplasm, although in mitotic division nucleus and cytoplasm come into close relationship during the process and the latter forms the threads of the 'nuclear' spindle[1]. It is, however, uncertain what part is played by the centrosomes, which are in fact absent from most plant-cells[2]. The mechanics of amitotic, and still more of the remarkable movements involved in mitotic, division are indeed quite unknown. It is, however, certain that they may be produced in a variety of ways, so that experiments with non-living materials do not afford definite evidence as to the nature of the physiological processes involved. Bütschli[3] was able to produce radiations resembling those shown by dividing nuclei by the contraction of air-bubbles embedded in solidifying gelatine and also in emulsions of oil and soap under special conditions[4]. Fischer[5] produced remarkable radiations arranged around the remains of the nucleus as a focus by precipitating albumose in dead cells of Elder-pith. In this case the nucleus acts merely as a centre of deposition, so that in the living cell it may also play a passive part in the production of the radiations formed around it. The grouping of particles of iron in a magnetic field yields similar configurations[6], but the magnetic properties of the cell constituents are incapable unaided of directly producing any such grouping in the strongest magnetic fields available[7]. No actual facts are, however, known as to the mode of movement in any single phase of the changes, and even if the motion of the chromosomes should prove to be due to the tension or pressure exercised by the threads of the spindle[8] we have still to determine the mode of action of these threads themselves.

The external conditions may influence the character and progress of cellular and

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[1] See R. Hertwig, p. 698; Strasburger, l.c., 1900, p. 118; Zimmermann, Morphologie u. Physiol. d. pflanzlichen Zellkerns, 1896, p. 48.

[2] Cf. Strasburger, Histologische Beiträge, Heft vi, 1900, p. 156; Ber. d. bot. Ges., 1901, p. 458; R. Hertwig, Abhandlg. d. Bayrisch. Akad. d. Wiss., 1898, Bd. XIX, p. 690; Mottier, Fecundation in Plants, 1904, p. 2.

[3] Bütschli, Unters. über Structuren, 1898, p. 156.

[4] Bütschli, Unters. ü. mikroskopische Schäume, 1892, pp. 29, 159, 166. Cf. also Strasburger, Bot. Zeitung, Referate, 1900, p. 300; Zacharias, Ber. d. bot. Ges., 1902, p. 298.

[5] A. Fischer, Fixirung, Färbung u. Bau d. Protoplasmas, 1899, p. 206.

[6] Cf. Errera, Compt. rend. de la Soc. royale de botanique de Belgique, 1890, T. XXIX, p. 17; Bütschli, l.c., 1898, p. 169; Rhumbler, Archiv f. Entwickelungsmechanik, 1903, Bd. XVI, p. 476; Seddig, Ann. d. Physik, 1903, Bd. II, p. 815.

[7] Ewart, Protoplasmic Streaming in Plants, 1903, p. 45.

[8] The theories concerning cell-division are mainly based upon preconceived hypotheses, so that nothing is to be gained by their discussion. Cf. Bütschli, l. c., 1892, p. 160; Ziegler, Verhandlg. d. deutsch. zoologischen Ges., 1895, p. 62; R. Hertwig, Abhandlg. d. Bayr. Akad., 1898, p. 694; Rhumbler, Archiv f. Entwickelungsmechanik, 1898, Bd. VII, p. 535; Ergebnisse d. Anatomie u. Entwickelungsgeschichte, 1898, Bd. VIII, p. 605; A. Fischer, l. c., pp. 224, 257; Bethe, Bot. Centralbl., 1902, Bd. LXXXIX, p. 513; Häcker, Praxis u. Theorie d. Zellen- u. Befruchtungslehre, 1899, p. 73.

of nuclear division to a greater or less degree. Thus, when a cell of *Spirogyra* which normally divides by mitosis is caused to divide amitotically by the action of ether, we have a change similar to the production of *Mucor* yeast occurring under special conditions[1]. The shape of other plants is, however, relatively little affected by the external conditions, and hence it is not surprising that in most cases the external conditions exercise little effect upon the character of the mitotic nuclear division. Certain abnormalities may often be produced, however[2], and in many cases changes in the external or internal conditions may result in one or in numerous amitotic divisions[3]. On the other hand, in the case of many lower organisms in which the nucleus normally divides by amitosis[4], mitotic nuclear divisions may possibly be produced under special circumstances. In any case transitions occur between typical mitosis and amitosis[5], and all forms of amitotic nuclear division characterized by the non-production of pronounced mitotic figures do not fall in the two categories proposed by Wasielewski[6].

Furthermore various instances are known of temporary and reversible differentiation in the protoplasm, and in fact the distinction between hyaloplasm and granuloplasm is one of this character. There is no positive evidence to support Strasburger's use of the terms trophoplasm or alveolarplasm, and kinoplasm or reticuloplasm as indicative of fixed structures[7]. Changes in the relative percentage of each according to the external conditions or the progress of development[8] are quite in accord with a unity of origin for both. Both Hertwig and Zacharias have opposed this doctrine of the existence of permanent organically distinct differentiation in the general cytoplasm.

The doctrine that continued existence and reproduction is impossible in the absence of mitotic nuclear division is, like the dogma as to the necessity of free oxygen for life, founded upon hasty, incorrect generalization. Nor is there any reason why full hereditary transmission should not be possible unless some of the reproductive living units, biophore, or pangens, group themselves into large visible chromatin-threads. It is quite possible, however, that such grouping previous to

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[1] Cf. Pfeffer, Sitzungsb. d. sächs. Ges. d. Wiss., 3. Juli, 1899.

[2] Blazek, Bot. Centralbl., 1902, Bd. xc, p. 548; Van Wisselingh, Flora, 1900, p. 373; Gerassimoff, Zeitschrift f. allgem. Physiol., 1902, Bd. i, p. 220; Strasburger, Histologische Beiträge, Heft vi, 1900, p. 127. On the lower animals cf. Doflein, Zell- u. Protoplasmastudien, 1900, p. 42; E. B. Wilson, Archiv f. Entwickelungsmechanik, 1901, Bd. xiii, p. 389; Wasilieff, Biol. Centralbl., 1902, Bd. xxii, p. 758; Werner, Bot. Centralbl., 1902, Bd. xc, p. 521; Wallengren, Zeitschr. f. allgem. Physiol., 1902, Bd. i, p. 67. R. Hertwig, Abhandlg. d. Bayr. Akad., 1898, Bd. xix, p. 687; Archiv f. Protistenkunde, 1902, Bd. i, pp. 11, 16, gives instances of variations in the nuclear figures at different stages of development.

[3] Wasielewski produced amitosis in roots by the aid of chloral hydrate (Jahrb. f. wiss. Bot., 1902, Bd. xxxviii, p. 377). See also Magnus, Jahrb. f. wiss. Bot., 1900, Bd. xxxv, p. 242; Chodat, Actes du Congrès international de Botanique, Paris, 1900, p. 23; Shibata, Jahrb. f. wiss. Bot., 1902, Bd. xxxvii, p. 648; Schimkewitsch, Bot. Centralbl., 1902, Bd. xxii, p. 605.

[4] R. Hertwig, Archiv f. Protistenkunde, 1902, Bd. I, p. 26.

[5] R. Hertwig, l. c., p. 25.

[6] L. c., p 401.

[7] Strasburger, Histologische Beiträge, Heft vi, 1900, p. 144.

[8] Strasburger, l. c., p. 144; R. Schrammen, Bot. Centralbl., 1902, Bd. xc, p. 551; R. Hertwig, Abhandlg. d. Bayrisch. Akad., 1898, Bd. xix, p. 690; Zacharias, Flora, 1895, Ergzbd., p. 259.

division might present certain advantages. The latest researches seem, however, to show that the nucleus is absent from, or at least not yet differentiated in, certain lower organisms[1]. It is still possible that the chromatin elements may be present, but diffusely distributed[2], although it is to be remembered that the structures to which this general term is given cannot be precisely identical in all organisms, but must exhibit greater or smaller dissimilarities capable of hereditary transmission.

Protoplasmic fusion. Contact must naturally precede fusion, but does not necessarily produce it, as for instance when similar or dissimilar organs of the cell, or dissimilar protoplasts, come into contact. Thus the closest contact does not produce fusion between the plasmodia of different species of Myxomycetes[3], whereas plasmodia of the same species readily unite. Even when a fragment of a foreign plasmodium is ingested by another species no fusion occurs between them[4]. In the case of the swarm-cells of *Aethalium* the capacity for fusion only appears at a certain stage of development, and hence it is possible under suitable conditions to permanently prevent the appearance of the fusion stage so that no plasmodium is formed[5]. Actual fusion does not occur in *Dictyostelium* and other Acrasiae, although the amoebae come into close contact and form an aggregate plasmodium[6]. Similarly, sperms do not fuse with one another, but readily unite with appropriate ova, in which the fusion of male and female pro-nuclei ultimately occurs. It is worthy of note that immediately after the entry into the ovum changes take place at the surface which prevent the penetration of additional sperms. Probably it was owing to the suppression of these changes by the agency of chloral hydrate that Hertwig was able to cause the entry of a number of spermatozoids into the egg of a sea-urchin[7]. The production of hybrids shows that the protoplasts of dissimilar species may unite, and it is possible that successful grafting involves the fusion of the interprotoplasmic connexions in the neighbouring cells of scion and stock[8].

In addition to intimate contact at some point or other, fusion involves the rupture of the intervening surface-tension films. This occurs naturally when the whole of the intervening medium is displaced at any one point, for the existence of the surface-tension film is dependent upon contact with a dissimilar non-wetting medium. Hence the presence of impurities on the surface of drops of mercury hinders their fusion greatly, and the same result will be attained whenever a thin layer of the surrounding medium is maintained between two drops of similar liquid[9]. It is owing

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[1] See especially in regard to bacteria, Hinze, Ber. d. bot. Ges., 1901, p. 369; Unters. ü. d. Bau von *Beggiatoa mirabilis*, 1902; Schaudinn, Archiv f. Protistenkunde, 1902, Bd. I, p. 335; Ernst, Centralbl. f. Bact., 1902, Bd. VIII, Abth. ii, p. 1; Bütschli, Protozoen, 1880, p. 107.

[2] R. Hertwig, l. c., 1902, p. 6.

[3] Cienkowski, Jahrb. f. wiss. Bot., 1863, Bd. III, p. 337.

[4] Celakovsky, Flora, 1892, Ergzbd., p. 215.

[5] Klebs, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 196.

[6] Cf. Zopf in Schenk's Handbuch d. Botanik, 1887, Bd. III, Abth. ii, p. 22; Potts, Flora, 1902, Ergzbd., p. 281.

[7] O. Hertwig, Zelle u. Gewebe, 1893, p. 93.

[8] Strasburger, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, pp. 586, 592; Meyer, Bot. Ztg., 1902, p. 173.

[9] Quincke, Pflüger's Archiv f. Physiol., 1879, Bd. XIX, p. 129; Berthold, Protoplasmamechanik, 1886, p. 107; Rhumbler, Biol. Centralbl., 1898, Bd. XVIII, p. 115.

to changes of surface-tension that the addition of alcohol to an emulsion of oil in water favours the fusion of the oil-drops, while, partly owing to this cause and partly owing to the solution of impurities, the addition of nitric acid to an emulsion of partially oxidized mercury produces a sudden coalescence of the droplets.

A high cohesion of the peripheral layers may aid in preventing fusion, as may also the secretion of gelatinous membranes; but the causes which determine fusion have not as yet been satisfactorily determined in a single case. Klebs[1] found that the gametes of *Protosiphon botryoides* do not conjugate at 26° to 27° C., although they develop and swarm at this temperature, but the causes of this behaviour, as well as for the absence of any power of fusion between the swarm-cells of *Aethalium* when first produced, are quite unknown. Townsend[2] found that fusion often does not occur between the fragments of the protoplast separated by plasmolysis, possibly because of the débris formed between them by the disorganization of connecting protoplasmic threads. When the latter remain intact fusion always occurs, since the most minute local union suffices to produce ultimate total fusion. The union of the plasmodia of Myxomycetes is not, however, prevented by the intervention of a thick layer of foreign substances, since the pseudopodia bore through it and unite. Similarly, the ectoplasm affords no obstacle to complete fusion, since its high cohesion is lost when it becomes withdrawn internally. Indeed the protoplast may, when necessary, dissolve away intervening cell-walls, while, on the other hand, the segmentation into separate protoplasts may take place without any production of dividing walls.

The ingestion and excretion of solid bodies. The continued existence of symbiotic algae in the cells of *Hydra viridis* and of certain Protozoa shows that special conditions determine whether foreign bodies are retained or rejected[3]. A tendency to the rejection of foreign bodies is shown even in dermatoplasts, as for instance when excreta, such as calcium oxalate crystals, are thrown into the cell-sap. Usually the excretion is aided by the existence of protoplasmic movement, whereas particles of various substances lying against the non-motile peripheral layer of a plasmolysed protoplast free from its investing cell-wall are usually not ingested. According to Rhumbler[4], differences of surface-tension and spreading tendencies are solely responsible for the ingestion of foreign bodies, but this can hardly apply to all cases. A solid body in contact with a drop of chloroform in water will be ingested by it as the result of the chloroform spreading over it and surrounding it. In the same way a glass fibre covered with shellac will be ingested by a drop of chloroform, and expelled when the shellac has been dissolved away, since as soon as the tip of the thread is exposed, the changed surface-tension and the tendency to spread causes the chloroform to be driven away from the thread by the water[5].

It is, therefore, quite possible that the digestion within the protoplast of an ingested body might produce the conditions for the excretion of indigestible remains.

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[1] Klebs, Bedingungen d. Fortpflanzung, 1896, p. 209.

[2] Townsend, Jahrb. f. wiss. Bot., 1897, Bd. XXX, p. 495.

[3] Pfeffer, Aufnahme u. Ausgabe ungelöster Körper, 1890, p. 174.

[4] Rhumbler, Archiv f. Entwickelungsmechanik, 1898, Bd. VII, p. 224.

[5] Rhumbler, l. c., p. 250.

The plasmodia of Myxomycetes may, however, with equal readiness ingest and expel indigestible particles such as grains of sand or of vermilion. In addition, mere contact with non-motile regions of the ectoplasm is insufficient to produce ingestion, which takes place usually only at those regions where amoeboid activity is shown.

PART II

THE INFLUENCE OF THE EXTERNAL CONDITIONS ON LOCOMOTION AND ON PROTOPLASMIC MOVEMENT

SECTION 65.

Under special external conditions the power of active locomotion may be inhibited without growth ceasing, and the contrary may also occur. A. Fischer[1] found that various bacteria become immotile in concentrated solutions in which they grow and develop motile cilia. The presence of carbolic acid, and in general any agency which when more intense suppresses growth, may produce the same effect. Temperatures lying near the maximum may act in the same way, but Matzuschita[2] did not determine to what degree the immotility was due to the production of non-ciliated developmental forms. Prolonged cultivation on solid media has, for instance, always this effect upon the motile aerobic forms of *Bacterium termo* used for testing the evolution of oxygen[3]. According to Ellis[4], the immotility is often due to the production of mucilage which mechanically prevents movement, while Ritter[5] found that facultatively anaerobic bacteria lost their motility in the continued absence of oxygen, but immediately regained it when oxygen was admitted.

Most locomotory and protoplasmic movements take place in darkness as well as in light, whereas the purple bacteria which develop normally in darkness[6] only begin to move when exposed to light, and fall into a condition of dark-rigor when it is withdrawn. In addition, other phototonic, thermotonic, and chemotonic actions upon locomotory activity are known. Many substances, such as ether and chloroform, which when concentrated

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[1] A. Fischer, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, pp. 48, 153.

[2] Matzuschita, Centralbl. f. Bact., Abth. ii, 1901, Bd. VII, p. 209.

[3] Ewart, Journ. Linn. Soc., 1896, Vol. XXXI, p. 364.

[4] Ellis, Centralbl. für Bact., 1902, Bd. IX, p. 546.

[5] Ritter, Flora, 1899, p. 337.

[6] [This appears to be an error. The purple chlorophyll-containing *Bacterium photometricum* and *Monas Okenii* will develop in feeble light but not in continued absolute darkness, even when sown on various solid and liquid nutrient media. The green bacteria (*Bacillus virens*, *Bacterium chlorinum*, and *Streptococcus varians*) may, however, be grown in darkness on gelatine-sugar media, but then lose their chlorophyll. Cf. Ewart, Journ. Linn. Soc., 1897, Vol. XXXIII, p. 123, and Annals of Botany, 1897, Vol. XI, p. 486.]

retard or inhibit movement may accelerate it when dilute. The fact that light causes certain zoospores, and meat extract those of *Saprolegnia*, to come earlier to rest[1] is due to the shortening of the period of development by these agencies. Whether the similar influence of magnetic forces is also of this character is, however, uncertain[2].

The existence of a power of rapid locomotion permits the shock-effects of sudden changes to become more readily perceptible. The sudden application of fatally injurious conditions often causes specially active irregular locomotion which reminds one of the spasmodic struggles of a poisoned or asphyxiating animal. Naturally shock-reactions are not always equally pronounced, and are not shown in all cases and with all agencies. Changes of temperature, of illumination, and of concentration, injuries and transitory anaesthetization, as well as many other agencies, may excite or accelerate protoplasmic streaming, and in some cases when once aroused, especially as the result of injury, it may persist until death. The direct action of a sudden change upon existent streaming is usually to cause a temporary retardation or even stoppage; but in some cases, especially with moderate rises of temperature, the velocity is temporarily accelerated beyond the value it ultimately assumes. Injurious external agencies, especially when suddenly applied, usually cause a contraction of amoeboid protoplasts to the spheroidal shape, but may occasionally increase the amoeboid activity.

Contact or the change to another medium causes the cilia of *Chlamydomonas* to straighten suddenly, and so produces a backward movement of the organism into the homogeneous medium, in which the ciliary and locomotory activity is resumed in one or more seconds[3]. A similar shock-movement is produced in *Bacterium photometricum* by sudden decreases of illumination, and this may cause it to move ten to twenty times its length backwards when it comes to the edge of an illuminated area to which it is, therefore, restricted. The transit from a concentrated to a more dilute solution produces a similar backward movement in many Bacteria, Infusoria, and Flagellatae, so that the organisms collect in the more concentrated medium. It is, however, not known whether this shock-movement is accompanied by a temporary cessation of the ciliary activity, although, according to Fischer, sudden changes of concentration do actually cause a temporary inhibition of the ciliary movement[4]. All motile organisms do not show shock-reactions of this character, and an organism sensitive to one form of shock may be insensitive to others. The shock-movement of *Bacterium photometricum* is produced only by the transit from light to darkness, and not by the reverse,

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[1] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, p. 467; Rothert, Flora, 1901, p. 374.

[2] Ewart, Protoplasmic Streaming in Plants, 1903, p. 52.

[3] Pfeffer, l. c., p. 444.

[4] A. Fischer, Jahrb. f. wiss. Bot., 1895, Bd. XXVII, p. 76.

whereas in *Pelomyxa palustris* the shock-movement is produced by sudden illumination, and not by the sudden withdrawal of light. Similarly, many bacteria show a shock-movement on passing from strong solutions to weak ones, but not on passing from regions of lower to ones of higher concentration. In addition, a pronounced deformation of the protoplasm is shown on transferring from an almost maximal temperature to a normal one, but not on raising to the higher temperature. The deformation is also absent on cooling to low temperatures, but it appears when the temperature is raised again. In the case of the streaming cells of *Chara* and *Nitella*, however, both the sudden application and the rapid removal of pressure, as well as sudden rises or falls of temperature or concentration, may produce a temporary shock-stoppage of streaming.

SECTION 66. **The Forms of Tactic Response to Tropic Stimuli.**

Whenever a tropic stimulus causes a definite orientation of the main axis of a freely motile organism, locomotion in a definite direction is assured, since in most cases the latter takes place along the main axis. Whether the movement is positive or negative in character will depend upon the direction of the anterior end in regard to the orienting stimulus. Local accumulation may also result from the fact that the organisms freely move towards regions of higher illumination or concentration, but experience a backward shock-movement on approaching regions of lower concentration or illumination. Passive accumulation also takes place when organisms which swim freely continually adhere to a mucilaginous region, or are suddenly killed on coming into contact with a poisonous area, or rapidly lose the power of movement in a zone deficient in oxygen.

Shock-stimulation is responsible for the accumulation of *Bacterium photometricum* in illuminated areas, as well as for the accumulation of various Bacteria and Infusoria in concentrated solutions. Whereas the phototactic movements of the zoospores of many Algae, and the chemotactic attraction of many antherozoids, and of the zoospores of *Saprolegnia* and of many Flagellatae, are the result of a tropic orientation of the body axis, as are also the geotactic and galvanotactic movements of various organisms. In both cases we are dealing with stimuli due to dishomogeneity in the surroundings, but the stimuli act upon dissimilar forms of irritability. The shock-stimulation is a temporary action repeated every time the required change of conditions is produced by the movements of the organism, whereas in the typical tropic orientation the inclination the organism assumes is maintained so long as the tropic agency is unaltered, even if the organism adheres to the same spot. Such organisms move with a definite aim, whereas forms like *Bacterium photometricum* may be said to possess a phobotactic irritability by which they avoid dark areas. Similarly, by chemo-phobotaxis we may indicate an irritability by which an organism is able to avoid or to remain in solutions of chemical substances owing to the backward shock-movement produced on entering or leaving them as the case may be[1]. In many cases the exact nature of the response is uncertain, and in others tropic and phobic actions may co-operate in producing the result observed.

In the case of small and active organisms it is difficult to determine whether a tactic or a phobic response is given, for during chemotactic attraction the individuals do not all travel along straight paths to the capillary containing the exciting substance, while at its mouth and within it the forms move about in the same way as organisms attracted in a phobic manner. Hence it was only after careful study and after using slowly moving forms that Jennings and Crosby were able to show that the attraction of Bacteria by chemical substances was the result of a phobic action, although Engelmann had previously shown that the attraction of *Bacterium photometricum* to illuminated areas was produced in this manner[2]. The phobic reaction and accumulation of various Infusoria and Flagellatae were demonstrated by Jennings[3], and were confirmed by Garrey[4] before the chemophobic responses of Bacteria were investigated.

It is possible that in many cases the same agency may excite a feeble phobic and a strong tactic, or a strong phobic and a feeble tactic response. This may explain the backward movement of the strongly chemotactic antherozoids of Ferns when they attempt to enter a capillary filled with a solution of malic acid. The phototactic zoospores of *Botrydium* also appear to be weakly photophobic[5], and some species of Bacteria may possess a strong power of chemotactic response in spite of Rothert's conclusions as to the general chemophobic reaction of Bacteria.

If a chemophobic action is always exercised when the organism

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[1] [There seems to be no reason for adopting the terms topotropism and topotaxis, as suggested by Pfeffer, to indicate the typical orienting movements, since the term 'phobism' put forward by Massart, Centralbl., 1902, Bd. XXII, p. 49, suffices to distinguish these special forms of tropic and tactic irritability from the more general case. It is still possible to use the term 'tropism' in the general sense (cf. Bot. Ztg., 1902, Referate, p. 17) instead of restricting it in the way that Massart (l. c., p. 49) and Nagel (Bot. Ztg., 1902, Ref., p. 24) do. Rothert's term 'apobatic' (Flora, 1901, p. 393) is both uncouth and unnecessary, nor can his term of 'strophotaxis' be adopted, since 'strophism' has already been used in an equally superfluous way to indicate movements produced by torsion. The error arises in supposing that a dissimilar response necessarily indicates a totally distinct form of irritability, and hence needs a new term, or that phenomena are made simpler or more easy to understand by giving them a classical terminology. The same applies to the use of the term 'argotaxis' (ἀργός, passive) to indicate purely physical, passive movements due to surface-tension, like those of a drop of oil in a soap-solution. In any case Nagel (Bot. Ztg., 1901, p. 297; 1902, Ref., p. 24) is in error in considering that phobic reactions alone arise from a special discriminatory sense.]

[2] Engelmann, Pflüger's Archiv f. Physiologie, 1882, Bd. XXX, p. 95; Jennings and Crosby, American Journal of Physiology, 1901, Vol. VI, p. 29; Rothert, Flora, 1901, Vol. VI, p. 29.

[3] Jennings, American Journal of Physiology, 1899, Vol. II; 1900, Vol. III.

[4] Garrey, Centralbl. f. Physiol., 1900, Bd. XIV, p. 105.

[5] See the literature quoted by Rothert, l. c., p. 386.

attempts to pass to a more dilute zone, an accumulation will be shown, however high the concentration may be. Phobic movements do not necessarily only result from a passage to zones of different concentrations, but may result from changes of position in regard to an orienting agency. Thus, owing to the unequal distribution of irritability over the surface of the organism, every displacement might exercise a shock-effect producing a return to the original orientation. From this point of view the typical tropic reactions of rapidly moving organisms might be regarded as phobic responses.

A reversal of both the tactic and phobic responses may take place with increasing concentration. Thus in the latter case, beyond a certain strength the phobic movement might be excited by the passage to regions of higher instead of to ones of lower concentration. In both cases, therefore, the organisms may collect at a definite distance from the mouth of the capillary from which the concentrated exciting solution is diffusing. Zoospores ciliated on one side only show this reversal of the tactic response especially well, for as the result of it they pass beyond the position of equilibrium and then turning round swim back again. If the base of such an organism were fixed it would presumably bend to a definite position as in the case of a rooted plant, and would assume a diatropic position at some intermediate point between the regions of repellent and attractive concentration. Usually, however, no diatropism can be detected in freely motile organisms, although, according to Verworn[1], the ciliated Infusorian *Spirostomum ambiguum* places itself at right angles to the direction of an electrical current, while *Oxytrichia* and other Infusoria, which creep about with their ciliated surface on the substratum may be said to be diathigmotropic. Similarly, certain Desmids as well as the chloroplastids of *Mesocarpus* assume diaphototropic positions in light of moderate intensity. Diatoms, on the other hand, are ortho-phototactic, although they may be made to assume plagio-phototropic positions by inclining the glass on which they glide at an angle with the light-rays.

Diatoms and other equipolar organisms may reverse their movement without turning round, and many such organisms which normally move to and fro are attracted in a definite direction merely by the movement to one side lasting longer than that towards the opposite one. In Amoebae and in plasmodia, however, the tropic attraction is attained by the excitation of amoeboid movement on one side. The backward shock-movement does not appear to be accompanied by any reversal of the organism, even when the latter is ciliated at one end only. At least no such reversal was observed by Engelmann in the case of the unipolarly-ciliated *Bacterium photometricum*[2]. If the impact against a glass plate alters the orientation

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[1] Verworn, Allgem. Physiol., 1901, 3. Aufl., p. 480.

[2] Cf. Rothert, l. c., p. 391; Jennings and Crosby, l. c., p. 36.

of the body, the resultant shock-movement will naturally take place in the new direction. Dorsiventral organisms like *Paramoecium*[1] assume definite positions as the result of every shock-movement, but whether this also applies to vegetable organisms is uncertain.

Since we are dealing with two distinct forms of irritability, one agency may induce a tactic and another a phobic movement, while in some cases the same stimulus may excite both forms of response. Many Infusoria are galvanotactic, but chemophobic and osmophobic, while certain Volvocineae are phototactic and also osmophobic[2]. According to Garrey[3] *Chilomonas* is chemophobic to the more active inorganic acids, and chemotactic to the feebler organic acids. It is in fact possible that in many cases the chemotactic attraction by weak solutions becomes a chemophobic repulsion when they are more concentrated.

In spite of the generally useful adaptive character of these responses, it is not surprising that in many cases a galvanotactic irritability should be shown, although it cannot have any practical importance. Similarly, although many organisms avoid injurious concentrations, others swim into these or even into poisonous solutions where they are killed. The best chemotactic agency can only attract or repel across relatively small distances, although light and gravity are more extended in their action. For biological purposes of attraction tactic stimulation is in general more advantageous, for the spermatozoids of Ferns, for instance, could hardly be drawn with certainty in any other way to the ovum. Phobic stimulation is, however, ample to attract and retain bacteria to special loci, or to prevent their penetration into injurious media.

Various orientations within the cell probably result from unilateral stimulation, but hitherto only the phototactic movements of chloroplastids and the traumatropic movements of the nucleus are known with certainty. The protoplasmic aggregation which results from various stimuli may be due either to a primary or secondary reaction—a distinction difficult to determine under the complicated relationships prevailing within the cell. The slow progress of the internal movements afford, however, strong evidence that they are not the result of shock-stimulation. In general, the power of movement is antecedent to tropic stimulation, and its rapidity is not perceptibly modified by the latter, although many instances may ultimately be found to exist in which a latent power of movement is first awakened by the tropic stimulus. Nägeli[4] found, however, that the phototactic stimulation of Algal zoospores, and Pfeffer[5] that the chemotactic

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[1] Jennings, Am. Journ. of Physiol., 1899, Vol. II.

[2] Rothert, l. c., p. 396.

[3] Garrey, The effects of ions upon the aggregation of flagellated Infusoria, 1900.

[4] Nägeli, Beiträge z. wiss. Bot., 1860, Heft ii, p. 102; Strasburger, Wirkung d. Lichts u. d. Wärme auf Schwärmsporen, 1878, p. 27.

[5] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. 1, p. 375.

stimulation of the sperms of Ferns produced no acceleration of movement. Nevertheless, if an organism whose movement is retarded or inhibited by a deficiency of oxygen or of a food-material is tropically stimulated by the unilateral access of oxygen or of the food-material, an acceleration of movement is bound to ensue at the same time that the tropic response is given[1]. Similarly, in the negatively photophobic *Bacterium photometricum* the power of movement is first awakened by exposure to light. Various tropic curvatures involve an acceleration or retardation of the average rate of growth, and in the nodes of grasses the awakening of growth is due to the geotropic stimulation which produces curvature.

Although certain tropic movements may have a purely physical origin, the reactions of plasmodia and of Amoebae are undoubtedly physiological responses, although Rhumbler and Verworn[2] consider those of the latter to be directly due to changes of surface-tension. The latter may act as stimuli and may also play an important part in the performance of movement, but nevertheless the fact that the amoeboid activity is shown in homogeneous media indicates that it is under the control of the organism. Hence the tactic movements of zoospores are no more to be regarded as the direct result of a modification of surface-tension by the external agency, than is the flying of a moth towards a candle or the curvature of a plant towards light.

The cilia of *Chlamydomonas* and of other forms appear thigmotropically excitable, for a rapid general response is shown when only the tip of a cilium is in contact with a foreign body. It is, however, uncertain whether the cilia are the perceptive organs for chemotactic and other tactic stimuli. Phototactic stimuli appear to be perceived neither by the cilia nor by the eye-spot of *Euglena*, but by its hyaline anterior end. In any case, the cilia being protoplasmic organs are able to transmit stimuli, and in the case of *Chlamydomonas* with considerable rapidity. Similarly, the latent period of induction and the duration of the after-effect are exceedingly short in rapidly motile zoospores. It is worthy of note that zoospores, even when radial, are capable of phototactic, geotactic, and chemotactic reactions, although, as the result of their continued rotation, they are in a similar condition to a plant rotated on a klinostat. Hence a rotating vertici-basal zoospore when it reacts to light must direct one end towards the source of illumination so that the axis of rotation is at right angles to the light rays. It is, however, also possible that the unequal stimulation of any pair of opposite sides might suffice to produce a tactic response, although none would be possible if the axis of rotation was at right angles to the direction of the orienting agency and both ends of the organisms were

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[1] Pfeffer, l. c., p. 463; 1888, Bd. II, p. 631.

[2] Verworn, Bewegung d. lebendigen Substanz, 1892, p. 44; Rhumbler, Ergebnisse d. Anatomie u. Entwickelungsgeschichte, 1899, Bd. VIII, p. 584.

equally excitable. A phobic response would, however, still be possible, for the time of a rotation is longer than the latent period of stimulation.

Individual differences appear to be of commoner occurrence among lower than among higher organisms; and, although critical researches are wanting, it appears that in the case of many Bacteria and Infusoria the irritability may vary according to the cultural conditions, so that a particular species may react at one time strongly, at another feebly or not at all to a particular agency[1]. It is even possible that races may be bred which are devoid of an irritability possessed by the common stock.

SECTION 67. **The Influence of Temperature.**

The maxima and minima for locomotion and streaming approximate to those for growth, although plants may be found able to grow at temperatures which do not permit of streaming or locomotory activity. Both forms of movement may, like growth, continue for a time at a supramaximal or supraminimal temperature which ultimately proves fatal. Zopf[2] observed, for instance, that *Bacterium vernicosum*, whose maximal temperature for growth is 45° to 46° C., continues to move for a time at 50° to 52° C. Streaming may still be present in the cells of *Chara*, *Nitella*, and *Elodea* after ten minutes' exposure to 50° C., and in *Elodea* after an even longer exposure to 55° C.[3] The determination of the optimum points is rendered difficult by the fact that even in the absence of any shock-effect the velocity assumed at high but not fatal temperatures is always more rapid than it becomes after prolonged exposure, as the cell becomes accommodated or fatigued[4]. On the other hand, after prolonged exposure to low temperatures a moderate rise may take some time to produce its full effect. In addition, the tone may be modified in other ways. Thus, according to Josing[5], streaming ceases within two minutes at 45° C., but not till after twenty minutes' exposure to this temperature in water containing 0·25 per cent. of ether[6]. Individual variations are also shown, for Ewart found that in some leaf-cells of *Vallisneria* streaming was retarded beyond 35° C., but in other cases not until 45° C. was reached, and an equally low optimum was obtained when the temperature was very gradually raised. Moderate rises of temperature influence the velocity of streaming in two ways—either by lowering the viscosity of the endoplasm or by increasing either the total amount of energy generated or the

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[1] Rothert, Flora, 1901, p. 417.

[2] Zopf, Beitr. z. Physiol. u. Morphol. niederer Organismen, 1892, Bd. I, p. 66.

[3] Ewart, Protoplasmic Streaming in Plants, 1903, p. 59.

[4] Id., p. 62.

[5] Josing, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 217.

[6] [Some doubt attaches to these results, for streaming may also continue for twenty minutes in the leaf-cells of *Vallisneria spiralis* at 45° C. in the absence of any ether. Cf. Ewart, l. c., p. 65.]

fractional amount of it directed into this channel. The former cause alone is sufficient to more than double the velocity of streaming when the temperature is raised from 2° to 32° C. Nevertheless, the increases of velocity within this range of temperature are much greater than this, and are hence mainly due to an increase in the amount of energy utilized. Above 30° C., however, the influence of the changes of viscosity becomes more prominent, the sudden stoppage occurring at 55° to 60° C. being due to the increase of viscosity which precedes coagulation[1].

The apparently higher optimum temperature observed for streaming as compared with that for growth is largely the result of the lesser duration of the observations in the former case, for prolonged exposure to temperatures of from 37° to 40° C. causes streaming to cease or become extremely slow in all the plants examined. In addition, the viscosity of the protoplasm may permanently increase during prolonged exposure, while the motor-mechanism may also be affected, a change of *tempo* ensuing.

The following cardinal points were obtained by various authors[2]:—

Author.	Plant.	Minimum.	Optimum.	Maximum.
Dutrochet	*Chara fragilis*	0° to 1° C.	—	45° C.
Sachs	*Cucurbita Pepo*	10° to 11° C.	30° to 40° C.	40° to 50° C.
	Solanum lycopersicum	12° C.		
	Tradescantia	12° C.		
Cohn	*Nitella syncarpa*	−2° C.	—	—
Velten	*Vallisneria spiralis*	0° to 1° C.	38·7° C.	45° C.
	Elodea canadensis	0° C.	36·2° C.	38·7° C.
	Chara foetida	0° C.	38·1° C.	42·8° C.
Klemm	*Trianea* and *Momordica*	−2° C.	—	45° to 48° C.
Hauptfleish	Streaming cells in general	0° C.	37° to 38° C.	41° to 42° C.

The discrepancy in these results is partly the result of the varying duration of the exposure, and is partly due to such factors as age, supply of oxygen, and previous treatment. Thus Ewart[3] obtained values varying only a degree or two from those of Hauptfleisch when the exposures were prolonged, whereas with short exposures an optimum of 40° C. and a maximum of 50° to 60° C. may frequently be obtained. In addition, the optimal and maximal temperatures are lower in young cells of *Chara* and *Nitella* than in old ones. Streaming may in fact continue during a short exposure of the latter to a temperature which causes subsequent death. Similarly, the absence of oxygen raises the optimum for short exposures, but lowers the optimum and maximum when the exposure is prolonged[4].

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[1] Ewart, Protoplasmic Streaming in Plants, 1903, pp. 20, 61.

[2] Dutrochet, Ann. sci. nat., 1838, pp. 25–7; Mémoires, 1837, T. I, p. 561; Sachs, Flora, 1863–4, p. 39; Cohn, Bot. Ztg., 1871, p. 723; Velten, Flora, 1876, pp. 210, 214; Klemm, Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, pp. 635–6; Hauptfleisch, ibid., 1892, Bd. XXIV. Corti was the first to observe the increase of velocity with rising temperature. See also Klebs, Biol. Centralbl., 1881, Nos. 16, 17, 19.

[3] L. c., p. 59.

[4] Ewart, Protoplasmic Streaming in Plants, 1903, p. 68.

When experiments are performed in water whose temperature is altered, as were those of Velten, lower optima and maxima are always obtained than when the objects are heated in moist air. This is in part due to the greater rapidity with which they gain the required temperature in the former case, although the deficiency in the supply of oxygen aids in prolonged exposures to lower the cardinal points. In any case, it is not easy to see how it was that Nägeli found streaming to increase in rapidity in the cells of *Nitella syncarpa* up to 37° C., when it suddenly ceased, unless the temperature was raised so rapidly as to exercise a shock-effect[1]. The existence of an optimum temperature is always shown more or less clearly[2], especially when the exposure is prolonged, although Schäfer's[3] attempt to give the detailed progress of the curve is largely futile owing to its variable character.

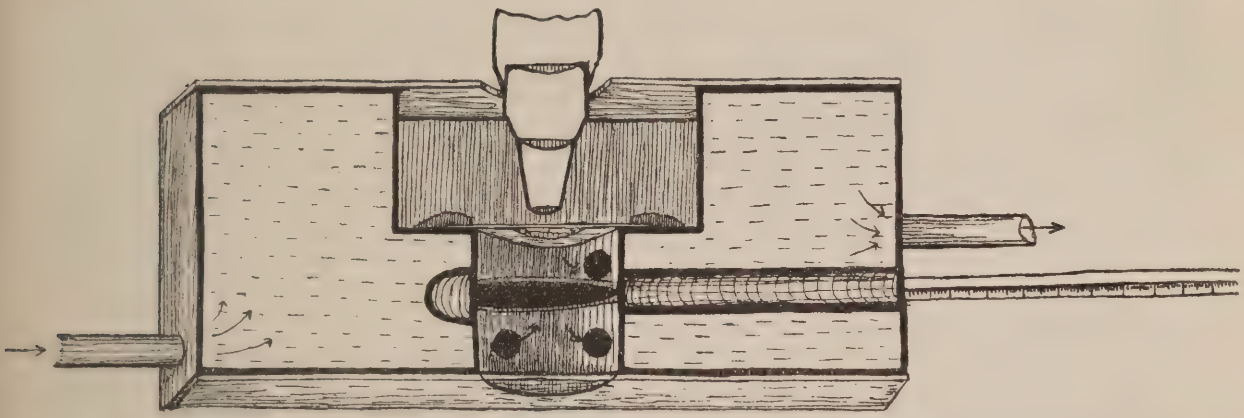

FIG. 52. Combined hot stage and gas-chamber. The three apertures lead to tubes projecting externally, and are used to ensure the better diffusion of dense gases. Through the upper aperture electrodes insulated at their bases may be inserted. (After Ewart.)

The zoospores of those Algae which grow at Spitzbergen at 0° C. to 1·8° C. are presumably motile at this temperature. The zoospores of *Vaucheria clavata*[4], *Ulothrix zonata*[5], and *Haematococcus lacustris*[6] are in fact motile in water at 0° C., whereas those of *Botrydium granulatum*[7] fall into cold rigor at 6° C. According to Strasburger, the optimum for the zoospores of *Haematococcus lacustris* lies between 30° and 40° C., the

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[1] Nägeli, Beitr. z. wiss. Bot., 1860, Heft ii, p. 77. Cf. Velten, Flora, 1876, p. 177.

[2] Schultze, Das Protoplasma d. Rhizopoden u. Pflanzenzellen, 1863, p. 48; Sachs, Flora, 1864, p. 65; Hofmeister, Pflanzenzelle, 1867, pp. 47, 53; Wigand, Botanische Hefte, 1885, 1, p. 216; Klemm, l. c., p. 635. For observations on streaming in the plasmodia of Myxomycetes see Kühne, Unters. ü. d. Protoplasma, 1864, pp. 47, 53.

[3] Schaefer, Flora, 1898, p. 135. Cf. Ewart, On the Physics and Physiology of Protoplasmic Streaming in Plants, 1903, p. 59.

[4] Unger, Die Pflanze im Momente d. Thierwerdung, 1843, p. 57.

[5] Dodel, Jahrb. f. wiss. Bot., 1876, Bd. x, p. 484.

[6] Strasburger, Wirkung d. Lichts u. d. Wärme auf Schwärmsporen, 1878, p. 62.

[7] Strasburger, l. c.

maximum at 50° C. Probably motile thermo-bacteria may remain capable of movement at 70° C. and over, and certain Oscillarias and Diatoms above 50° C. Most Bacteria, Infusoria, Vorticellae, and Rotifers cease to move, sooner or later, at from 40° to 45° C.[1]

A sudden change of temperature may awaken streaming in quiescent cells[2], and may produce a more or less pronounced disturbance in cells which already show streaming. This may be evidenced either by a temporary acceleration or retardation or by a succession of both. A rapid rise to a supraoptimal temperature commonly produces an irregular feverish activity of streaming[3]. A sufficiently sudden and pronounced rise or fall of temperature always produces a temporary or permanent shock-stoppage of streaming in cells which normally show this form of activity; but if the streaming has been induced by previous stimulation, the superimposed effect of a sudden change of temperature is naturally less evident[4]. It was probably owing to this reason, and to the insufficient rapidity with which the temperature altered, that Velten[5] was unable to detect any shock-disturbance at all. The existence of a shock-effect is well shown by the fact that localized cold or heat suddenly applied to one end of a cell of *Chara* or *Nitella* causes a temporary stoppage of streaming over the entire cell.

In all cases, however, the protoplasm rapidly accommodates itself to the new conditions if their action is not of too great intensity. Thus when streaming is resumed after the application of localized cold[6], it is slower in the cold area largely owing to the higher viscosity of the endoplasm[7], and this causes an accumulation of protoplasm at that point.

Schultze, Kühne[8], and Sachs[9] observed that exposure to high or low temperatures produced a pronounced deformation, fragmentation, or vacuolation of the protoplasm, such as may also be caused by the action of induction-shocks or poisons. Klemm[10] found that these changes only take place when the cell is returned to a normal temperature, and that they may be accompanied by spasmodic feverish streaming until the cell becomes normal again. The return to a normal temperature appears, therefore,

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[1] Ewart, Protoplasmic Streaming in Plants, 1903, p. 62. A few details concerning *Oscillaria* are given by Meyen, Pflanzenphysiologie, 1832, Bd. III, p. 565; on antherozoids see Hofmeister, Pflanzenzelle, 1867, p. 33, and Voegler, Bot. Ztg., 1891, p. 675.

[2] Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 210.

[3] Dutrochet, Ann. sci. nat., 1838, p. 27; Hofmeister, l. c., p. 53; Kühne, Unters. ü. d. Protoplasma, 1864, p. 102; de Vries, Matériaux p. la connaissance de l'influence de la température s. l. plantes, 1870, p. 8 (reprint from Arch. Néerlandaises, T. V); Klemm, Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 640; Hörmann, Studien ü. d. Protoplasmaströmung bei d. Characeen, 1898, p. 45.

[4] Ewart, l. c., p. 66. The same effect may be produced by feeble etherization. Josing, l. c., p. 220.

[5] Velten, Flora, 1876, p. 214.

[6] Hörmann, l. c., p. 46; Ewart, l. c.

[7] Ewart, l. c., p. 48.

[8] Kühne, l. c., pp. 64, 87, 101.

[9] Sachs, l. c., pp. 39, 66.

[10] L. c.

to exercise a different effect to exposure to either extreme, but whether this applies generally is uncertain. Similar reactions are, however, shown by the plasmodia of Myxomycetes, in which moderate changes of temperature induce a temporary tendency to assume a spheroidal shape[1]. Possibly also sudden changes of temperature may produce shock-movements in many plant-zoospores. At least when suddenly exposed to high temperatures they dart actively in all directions, like ants disturbed in their nest[2].

THERMOTAXIS.

Paramoecium and other Infusoria are strongly thermotactic, being positively so up to a certain temperature, beyond which they swim towards the colder zones (negative thermotaxis)[3]. De Wildeman[4] ascribes positive thermotaxis to *Euglena*, not only in water, but also when on wet sand, and this irritability may possibly be possessed by many free-swimming plant-organisms, although the evidence brought forward by Schenk[5] is unsatisfactory. Stahl[6] has, however, shown that the plasmodium of *Aethalium septicum* moves towards the warmer side, when resting on a strip of wet filter-paper, one end of which lies in water at 30° C. and the other in water at 7° C. According to Wortmann[7], the movement is reversed and becomes negatively thermotactic when the temperature on one side rises above 36° C.

In creeping organisms a reaction of this kind may be of great utility, whereas small free-swimming plants are likely to have their thermotactic tendencies overcome by the convection currents set up by the difference of temperature. This is, however, not the case where it is the surface layers which become warmer, so that a thermotactic irritability is most likely to occur in strongly motile surface organisms found in ponds exposed to full insolation. It is evident that the slow response of plasmodia cannot be phobic in character, but this does not necessarily apply to free-swimming organisms, which may be capable of either thermotactic or thermophobic responses.

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[1] Kühne, Unters. ü. d. Protoplasma, 1864, p. 87.

[2] On the influence of temperature on pulsating vacuoles and nuclear division cf. Matruchot et Molliard, Rev. gén. de Bot., 1903, T. XV, p. 193.

[3] Mendelssohn, Pflüger's Archiv f. Physiol., 1895, Bd. LX, p. 1; Zeitschrift f. allgem. Physiol., 1902, Bd. II, p. 38.

[4] De Wildeman, Bot. Centralbl., 1894, Bd. LX, p. 176.

[5] Schenk, Centralbl. f. Bact., 1893, Bd. XIV, p. 37. Beyerinck (ibid., 1894, Bd. XV, p. 799) observed that *Bacterium Zopfii* spread on gelatine to the warmer side, because growth and reproduction are more rapid in that direction. [Zikes, Centralbl. f. Bact., 1903, Abth. ii, Bd. XI, p. 59.]

[6] Stahl, Bot. Ztg., 1884, p. 174. See also Clifford, Annals of Botany, 1897, Vol. XIV, p. 179.

[7] Wortmann, Ber. d. bot. Ges., 1885, p. 117. A negatively thermotactic reaction was observed by Verworn (Psycho-physiolog. Protistenstudien, 1889, p. 63) in the case of *Amoeba*.

SECTION 68. **The Influence of Illumination.**

Numerous plants and organs which develop in darkness also show locomotion or streaming, while, even when normal development takes place only in light, the power of movement is often retained for a long time, or even until death ensues. This applies especially to streaming movements, which usually appear in organs etiolated by development in darkness[1]. The zoospores of *Vaucheria* and of other chlorophyllous plants are motile even when formed in darkness[2], and the period of swarming of asexual zoospores is frequently prolonged in the absence of light. Thus Strasburger[3] found that when developed in darkness the zoospores of *Ulothrix zonata* remained motile for over three days, and those of *Haematococcus lacustris* for more than two weeks, whereas in favourable illumination the latter more especially come to rest in a few minutes. This peculiarity is not always so pronounced, but it aids in enabling the fixed form to be developed where a suitable photic ration is assured. Many of the zoospores, in fact, die in continued darkness without ever coming to rest and germinating.

Apart from any transitory shock-effect, the activity of movement of zoospores is not directly affected by the withdrawal of light, and the same applies to streaming, when this is either normally present, or persists for a long time when aroused by stimulation[4]. In all plants incapable of indefinite existence in darkness, streaming is ultimately retarded more or less, but only as the indirect result of the absence of light[5], and the same effect is shown among Oscillareae[6] and Volvocineae[7]. According to Engelmann[8], movement is excited in purple bacteria when they are exposed to light, whereas they come to rest again in darkness or in constant illumination. Winogradsky[9] observed, however, a continuance of the movement in darkness, possibly as the result of racial or cultural peculiarities. According to Sorokin[10], streaming ceases in the plasmodium of *Dictydium ambiguum* in darkness, and is reawakened by illumination.

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[1] Dutrochet, Ann. sci. nat., 1838, 2e sér., T. IX, p. 30; Nägeli, Beitr. z. wiss. Bot., 1860, Heft ii, p. 78; Sachs, Bot. Ztg., Beilage, 1863, p. 3; Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 210; Ewart, Journ. Linn. Soc., Vol. XXXI, 1896, pp. 564, 573; Josing, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, pp. 198, 210.

[2] Klebs, Die Bedingungen d. Fortpflanzung u. s. w., 1896, p. 19; Walz, Jahrb. f. wiss. Bot., 1866–7, Bd. V, p. 132.

[3] Strasburger, Wirkung d. Lichts u. d. Wärme auf Schwärmsporen, 1878, pp. 27, 53.

[4] Nägeli, l. c., p. 102; Strasburger, l. c., p. 27. On streaming cf. Hauptfleisch, l. c.; Josing, l. c., p. 198.

[5] Ewart, Protoplasmic Streaming in Plants, 1903, p. 71.

[6] Famintzin, Jahrb. f. wiss. Bot., 1867–8, Bd. VI, p. 31; Hansgirg, Bot. Centralbl., 1882, Bd. XII, p. 361.

[7] Oltmanns, Flora, 1892, p. 196.

[8] Engelmann, Bot. Ztg., 1888, p. 663; Pflüger's Archiv f. Physiologie, 1882, Bd. XXX, p. 103.

[9] Winogradsky, Beitr. z. Morphol. u. Physiol. d. Bact., 1888, p. 90.

[10] Sorokin, Bot. Jahresb., 1878, p. 471.

Further instances of such actions may ultimately be discovered, and much depends upon the condition of tone of the organism, which largely depends upon external circumstances.

According to Josing[1], the action of ether or the withdrawal of carbon dioxide causes streaming to cease in darkness and to recommence on illumination, whereas under normal conditions it is about as rapid in darkness as in light. Thus Josing states that in leaf-cells of *Vallisneria spiralis* in water containing from 0·25 to 1 per cent. of ether, streaming ceases after darkening for ten minutes to half an hour, and recommences thirty seconds to five minutes after reilluminating. Chloroform acts in the same way, but not alkaloids or alcohol[2]. Similar, but slower, reactions are shown when hanging-drop preparations are made in a gas-chamber, the floor of which is covered by caustic soda. If, however, a non-volatile acid is added (1 of phosphoric acid or of citric acid in 10,000, and 20,000 of water respectively), the streaming persists in darkness as well as in light. Since non-chlorophyllous objects react in the same way, the recommencement of streaming on exposure to light cannot be due to the photo-synthetic production of oxygen.

[It is doubtful whether the action of ether actually depends upon the condition of phototonus. Very dilute solutions of ether may slightly accelerate streaming, but solutions of the strength given retard it[3]. The rise of temperature produced in a strongly illuminated gas-chamber will cause ether to pass into the air of the chamber, and the hanging drop to contain less ether, whether the floor of the chamber is covered with a similar solution of ether or not and whether the chamber is open or closed. In this way the retarding action exercised in darkness would be lessened on illumination, and might even be converted into an acceleration. Josing states, however, that it is the blue rays, and not the red ones, which excite streaming in the etherized preparations. In any case I am quite unable to confirm the statements of Josing in regard to the effects of the withdrawal of carbon dioxide, streaming continuing on the average equally long in similar preparations of *Vallisneria* kept in darkness, whether small amounts of carbon dioxide were present or not, sometimes the one and sometimes the other coming to rest first. Further, cells of *Vallisneria* frequently continued to show streaming for more than a day in darkness, although the carbon dioxide was continually removed and no external acidity was present. Any considerable accumulation of carbon dioxide retards streaming both in light and darkness, and cells of *Chara* and *Nitella* continued to show slow streaming, although the carbon dioxide was continually withdrawn and the plants kept in darkness for as long as six weeks[4]. Finally, the 0·01 per cent. solution of phosphoric acid which, according to Josing, causes streaming to continue in darkness, produces a stoppage of streaming in *Chara* and *Nitella* within an hour or two, and in *Elodea* and *Vallisneria* within a day[5].]

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[1] Josing, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, pp. 198, 210.

[2] Josing, l. c., p. 214.

[3] See Ewart, Protoplasmic Streaming in Plants, 1903, p. 86.

[4] Ewart, l. c., p. 42.

[5] Cf. Ewart, l. c., p. 77.

A sufficient increase in the intensity of the light always produces a retardation of locomotion and streaming[1]. By localized action local retardations or interruptions of streaming may be caused[2], as well as various protoplasmic deformations or vacuolation[3]. Owing to the fact that the plasmodia of Myxomycetes are killed by exposure to light of moderate intensity, even feeble illumination distinctly retards the amoeboid activity of these organisms, and hence also the streaming of the endoplasm[4]. Similarly, after several hours' exposure to continuous direct sunlight, streaming ceases or becomes extremely slow in *Elodea* and *Chara*, but may become active again in feeble light[5]. Other instances in which submaximal intensities of illumination produce a retardation of movement will probably be discovered.

A striking instance of shock stimulation is afforded by *Bacterium photometricum* and other purple bacteria, which perform a pronounced backward movement when the illumination suddenly decreases, but not when it increases. No fatigue is shown in this case, however rapidly the stimulation is repeated[6]. According to Engelmann[7], *Bacterium photometricum*, which Winogradsky[8] considers to be a small *Chromatium*, also performs a shock-movement when the percentage of carbon dioxide suddenly alters, but not when the air is suddenly replaced by hydrogen. In the case of the Rhizopod *Pelomyxa palustris* Engelmann[9] found that sudden illumination causes the pseudopodia to be rapidly withdrawn, and the plasmodia of Myxomycetes seem to react much in the same way although more feebly. A shock-movement is, on the other hand, produced in many lower animals by the sudden withdrawal of light[10], and, to a slight extent, also in the zoospores of *Botrydium granulatum*[11]. In the case of the zoospores of *Bryopsis plumosa*, however, sudden illumination produces a temporary irregularity of movement. In many other organisms and zoospores Strasburger could detect no perceptible photic shock-effect, and sudden

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[1] Cf. Ewart, Protoplasmic Streaming in Plants, 1903, p. 69; Annals of Botany, 1898, Vol. XII, pp. 383-90.

[2] Pringsheim, Jahrb. f. wiss. Bot., 1879, Bd. XII, pp. 334, 367.

[3] Klemm, ibid., 1895, Bd. XXVIII, p. 647.

[4] Baranetzsky, Mém. de la Soc. d. sci. nat. de Cherbourg, 1876, T. XIX, pp. 328, 340; Hofmeister, Pflanzenzelle, 1867, p. 21. Cf. also Lister, Annals of Botany, 1888-9, Vol. III, p. 13.

[5] Ewart, Protoplasmic Streaming in Plants, 1903, p. 70.

[6] Engelmann, Pflüger's Archiv f. Physiologie, 1882, Bd. XXX, p. 103; Bot. Ztg., 1888, p. 666; Winogradsky, Beiträge z. Morphol. u. Physiol. d. Bacterien, 1888, p. 95.

[7] Engelmann, 1882, l. c., p. 112; 1888, l. c., p. 689.

[8] Winogradsky, Bot. Ztg., 1888, p. 90.

[9] Engelmann, Pflüger's Archiv f. Physiologie, 1878, Bd. XIX, p. 3; Blochmann, Biol. Centralbl., 1894, Bd. XIV, p. 85.

[10] See Loeb, Pflüger's Archiv f. Physiol., 1897, Bd. LXVI, p. 459; Nagel, Bot. Ztg., 1901, Ref., p. 289.

[11] Strasburger, Wirkung d. Lichts u. d. Wärme auf Schwärmsporen, 1878, p. 25; Stahl, Bot. Ztg., 1880, p. 410 (*Euglena*).

illumination or darkening exercises no apparent effect upon protoplasmic streaming. If, however, preparations which have been kept in darkness for some time are suddenly exposed to concentrated sunlight, a temporary stoppage lasting from a few seconds to a minute or a distinct retardation may often be seen. The latter may be followed by a slight acceleration, after which streaming rapidly decreases and ultimately ceases if the exposure is continued[1]. A shock-effect may possibly always be exercised when a sudden change is made from prolonged darkness to sufficiently intense light, but the reverse does not hold good, since intense light rapidly proves fatal. Plants may, however, exist in which both sudden darkening and sudden illumination produce the same shock-effect.

SECTION 69. **The Tropic Action of Light on Freely Motile Organisms.**

As in the case of rooted plants, varying degrees and forms of irritability are shown. More especially the sensitive and actively motile zoospores place their long axes immediately parallel to the direction of illumination and swim in a definite direction instead of all ways as they do in uniform diffuse light. The anterior end is turned towards the source of illumination when this is of moderate strength, but away from it when intense, and the direction of movement follows suit. The velocity is little if at all altered, and if the organism comes into contact with a glass plate or adheres by its hinder end, it may still show the same tropic orientation as before. In fact, under these circumstances, Stahl[2] found that the positively phototropic orientation of *Euglena viridis* became negative in intense light. Oscillarias and Diatoms also place their long axes parallel to the direction of the light falling from one side only, and move towards or away from it according to its intensity. Various Desmids behave similarly, and some forms are plagio-phototropic in light of medium intensity.

An accumulation of *Bacterium photometricum* is, however, also possible by means of the backward shock-movement experienced every time the organism passes to a dark region. Engelmann[3] was unable to produce any distinct local accumulation by unilateral illumination, so that a gradual decrease in the intensity of the illumination does not appear to act as a phobic stimulus. It is, therefore, uncertain whether the attraction observed by Winogradsky, and the repellent action of light on *Beggiatoa*, are phobic or tropic in origin[4].

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[1] Ewart, Protoplasmic Streaming in Plants, 1903, p. 71.

[2] Stahl, Bot. Ztg., 1880, p. 410.

[3] Engelmann, Pflüger's Archiv f. Physiol., 1882, Bd. XXX, p. 121.

[4] Winogradsky, Beiträge z. Morphol. u. Physiol. d. Bact., 1888, Heft i, p. 94; Bot. Ztg., 1887, p. 517.

The negatively phototactic movement of the plasmodia of Myxomycetes is possibly directly due to the retarding action of the strong illumination upon the amoeboid activity of the exposed side, but it is uncertain whether similar phototropic movements and aggregations may be produced within cells covered by cell-walls, apart from those shown by the chloroplastids of *Mesocarpus* and other plants.

In many cases a sufficient rise in the intensity of the illumination causes the positive phototaxis to become negative, so that Weber's law can only apply within certain limits. Strasburger[1] observed only an attraction to the light in the case of the zoospores of *Botrydium granulatum*, and of the Flagellate Infusorian *Chilomonas curvata*. This was possibly due to the fact that the organisms were temporarily adapted to high intensities of light, since Stahl[2] found that the zoospores of *Botrydium granulatum* readily performed negatively phototactic movements. Moderately strong sunlight is sufficient to produce this in most zoospores, but in others comparatively feeble light suffices, as, for instance, in the case of most Diatoms, while no positive phototactic action at all has been detected in Myxomycetes.

Zoospores hence usually collect at a certain distance from the source of illumination, but instead of coming to rest, continually cross and recross the imaginary line of equilibrium, where, we may assume, they would take on a diaphototropic position if incapable of locomotion. Owing to the unequal irritability of different individuals, the position of equilibrium varies even in the same species. In addition, periodic autogenic changes of tone may occur, which, under constant conditions, may cause the zoospores to swim at intervals from one side to the other of a drop of water in the path of the light[3]. In some cases this reversal is slowly produced, but in the zoospores of *Ulothrix zonata* it may take place so rapidly, that the zoospore, immediately it has reached one side, swims back to the other. Another instance of autogenic reversal is afforded by the fact that the Desmid *Closterium moniliferum* turns first the young end and then the older one towards the light at intervals of six to thirty-five minutes[4].

Changes of tone also occur during development[5], and they may be induced to a greater or less extent by alterations in the cultural and external conditions. Thus it requires a stronger illumination to change positive into negative phototaxis when zoospores are used which have developed in strong light than when they have developed under feeble illumination[6]. Similarly,

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[1] Strasburger, Wirkung d. Lichts u. d. Wärme auf Schwärmsporen, 1878, p. 26.

[2] Stahl, Einige Bemerkungen ü. d. richtenden Einfluss d. Lichts auf Schwärmsporen, 1879. Reprint from Verh. d. phys.-med. Ges. zu Würzburg, N. F., Bd. XIV.

[3] Strasburger, l. c., pp. 17, 38.

[4] Stahl, Bot. Ztg., 1880, p. 396.

[5] Cf. Strasburger, l. c., p. 38; Oltmanns, Flora, 1892, p. 187.

[6] Strasburger, l. c., p. 39; Oltmanns, l. c., p. 191.

a rise of temperature with constant illumination causes the zoospores to move to the further side of the drop, and this, presumably, because their photic irritability is raised [1]. In addition, *Chromulina Woroniniana* shows at 5° C. a negatively, but at 20° C. a positively phototactic response to the same intensity of light [2], while Strasburger found that a deficiency of oxygen raises the phototactic tone. In the absence of oxygen the zoospores of Algae retain their phototactic irritability so long as they remain capable of movement [3], but it must be remembered that the exposure to light provides not only the stimulus to movement, but also the energy for it by the agency of photosynthesis. Although no thorough researches have been performed upon the influence of chemical agencies, Elfving [4] has shown that etherization raises the sensitivity of *Chlamydomonas pulvisculus*, and also its phototactic tone. According to Elfving, chloroform inhibits the phototactic irritability without suspending the power of movement, but these results are not in entire agreement with those of Rothert [5]. It is evident, however, that various combinations of factors may be responsible for the appearance of organisms on the surface at certain times of the day or year, whereas at others they sink to a greater or less depth below it.

Engelmann found that *Euglena* only responded to an incident ray of light when it fell upon the clear hyaline anterior end, and that it did so before the light reached the eye-spot [6]. It does not follow that a similar localization of irritability is shown in all cases, while the assumption as to the function of the pigment-spot as an eye [7] is devoid of proof, and is merely based upon the analogy with the pigmented ocelli and eye-spots of lower animals. In fact, many zoospores are phototactic, although they have no pigment-spot.

When the zoospores are exposed to strong light which has been passed through a prism filled with diluted indian ink, so that the intensity diminishes along a plane at right angles to its direction, they move towards the feebler light and across the incident rays. Diatoms and Desmids behave in the same way, but nevertheless, these observations fail to prove

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[1] Strasburger, l. c., p. 56. Strasburger finds (l. c., p. 52) that a sudden fall of temperature produces a transitory backward movement.

[2] Massart, Bull. de l'Acad. royale de Belgique, 1891, 3e sér., T. XXII, p. 164.

[3] Celakovsky, Ueber d. Einfluss d. Sauerstoffmangels auf die Bewegung einiger aëroben Organismen, 1898, pp. 11, 28. Reprint from the Bull. de l'Acad. d. sciences de Bohême.

[4] Elfving, Ueber d. Einwirkung von Aether u. Chloroform auf Pflanzen, 1886, p. 13. Reprint from the Öfversigt af Finska Vetensk. Soc. Förh., Bd. XXVIII.

[5] Rothert, Jahrb. f. wiss. Bot., 1903, Bd. XXXIX, p. 1.

[6] Engelmann, Pflüger's Archiv f. Physiologie, 1882, Bd. XXIX, p. 396.

[7] Klebs, Unters. a. d. bot. Inst. zu Tübingen, 1883, Bd. I, p. 263; Overton, Bot. Centralbl., 1889, Bd. XXXIX, p. 114; Franzé, ibid., 1894, Bd. LVII, p. 81; Schütt, Peridineen, 1895, p. 98; Zimmermann, Beihefte z. Bot. Centralbl., 1894, Bd. IV, p. 161; Senn, in Engler u. Prantl, Natürl. Pflanzenfamilien, 1900, I. Th., Abth. i, p. 102; Kohl, Carotin, 1902, p. 15. On the structure of the eye-spot cf. also Strasburger, Histologische Beiträge, 1900, Heft vi, p. 193.

that it is the intensity of the light and not its direction which acts as the orienting agency.

Zoospores. Various groupings were observed by Colomb and by Olivi[1], as well as by Nägeli, Cohn, and Famintzin[2], but up to the time of Stahl[3] and Strasburger insufficient attention was paid to the mechanical influence of currents in the water. Sachs[4] has, in fact, shown that the slight warming due to unilateral illumination causes currents sufficient to produce special grouping of non-motile drops of oil suspended in a mixture of alcohol and water. The movements are, however, largely due to the changes of surface-tension as the alcohol evaporates, and if pure water is used and evaporation checked the streaming in the liquid is much feebler[5], and is insufficient to prevent the normal phototactic orientation[6]. Thus, in a mixture of dissimilar zoospores, one kind may show a negative, the other a positive action, while non-reacting or dead forms become uniformly distributed, or at least not definitely grouped. Active living zoospores, however, assume a suitable position in one or more minutes.

Most chlorophyllous zoospores such as those of *Ulothrix zonata*, *Ulva*, *Enteromorpha*, *Bryopsis plumosa*, *Scytosiphon lomentarius*, as well as *Euglena* and other green Flagellatae, and the unicellular and colonial Volvocineae, show various grades of phototactic irritability[7]. The zoospores of *Vaucheria*[8], as well as the small yellow zoospores of *Bryopsis plumosa*, but not the large green ones, are irresponsive to light. According to Thuret, the zoospores of *Codium tomentosum* and *Ectocarpus firmus* hardly show any phototactic irritability, although the colourless zoospores of *Chytridium vorax* and *Polyphagus euglenae* are strongly phototactic[9], and the same applies to one species at least of *Bodo*[10]. A phototactic irritability will obviously aid the zoospores of parasites in seeking out regions where their hosts live, but chemotactic stimuli are even more effective, and hence the zoospores of

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[1] Usteri, Annal. d. Botanik, 1793, Stück VI, p. 30.

[2] For the literature see Strasburger, Wirkung d. Lichts u. d. Wärme auf Schwärmsporen, 1878, p. 1.

[3] Stahl, Bot. Ztg., 1878, p. 715; Verhandlg. d. physik.-med. Ges. zu Würzburg, 1879, Bd. XIV, p. 7.

[4] Sachs, Flora, 1876, p. 241.

[5] Berthold, Protoplasmamechanik, 1886, p. 113.

[6] Cf. Strasburger, l. c., pp. 6–8.

[7] Strasburger, l. c.; Stahl, l. c.; Famintzin, Jahrb. f. wiss. Bot., 1867–8, Bd. VI, p. 1; Woronin, Bot. Ztg., 1880, 629 (*Chromophyton*); Berthold, Fauna u. Flora des Golfs von Neapel, 1882, p. 11; Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 443; Overton, Bot. Centralbl., 1889, Bd. XXXIX, p. 68; Oltmanns, Flora, 1892, p. 187 (*Volvox*); Kolkwitz, Bot. Centralbl., 1897, Bd. LXX, p. 187; Holmes, ibid., 1903, Bd. XCIII, p. 18 (*Volvox*). According to Borzi (Bot. Jahresb., 1883, Bd. I, p. 26), the zoospores of *Enteromorpha compressa* lose their phototactic irritability on copulation.

[8] Thuret, Ann. sci. nat., 1850, 3e sér., T. XIV, p. 246; Woronin, Bot. Ztg., 1869, p. 139; Strasburger, l. c., p. 42.

[9] Strasburger, l. c., p. 18. Cf. also Kolkwitz, l. c., p. 187.

[10] Rothert, Flora, 1901, p. 372.

Saprolegnia and of many colourless Flagellatae are not phototactic[1]. The same applies to the antherozoids of Ferns[2], whereas those of *Sphaeroplea*[3] and *Fucus*[4] respond readily to light, although Bordet[5] obtained negative results in the latter case.

All chlorophyllous Diatoms appear to be phototactic[6], but not the colourless forms[7]. The orienting action is feeble, however, so that the oscillating forms pursue irregular paths towards or from the light. The negative phototaxis is shown with light of moderate intensity, and commonly causes the Diatoms to creep into the mud. Chlorophyllous Oscillariaceae place themselves parallel to the incident rays, and creep towards the light even when it is moderately intense[8].

Desmids. Most motile forms show phototactic reactions, although these are often feeble[9], and the irritability may vary in different individuals of the same species. Hence Aderhold and Stahl found that intense illumination caused them in most cases to show negative phototaxis, whereas Klebs could only detect positive phototaxis even on re-examining the same species. Such forms as *Pleurotaenium*, *Micrasterias*, and *Penium* respond especially well and glide slowly to or from the light according to its intensity. Such forms as *Closterium moniliferum* and other species of the same genus which regularly turn over and attach the free end to the substratum continue the same movement when exposed to light, but then progress to or from the source of illumination as the case may be.

According to Stahl and Aderhold the long axis is approximately parallel to the direction of the light during positive, but at right angles to it during negative phototaxis. Klebs, however, doubts the existence of any such orientation, and, according to Braun[10], the younger end of *Penium curtum* is always turned towards the light. Probably various grades of irritability

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[1] Strasburger, l. c., p. 18; Cohn, Bot. Ztg., 1867, p. 178; A. Fischer, Jahrb. f. wiss. Bot., 1882, Bd. XIII, p. 297; Kolkwitz, l. c. In regard to animals see J. J. Loeb, Der Heliotropismus d. Thiere, 1890; Verworn, Psycho-physiolog. Protistenstudien, 1889, p. 35; Herbst, Biol. Centralbl., 1894, Bd. XIV, p. 659; Jourdan, Die Sinne u. die Sinnesorgane d. niederen Thiere, 1891; Nagel, Der Lichtsinn augenloser Thiere, 1896.

[2] Pfeffer, l. c., p. 372.

[3] Cohn, Ann. sci. nat., 1856, 4e sér., T. V, p. 201.

[4] Thuret, Ann. sci. nat., 1854, 4e sér., T. II, p. 210.

[5] Bordet, Bull. de l'Acad. royale de Belgique, 1894, 3e sér., T. XXVII, p. 894. Cf. Winkler, Ber. d. bot. Ges., 1900, p. 304.

[6] Cohn, Jahrb. d. schles. Ges. f. vaterl. Cultur, 1863, p. 102; Bot. Ztg., 1867, p. 171; Stahl, Bot. Ztg., 1880, p. 400; Verworn, l. c., p. 46.

[7] Benecke, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 554.

[8] Dutrochet, Mém. d. végétaux et d. animaux, Bruxelles, 1837, p. 340; Famintzin, Jahrb. f. wiss. Bot., 1867–8, Bd. VI, p. 27; Hansgirg, Bot. Centralbl., 1882, Bd. XII, p. 361; Verworn, l. c. p. 50.

[9] Stahl, Bot. Ztg., 1880, p. 392; Verhandlg. d. physik.-med. Ges. zu Würzburg, 1879, N. F., Bd. XIV; Klebs, Biol. Centralbl., 1885, Bd. V, p. 353; Aderhold, Jenaische Zeitschrift f. Naturw. 1888, N. F., Bd. XV, p. 323.

[10] Braun, Verjüngung in d. Natur, 1851, p. 217.

exist, for in certain cases clear and definite orienting responses seem to be given.

Myxomycetes. Stahl and Baranetzsky only observed negative phototaxis in the plasmodia of Myxomycetes, and it is possible that they respond to the intensity of the light rather than to its direction. It is, however, doubtful whether very feeble light induces positive phototaxis, as Hofmeister states[1]. The plasmodia of Acrasieae appear also to be phototactic[2]. Strasburger[3] suggests that a change of phototactic tone may be responsible for the upward movement during fruiting, but since this movement is also shown in darkness other directive factors must enter into play which are able to overcome the negative phototaxis induced by exposure to light.

Coloured light. Phototaxis, like phototropism, is mainly or entirely excited by the more refrangible rays. Strasburger[4] was in fact unable to detect any phototaxis in zoospores exposed to red or green light, whereas the maximum action is shown in the indigo region of the spectrum. The same applies to *Euglena* according to Engelmann[5], and to Diatoms according to Verworn[6], whereas all the visible rays of the spectrum appear to act as phototactic stimuli to *Oscillaria.* Since similar peculiarities exist in the case of colourless organisms[7], it does not follow that the general response of *Oscillaria* is due to the special absorptive activity of the phycocyanin. Various instances are known among animals in which the more refrangible rays are not the most active in phototaxis, and to our eyes the yellow rays are brighter than the blue and red.

In the case of purple bacteria, however, the most pronounced phobic action is exercised by the ultra red rays[8], and owing to the association of bacterio-purpurin with the chlorophyll of these organisms, these are also the rays which are most readily absorbed. On the other hand, the phototactic movements of plasmodia[9] and of chloroplastids are mainly produced by the more refrangible rays, and according to Josing it is the blue and not the green or red rays which excite streaming in etherized cells[10]. Similarly, the injurious action of intense light is mainly due to the more refrangible rays, and the disorganization observed by Borsčow and Luerssen[11]

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[1] Hofmeister, Pflanzenzelle, 1867, p. 20; Allgemeine Morphologie, 1868, p. 625; Baranetzsky, Mém. de la Soc. d. sci. nat. de Cherbourg, 1876, T. XIX, p. 328; Stahl, Bot. Ztg., 1884, p. 167.

[2] Olive, Proceedings of the Boston Society of Natural History, 1902, Vol. XXX, p. 485.

[3] Strasburger, Wirkung des Lichts u. d. Wärme auf Schwärmsporen, 1878, p. 70.

[4] Strasburger, l. c., p. 44. Cf. also Cohn, Bot. Ztg., 1867, p. 171.

[5] Engelmann, Pflüger's Archiv f. Physiol., 1882, Bd. XXIX, p. 398.

[6] Verworn, Psycho-Physiologische Protistenstudien, 1889, p. 49. When oxygen is deficient the organisms may collect in the red and yellow regions of the spectrum where photosynthesis is most active. Cf. Engelmann, l. c., p. 390.

[7] Cf. Nagel, Bot. Ztg., 1901, Ref., p. 293.

[8] Engelmann, Bot. Ztg., 1888, p. 677.

[9] Baranetzsky, l. c., p. 331.

[10] Josing, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 208.

[11] Borsčow, Bull. de l'Acad. de St. Pétersbourg, 1868, T. XII, pp. 211, 230; Luerssen, Einfluss d.

in plant-cells kept in light which had passed through potassium bichromate solution was probably due to some accessory heating or other effect. Reinke and Kraus[1] were in fact unable to detect any such deformations in the protoplasm of epidermal hairs under similar exposure.

SECTION 70. **The Photic Orientation of Chloroplastids.**

The movements produced by the action of light serve not only to bring the chloroplastids into suitable functional positions, but also to withdraw them from the action of intense light. Other agencies such as temperature, chemical actions, and the withdrawal of water may also affect the position, and autogenic alterations of the normal position are also possible[2]. In addition, when active streaming is excited by an injury to the leaves of *Vallisneria* and *Elodea*, the chloroplastids may be carried with the plasma for a variable length of time until the resting condition is again assumed[3]. During normal streaming either none or only occasional chloroplastids are carried with the streaming protoplasm. Pringsheim found[4] that the chloroplastids bleached by sunlight in cells of *Nitella* were carried away by the streaming endoplasm, whereas in cells of *Chara* they retain their original positions[5], and the most varied agencies fail to cause them to leave the ectoplasm in *Nitella*[6]. Nevertheless, slight disturbances of position are probably easily produced, and these are very pronounced in such Diatoms as *Rhipidophora* and *Striatella*, for mechanical vibrations cause their chloroplasts to retract and become spherical[7].

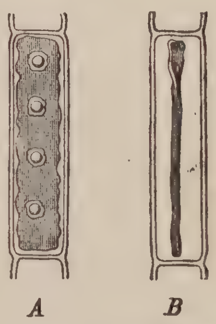

FIG. 53. Cells of *Mesocarpus* illuminated from beneath. *A*, face position in moderate light; *B*, profile position in strong light.

A phototropic orientation is especially evident in the chlorophyll plates of *Mougeotia* and *Mesocarpus*, which under favourable conditions place themselves at right angles to the incident rays (Fig. 53 *A*), but in strong light twist round until a profile position is assumed with the flat surface parallel to the direction of the light[8]. In other cases,

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rothen u. blauen Lichtes auf die Strömung d. Protoplasmas, 1868. Cf. also Velten, Die physikal. Beschaffenheit d. pflanzl. Protoplasmas, 1876, p. 14 (reprint from the Sitzungsb. d. Wiener Akad., 1876, Bd. LXXIII, Abth. i); Famintzin, Jahrb. f. wiss. Bot., 1867–8, Bd. VI, p. 38.

[1] Reinke, Bot. Ztg., 1871, p. 800; G. Kraus, Bot. Ztg., 1876, p. 584.

[2] See Fr. Schmitz, Die Chromatophoren, 1882; Schimper, Jahrb. f. wiss. Bot., 1885, Bd. XVI, p. 203; Hauptfleisch, l. c.; Haberlandt, Physiol. Pflanzenanat., 2. Aufl., 1896, p. 232.

[3] Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 192.

[4] Pringsheim, Jahrb. f. wiss. Bot., 1879, Bd. XII, p. 333.

[5] Ewart, Journ. Linn. Soc., 1897, Vol. XXXI, p. 574.

[6] Pfeffer, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 723.

[7] Lüders, Bot. Ztg., 1862, p. 42; Schmitz, Chromatophoren, 1882, p. 82; Schimper, l. c., p. 218.

[8] Stahl, Bot. Ztg., 1880, p. 299; Moore, Journ. of Linn. Soc., 1888, Vol. XXIV, p. 366;

however, where the chloroplastids are numerous and usually lens-shaped they move in the protoplasm lining the cell to the face or profile positions. It is in this way that the chloroplastids in a filament of *Vaucheria* collect in two parallel rows along its upper and under-surface when feebly illuminated from beneath, but along its sides when the light is intense and a profile position is assumed. Similar reactions are shown in the leaves of Mosses and of *Elodea*, as well as in the fronds of Lemna and in Fern-prothallia [1]. Under moderate vertical illumination the chlorophyll bodies assume the face position by placing themselves upon the outer and inner walls, whereas in intense light they group themselves upon the side walls (Fig. 54 *B*). Owing to the special internal relationships the chloroplastids do not spread themselves uniformly in darkness, but place themselves upon the inner and side walls (Fig. 54 *C*).

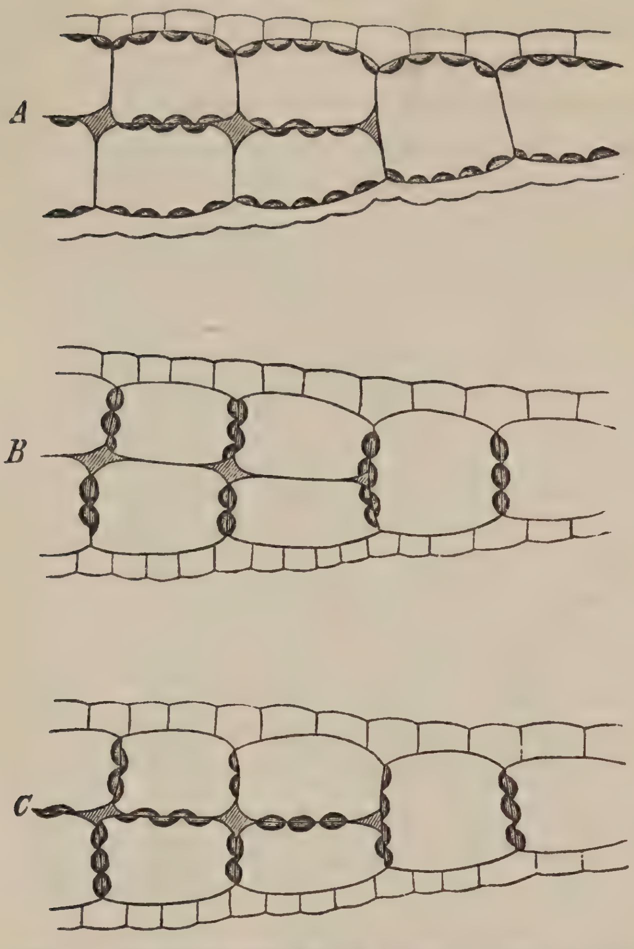

FIG. 54. Transverse section through the leaf of *Lemna trisulca* (after Stahl). *A*, surface position (day position). *B*, arrangement of the chlorophyll grains in intensive light. *C*, position assumed in darkness.

In very intense light irregular aggregations and groupings of the chloroplastids are often shown, not only in the simple tissues mentioned, but also in the more complex ones of higher plants [2]. Aggregation is rapidly produced in the chloroplastids of *Acetabularia mediterranea* [3], whereas in *Vaucheria* long exposure is necessary and in *Nitella* no aggregation at all is shown [4]. We are here dealing with internal

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Oltmanns, Flora, 1892, p. 207; Lewis, Annals of Botany, 1898, Vol. XII, p. 418. Wittrock observed (Stahl, l. c.) that the chlorophyll plates of Gonotonema reacted similarly.

[1] Frank, Jahrb. f. wiss. Bot., 1872, Bd. VIII, p. 216; Schimper, Jahrb. f. wiss. Bot., 1885, Bd. XVI, p. 203; Stahl, l. c.; Haberlandt, Ber. d. bot. Ges., 1886, p. 206; Moore, l. c.; Oltmanns, l. c.; Kohl, Carotin, 1902, p. 103. According to Prillieux (Compt. rend., 1874, T. LXXVIII, p. 506), the chlorophyllous plasma in certain leaf-cells of *Selaginella Martensii* forms masses which glide in the same way over the cell-wall. Cf. also Haberlandt, Physiol. Pflanzenanatom., 2. Aufl., 1896, p. 229.

[2] Böhm, Sitzungsb. d. Wiener Akad., 1856, Bd. XXII, p. 479; 1859, Bd. XXXVII, p. 453; Stahl, Bot. Ztg., 1880, p. 340; Schimper, l. c., p. 225.

[3] de Bary, Bot. Ztg., 1877, p. 731.

[4] Stahl, l. c., p. 324.

disturbances which have no relation to the direction of the light, and which may also be produced by temperature extremes as well as by injuries and various mechanical agencies[1]. On the other hand, the orienting action of ordinary light is well shown by the fact that oblique illumination may cause the chloroplastids to collect at the opposite corners of the cells in the unilamellar leaf of a Moss[2]. In addition, the chloroplastids in *Bryopsis* move towards the better illuminated portion of the cell[3].

Even when we are dealing with simple tissues and responsive chloroplastids, the positions assumed do not always correspond precisely to the above rules, partly owing to the shape of the cells and their relationships to neighbouring ones. The position of the chloroplastids in the palisade-cells of leaves is but little or not at all influenced by light, and the same applies to other cells as well. This may either be due to the absence of any phototactic irritability or to the suppression of any aitiogenic response by more powerful aitiogenic factors. In addition, the light-rays may be concentrated by refraction or reflection upon particular areas, as in the protonema of *Schizostega* (*Schistostega*), or the light may be so dispersed that a cell or cells in the interior may be uniformly illuminated on all sides even when the leaf is under unilateral external illumination.

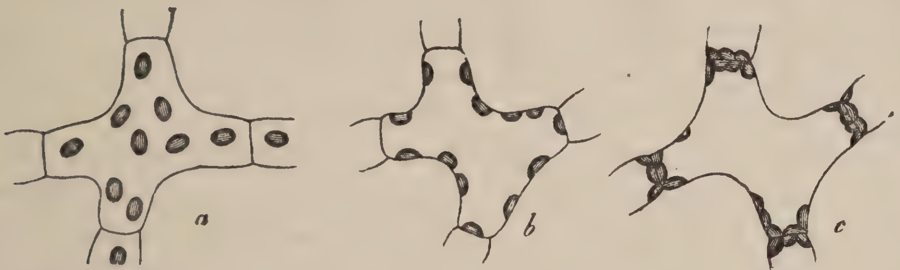

FIG. 55. Mesophyll-cells from the under-surface of the leaf of *Oxalis acetosella* seen from above: (*a*) face position of chloroplastids in diffuse light; (*b*) profile position after short exposure to sunlight; (*c*) after longer insolation (after Stahl).

In the tissues of many of the higher plants the choroplastids show similar groupings in response to light as do those in the leaf-cells of Mosses. Thus in the spongy mesophyll of *Oxalis acetosella* the chloroplastids arrange themselves upon the walls parallel to the surface in diffuse light (Fig. 55 *a*), whereas in direct sunlight a profile position is assumed (Fig. 55 *b*), and after long exposure the balling together shown in Fig. 55 *c* takes place. In the leaf-cells of *Sempervivum* and *Sedum*, according to Stahl (l.c.), the face position is assumed in shade, an intermediate position in bright diffuse light, and an aggregated position in sunlight.

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[1] Cf. Frank, l. c., pp. 261, 295; G. Kraus, Bot. Ztg., 1874, p. 206; Haberlandt, Ueber d. Einfluss d. Frostes auf die Chlorophyllkörner, 1876, p. 6 (reprint from the Oester. Bot. Zeitschrift); Schimper, l. c., pp. 166, 235; Moore, l. c., pp. 206, 371.

[2] Stahl, l. c., p. 346.

[3] Winkler, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 455.

As the result of the dispersal of the penetrating rays, a tropic orientation of the chloroplastids will be less useful in the interior of a tissue than it is on the surface. Nevertheless it is at the surface where the light is strongest that protective movements are of most importance, while in feeble light the position the superficial chloroplastids assume still further darkens the interior of the tissue, especially in thick leaves. This is one of the reasons for the thinness of shade leaves, since in this way they acquire greater adaptability to varying intensities of illumination. All chloroplastids do not, however, show a power of photic orientation, even when in superficial cells. This power is in fact absent from the cells of *Cladophora*, *Nitella*, *Spirogyra*, and from most palisade parenchyma cells. In these the accumulation of the chloroplastids at the upper ends of the cells would hinder instead of favouring the utilization of the light rays, which is best performed when they lie on the side walls. Stahl[1] and Haberlandt[2] have, however, shown that light exercises a strong orienting action upon the chloroplastids in the palisade-cells of many plants, which Haberlandt found to be especially pronounced when the light was at right angles to the long axis of a palisade-cell exposed by sectionizing.

A certain advantage is attained by the fact that the immovable chloroplastids of palisade-cells bulge inwards during moderate illumination, but flatten themselves against the wall when the light is intense. This was first discovered by Micheli[3], while Stahl observed the following changes of shape of the chloroplastids of *Ricinus* in shade and sunlight:—

	Diameter of base parallel to cell-wall.	Height at right angles to cell-wall.
In shade	0·0063 mm.	0·0057 mm.
In sunlight	0·0083 mm.	0·0036 mm.

In this way the chloroplastids are less exposed to intense illumination, but intercept more light when the latter is less intense. These and other changes of shapes are not restricted to the chloroplastids of palisade-cells, but are shown in others also, and may not only be produced by intense illumination but also by various other agencies, such as continued darkness, extremes of temperature, saline solutions, and chemical substances[4].

Neither the mode of stimulation nor the mechanism of movement of the chloroplastids is as yet known, apart from the fact that chloroplastids may be passively carried by streaming protoplasm. It is even uncertain whether the chloroplastid

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[1] Stahl, Bot. Ztg., 1880, p. 377.

[2] Haberlandt, Physiol. Pflanzenanat., 2. Aufl., 1896, p. 210.

[3] Micheli, Arch. d. sci. de la Bibl. univers. de Genève, 1876, T. XXIX, p. 26; Stahl, l. c., p. 357.

[4] Stahl, l. c., 1880, pp. 303, 361; Schmitz, l. c., 1882, p. 82; Berthold, Jahrb. f. wiss. Bot., 1882, Bd. XIII, p. 691; Klebs, Unters. a. d. bot. Inst. zu Tübingen, 1883, Bd. I, p. 268; 1886, Bd. II, p. 557; Schimper, l. c., p. 240; Moore, l. c., p. 643; Haberlandt, Flora, 1888, p. 296; de Vries, Ber. d. bot. Ges., 1889, p. 19; Tswett, Bot. Centralbl., 1897, Bd. LXXII, p. 329; Kolkwitz, Festschrift f. Schwendener, 1899, p. 271.

makes use of the locomotory energy of the surrounding cytoplasm or whether changes of surface-tension of its own production are responsible for its movement. The chloroplastids may indeed possess no power of photic reaction at all and may be carried to or from the light by the cytoplasm, but this can hardly apply to the orientation of the chlorophyll-bands of *Mougeotia* or of the chloroplastids of *Vaucheria* and of Moss-leaves. The nucleus, for instance, does not accompany the movement of the chloroplastids, and it is only in a few cases that a certain accumulation of protoplasm is shown where they collect[1]. It remains, however, to be determined whether the phototactic chloroplastids merely act as directive agencies or are directly responsible for their own movement. The 'active' view supported by Velten[2] and Stahl[3] is as devoid of proof as is that according to which the movement is passive (Frank[4], Moore[5], and Oltmanns[6]). In any case, isolated chloroplastids show no power of orientation however long they may remain living and capable of photosynthesis, and in whatever media, apart from the cytoplasm, they may be placed. Nor do dead chloroplastids show any phototactic orientation within a living cell[7].

Although the orientation of the chlorophyll-band of *Mougeotia* and of the chloroplastids of *Vaucheria* and Mosses appears to be due to the direction of the light-rays, it is possible that in other cases the movements may be produced in response to changes in the general intensity of diffuse illumination. Haberlandt[8] considers the latter to be the case in Moss-leaves and Fern-prothallia, but the evidence given above points rather to the opposite conclusion. It must be remembered that rays falling perpendicularly to the surface of a Moss-cell mostly penetrate, whereas those with an oblique incidence are mostly reflected. Hence a directive action may be exercised even in diffuse light or when the plant is rotated on a klinostat. The condition is the same as when a cylinder containing zoospores is rotated in diffuse light, but has strips of partially opaque paper pasted on its sides. A phototactic response will be shown towards the better illuminated areas in feeble light, but away from them when the light is intense.

Within the tissues where the light is dispersed in all directions, responses may be more commonly produced by changes in the intensity of the illumination; and in fact when very intense illumination produces changes of position and a balling together of the chloroplastids, this is not the result of any tropic stimulation. When moderately strongly illuminated on one side the chloroplastids of *Vaucheria*, Moss-leaves, and Fern-prothallia collect on the opposite sides of the cell. This cannot be due to their possessing dissimilar powers of reaction, since they retain their original position when the shaded under-surface of a prothallus is exposed to light[9]. The chloroplastids are, therefore, not dorsiventral, and in fact they appear to respond as a whole and not individually to changes in the direction and intensity of the illumination. The chlorophyll plate of *Mougeotia* is also isobilateral but diaphototropic.

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[1] Frank, Jahrb. f. wiss. Bot., 1872, Bd. VIII, p. 283.

[2] Velten, Aktiv oder passiv? Oester. Bot. Zeitschr., 1876, No. 3.

[3] Stahl, Bot. Ztg., 1880, p. 351.

[4] Frank, l. c., p. 282.

[5] Moore, Journ. Linn. Soc., 1888, Vol. XXIV, pp. 203, 264.

[6] Oltmanns, Flora, 1892, p. 211.

[7] Ewart, Protoplasmic Streaming in Plants, 1903, p. 108.

[8] Haberlandt, Physiol. Pflanzenanat., 2. Aufl., 1896, p. 234.

[9] Stahl, l. c., p. 350.

The orientation cannot be determined by the assimilatory activity, since it is produced almost solely by the more refrangible rays, and hardly at all, or not at all, by the less refrangible ones which are most active in photosynthesis[1]. According to Frank, light which has passed through a solution of potassium bichromate exercises a feeble action, but Borodin and Schmidt could detect no action at all, possibly owing to the use of more concentrated solutions or thicker screens. Chromoplasts, leucoplasts[2], and etiolated chloroplastids[3] show no power of phototactic orientation, but it must be remembered that we are dealing with a special irritability which is not developed by all chloroplastids. Chromoplastids may, however, occur in plants which are capable of phototactic responses, such as are shown by certain non-chlorophyllous zoospores, and by the pigment cells of such animals as the chameleon[4]. According to Berthold[5], peculiar plasmatic plates occur in *Chylocladia* which are capable of phototactic reaction like chloroplastids. No evidence as to the mode of orientation is, however, afforded by the fact that it ceases in the absence of oxygen[6], or as the result of etherization[7], and is also more or less influenced by the external conditions in general.

An unequal distribution of the chloroplastids may either be produced purely mechanically as the result of the shape of the cell, or by gravitational or surface-tension forces, or it may be due to the physiological polarity of the protoplasm, or to the action of the external conditions. In darkness the chloroplastids in the leaf-cells of a Moss collect upon the walls at right angles to the surface, while those in the interior of tissues have a tendency to avoid the surfaces and to collect on the walls bordering the intercellular spaces where air is present[8]. The utility of this arrangement is obvious, but according to Haberlandt the chloroplastids have a general tendency to avoid those walls through which continuous translocation occurs. Frequently the chloroplastids leave the peripheral protoplasm and they often tend to collect around the nucleus, so long as they contain no large starch-grains[9].

Rapidity of the reaction. This is especially pronounced in the chlorophyll-bands of *Mesocarpus*[10], but the chloroplastids of *Funaria* and other plants may pass in less

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[1] Borodin, Ueber die Wirkung d. Lichts auf die Vertheilung der Chlorophyllkörner, 1869, p. 58 (Mélanges biologiques, Bd. VII); P. Schmidt, Ueber einige Wirkungen des Lichts auf Pflanzen, 1870, p. 27; Frank, Bot. Ztg., 1871, p. 228.

[2] Schimper, l. c., p. 204.

[3] According to observations by Senn.

[4] O. Hertwig, Die Zelle u. d. Gewebe, 1893, p. 81.

[5] Berthold, Jahrb. f. wiss. Bot., 1882, Bd. XIII, p. 690.

[6] Demoor, L'étude de la physiol. de la cellule, 1894, p. 54 (reprint from the Archives de Biologie, Bd. XIII). Lewis (Annals of Botany, 1898, Vol. XII, p. 421) observed a phototactic reaction of the chlorophyll plate of *Mesocarpus* in an atmosphere of hydrogen, but in this case oxygen is provided by the assimilation of the carbon dioxide produced within the cell.

[7] Elfving, Ueber die Einwirkung von Aether u. Chloroform auf d. Pflanze, 1886, p. 16 (reprint from the Öfversigt af Finska Vetensk. Soc. Förh., Bd. XXVIII).

[8] Stahl, Bot. Ztg., 1880, p. 332; Haberlandt, Ber. d. bot. Ges., 1886, p. 217.

[9] Schimper, l. c., p. 206; Berthold, Protoplasmamechanik, 1886, pp. 140, 169; Haberlandt, Flora, 1888, p. 304.

[10] See Stahl, l. c., p. 301; Oltmanns, l. c.; Lewis, l. c., p. 418. Lewis investigated the induction-period and after-effect.

than an hour from the night to the day position, whereas in less readily responsive plants a few hours may be required. As is generally the case, the new position is assumed more rapidly than the original position is regained when the stimulus is removed. In plants which react rapidly enough, the chloroplastids therefore undergo daily changes of position. Such parts as the thallus of *Marchantia*, in which light causes the chloroplastids to collect upon the outer walls, will assume a deeper green when illuminated [1]. The continued paling shown by many plants in prolonged darkness is, however, in part the result of pathological changes in the chloroplastids, coupled with a decomposition of the chlorophyll. The shadow figures produced by Sachs [2] by partially covering leaves with tinfoil or black paper are not solely the result of the primary photic reaction. Similarly, the paling of leaves in intense light [3] though in the first instance partly due to movements of the chloroplastids, is mainly the result of the partial decomposition of the chlorophyll [4].

Historical. The changes of position of the chloroplastids in the leaves of *Crassulaceae*, when exposed to sunlight, were discovered by Böhm [5], and the details of the process, as well as the change of the reaction with increasing intensity of illumination, were investigated by Famintzin, Borodin, and especially by Frank [6]. Frank considered the changes of position to be due to diffuse phototonic stimulation, whereas Stahl [7] considers them to be phototactic orienting responses to the direction of the illumination. Many undoubted instances of phototactic or phototropic orientation are given by Stahl, but diffuse actions may also be exercised, as was shown by Schimper and Haberlandt [8]. Frank [9] used the term 'epistrophe' to indicate the normal orientation of the chloroplastids in light, and 'apostrophe' for that assumed in darkness, or owing to the action of other factors. Schimper [10], and also Moore [11], used Frank's terms in a slightly different sense, and distinguished the balling together of the chloroplastids as 'systrophe.' None of these terms are, however, really necessary, since light-position, dark-position, superficial, lateral, and aggregated positions indicate all the possible movements in the cell, and profile and face positions, flattened and convex shapes, describe those of the chloroplastid.

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[1] See Stahl, Bot. Ztg., 1880, p. 329; Schimper, l. c., p. 225; Moore, l. c., p. 233. First observed by Borodin and Frank.

[2] Sachs, Sitzungsb. d. Sächs. Ges. d. Wiss., 1859, p. 226; Stahl, l. c.

[3] First observed by Marquart, Die Farben d. Blüthen, 1835, p. 47.

[4] Pringsheim, Pringsh. Jahrb., 1879–81, Bd. XII, p. 374; Keeble, Annals of Botany, 1895, Vol. IX, p. 63; Ewart, Annals of Botany, 1898, Vol. XII, p. 384.

[5] Böhm, Sitzungsb. d. Wiener Akad., 1856, Bd. XXII, p. 479; 1853, Bd. XXXVII, p. 453.

[6] Famintzin, Jahrb. f. wiss. Bot., 1867–8, Bd. VI, p. 45; Borodin, Bull. de l'Acad. de St. Pétersbourg, 1867, T. IV, p. 482; Mélanges biologiques de St. Pétersbourg, 1869, Bd. VII, p. 50; Frank, Jahrb. f. wiss. Bot., 1872, Bd. VIII, p. 216.

[7] Stahl, Bot. Ztg., 1880, p. 297.

[8] Schimper, Jahrb. f. wiss. Bot., 1885, Bd. XVI, p. 203; Haberlandt, Ber. d. bot. Ges., 1886, p. 209.

[9] Frank, l. c., p. 221.

[10] Schimper, l. c.

[11] Moore, Journ. Linn. Soc., 1888, Vol. XXIV, p. 200.

SECTION 71. **The Action of Gravitational and Centrifugal Forces.**

Mechanical Actions.

Small particles only respond slowly to the action of gravity in water, and still less in more viscous liquids or ones of nearly the same density. Hence very slight agitation suffices to keep particles suspended in a liquid. Strong centrifugal forces may, however, effect rapid separation such as gravity is unable to perform. Crystals and particles of precipitated methyl blue[1] sink rapidly in the cell-sap, and only slowly, or not at all, in the protoplasm according to its viscosity. The nuclei and chloroplastids, although denser than the cytoplasm, as well as the vacuoles and oil-drops which are less dense, do not appear to have their position in the cell influenced by gravity so long as they are embedded in cytoplasm. The latter, even when thin, does not collect on the under side of the cell, although denser than the cell-sap. In streaming endoplasm of low viscosity, however, a feeble gravitational accelerating or retarding action upon floating particles of less and greater density can frequently be observed[2], and the denser particles come perceptibly nearer to the periphery on the under side of the cells of *Chara* and *Nitella*[3]. When large crystals of calcium oxalate or large starch-grains occur in the protoplasm they are commonly found on the under side[4], and the starch-grains carry with them the attached chloroplastids or leucoplastids. The movements of the starch-grains are shown very well in the starch-bearing endodermal cells, as well as in the cells of the root-cap, and when inverted the change of position may begin at favourable temperatures in a few minutes and be completed in from ten to twenty minutes. At low temperatures the movement is slower[5] owing to the higher viscosity of the protoplasm[6]. The starch-grains in the cells of such an organ when rotated once every half-hour or hour on a klinostat in a warm room will, as Dehnecke found, be in continual movement, and the changes of position of the starch-grains are now considered to aid largely in the perception of geotropic stimuli[7].

In cells subjected to strong centrifugal action starchless chloroplastids,

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[1] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1886, Bd. II, p. 189; Zimmermann, Beiträge z. Morphol. u. Physiol. d. Pflanzenzelle, 1893, p. 68.

[2] Ewart, Protoplasmic Streaming in Plants, 1903, p. 23.

[3] Nägeli, Beitr. z. wiss. Bot., 1860, Heft ii, pp. 67–74.

[4] Dehnecke, Ueber nicht assimilirende Chlorophyllkörper, 1880, p. 10; Heine, Ber. d. bot. Ges., 1885, p. 189, Landw. Versuchsst., 1888, Bd. XXXV, p. 170.

[5] Němec, l. c., 1901, p. 129.

[6] Ewart, Protoplasmic Streaming in Plants, 1903, pp. 16–20; W. Ostwald, Zool. Jahrb., 1903, Bd. XVIII, p. 3.

Němec, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, pp. 108, 127; Ber. d. bot. Ges., 1902, p. 342; Haberlandt, Ber. d. bot. Ges., 1902, p. 190; Jahrb. f. wiss. Bot., 1903, Bd. XXXVIII, p. 487.

the nucleus and the greater part of the cytoplasm when a vacuole is present, are driven to the outer end of the cell, only a very thin peripheral film and fine threads remaining at the other end[1] (Fig. 56). The oil-drops in chloroplastids of *Vaucheria* move with the chloroplastids, whereas free drops or masses of oil move in the opposite direction. Displacements of this kind were found by Mottier to be produced in most plant-cells by centrifugal forces 1,900 times more powerful than that of gravity after exposures of from half an hour to several hours. In a few thin filamentous Algae, however, only slight changes of configuration were shown, probably owing to the small diameter of the cell coupled with the properties and mode of arrangement of the cell-contents[2]. Similarly, owing to the packing of the cell with grains of starch and aleurone, Andrews only observed slight displacements in the cells of turgid cotyledons of *Vicia sativa* and *Pisum* when exposed to a centrifugal force of 4,400 g., whereas a pronounced displacement was shown as soon as a portion of the reserve-materials had been consumed. Usually, no apparent effect is produced by centrifugal forces of 100 g. strength, but in a few cells relatively feeble gravitational forces may produce pronounced displacement. The fact that a thin film always remained adherent to the cell-wall is explained by the increased degree of cohesion as the membrane becomes thinner, and by the fact that in short cells the centrifugal action is unable to overcome the osmotic pressure which keeps the plasmatic membrane pressed against the cell-wall. Similarly, in thin threads the surface-tension pressure becomes so great as to render them relatively rigid.

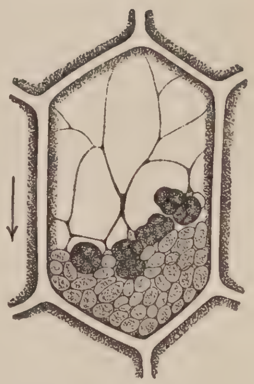

FIG. 56. Leaf-cell of *Calypogeia trichomanis*, after exposure to a centrifugal force of 4,400 g. in the direction shown by the arrow. The chloroplastids, large oil-bodies, and most of the cytoplasm, have collected at the lower (outer) end of the cell. Magn. 700. (After Andrews.)

The tearing away of the chloroplastids acts injuriously and even fatally upon Characeae, but Mottier found that other plants remained living. This applies even to the cells of *Spirogyra* in which the chlorophyll-band had been driven to one end by centrifugal action. The original positions are restored in less than half an hour in cells showing active streaming, whereas the original configuration is not entirely resumed until after a few days in the case of *Spirogyra*, and after one or more weeks in the case of *Cladophora*. The restoration was found to be still slower by Andrews, in cells of the cotyledons of *Helianthus* and *Cucurbita*, filled with reserve-materials, if growth was pre-

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[1] Mottier, Annals of Botany, 1899, Vol. XIII, p. 325; Andrews, Jahrb. f. wiss. Bot., 1902, Bd. XXXVIII, p. 1; Miehe, Flora, 1901, p. 109.

[2] On the influence of these factors upon the resistance to movement within cells cf. Ewart, Protoplasmic Streaming in Plants, 1903, pp. 16-33.

vented. When growth took place the removal of the reserve-materials allowed more rapid readjustment to occur.

Dehnecke[1] found that chloroplastids containing starch when kept in movement by long-continued rotation on a klinostat ultimately expelled the contained starch-grains and became more or less deformed, but the exact origin of this effect is uncertain. The displacements produced by high centrifugal action cannot be supported indefinitely, and Andrews[2] found that a disturbance of growth was produced even by short exposure.

It is evident from these experiments that the nucleus, and also the cytoplasm, have a higher density than the cell-sap, while the nucleolus and chromatin have a higher density than the rest of the nucleus. The latter may, in some cases, be driven out of the nucleus by very high centrifugal forces[3]. According to Němec[4], the nuclei in the cells of the root-cap move upwards when the root is inverted. Since this movement is in the opposite direction to that expected from their density, we must at present ascribe a geotactic irritability to the nucleus, although the phenomenon may result merely from the downward movement of the starch-grains.

Starchless chloroplastids, and all chromatophores excepting those in the petals of *Caltha palustris*[5], are denser than the cell-sap. The centrifugal movement of the oil-bodies of Hepaticae show that they do not consist solely of oil, which, being less dense, moves centripetally[6]. Latex may be separated by centrifugal action in the same way as milk[7]. It has not yet been determined whether a permanent displacement can be produced without the plant being killed. Mottier was, however, able to produce unequal cell-division as the result of the accumulation of the protoplasm on one side[8], while Miehe[9] was successful in reversing the polarity of the initial cell of a stoma by centrifugal action.

SECTION 72. **Geotactic Reactions.**

According to Schwarz[10], *Euglena viridis* and *Chlamydomonas pulvisculus* are negatively geotactic, and the same applies, according to Aderhold, to *Haematococcus lacustris*, and in a less degree to the zoospores of *Ulothrix tenuis*. The experiments were performed in darkness, and partly

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[1] Dehnecke, Ueber nicht assim. Chlorophyllkörper, 1880, p. 11.

[2] Andrews, l. c., p. 21.

[3] Andrews, l. c., p. 36; Mottier, l. c., p. 352.

[4] Němec, Ber. d. bot. Ges., 1902, p. 344. Cf. Andrews, l. c., p. 35.

[5] Andrews, l. c., p. 37.

[6] Andrews, l. c., p. 34.

[7] Andrews, l. c., p. 24.

[8] Mottier, l. c., pp. 331, 357.

[9] Miehe, Flora, 1901, p. 109.

[10] Fr. Schwarz, Ber. d. bot. Ges., 1884, p. 51.

[11] Aderhold, Jenaische Zeitschrift f. Naturwiss., 1888, N. F., Bd. XV, p. 321; Massart, Bull. de l'Acad. royale de Belgique, 1891, 3e sér., T. XXII, p. 164; Jansen, Bot. Centralbl., 1893, Bd. LVI, p. 20.

in capillaries filled with water and open at both ends. Schwarz also observed an ascent through wet sand. Massart[1] found that *Chromulina Woroniniana* behaves similarly at 15° to 20° C., but becomes positively geotactic at 5° to 7° C. Changes of geotactic tone according to the temperature may possibly be used by many motile organisms to enable them to collect in zones at a suitable temperature, and changes of geotactic tone do actually occur among Infusoria[1]. Aderhold found, however, that *Euglena viridis* and *Chlamydomonas pulvisculus* remained negatively geotactic at 0° C.[2], while Schwarz could detect no geotactic reaction below 5° or 6° C.[3]

No geotaxis appears to be shown by Oscillariae and Diatomaceae, although certain Desmids may possess this irritability to a feeble degree[4]. Various Infusoria, including *Polytoma uvella*, afford instances of geotactic non-chlorophyllous objects[5]. Massart found one species of *Spirillum* to be negatively, and another species under the same conditions was found to be positively geotactic[6]. Stahl[7] considers that the plasmodia of Myxomycetes have no geotactic irritability, the creeping up to the surface of the substratum before fruiting being due to the change of the previous positive into negative hydrotropism. Rosanoff and Baranetzsky[8] had previously assumed the existence of negative geotaxis in plasmodia, but Strasburger[9] threw doubt upon this view.

We can hardly speak of geotactic irritability when an organism rises or sinks owing to autogenic changes of its specific gravity, or when the position of the centre of gravity causes the axis of the organism and the direction of movement to be parallel to the perpendicular[10]. That the geotactic responses are not produced in this way is shown by the fact that many zoospores with excentric centres of gravity show no geotaxis, while *Chromulina*, according to its tone, is negatively or positively geotactic. According to Jensen[11], *Euglena viridis*, in virtue of the position of its centre of gravity, would react positively, instead of being negatively

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[1] Massart, Bull. de l'Acad. royale de Belgique, 1891, 3e sér., T. XXII, p. 164; Sosnowsky, Bot. Centralbl., 1901, Bd. LXXXVIII, p. 199.

[2] Aderhold, l. c., p. 320.

[3] [In all cases the possibility of the existence of passive movements due to convection or thermo-diffusion currents needs to be considered.]

[4] Aderhold, l. c., pp. 322, 359; Klebs, Biol. Centralbl., 1885, Bd. V, p. 360.

[5] Massart, l. c., pp. 162, 166; Jensen, l. c.; Mendelsohn, Centralbl. f. Physiol., 1895, Bd. IX, p. 374. In regard to other animals see Loeb, Centralbl. f. Physiol., 1891, p. 429; 1893, Bd. VII, p. 304.

[6] Zikes, Centralbl. f. Bact., Abth. ii, 1903, Bd. XI, p. 59.

[7] Stahl, Bot. Ztg., 1884, p. 168.

[8] Rosanoff, Mém. de la Soc. de sci. nat. de Cherbourg, 1869, T. XIV, p. 149; Baranetzsky, ibid., 1876, Bd. XIX, p. 322.

[9] Wirkung d. Lichts u. d. Wärme auf Schwärmsporen, 1878, p. 71.

[10] Cf. Verworn, Psycho-physiol. Protistenstudien, 1889, p. 122.

[11] Jensen, Bot. Centralbl., 1893, Bd. LVI, p. 21.

geotactic as it actually is. Such forms as *Euglena viridis* and *Chlamydomonas pulvisculus* only have their negative geotaxis mechanically overcome when they are subjected to centrifugal forces eight times greater than that of gravity, while the limit of geotactic perception seems to lie between 0·2 to 0·3 g., according to Schwarz. It is, however, uncertain whether the perception arises from the movements of the denser particles in the organism or is aroused by differences of pressure in the medium.

SECTION 73. **Diffuse Chemical Actions.**

Locomotion and intercellular movement, like all forms of vital activity, are dependent upon metabolism, and hence cease sooner or later when the latter is partially or completely suppressed. The same is the case when oxygen is removed from an aerobic organism, although growth and movement may be maintained under relatively low partial pressures of oxygen. On the other hand, the access of air to obligate anaerobes, as well as a sufficient increase of the partial pressure of oxygen upon aerobes, retards and ultimately inhibits their powers of growth and movement. Among certain facultatively anaerobic bacteria, however, the absence of oxygen causes movement to cease although growth continues[1]. The power of movement is, however, retained, and is at once shown when oxygen is admitted. Possibly in other cases the removal of oxygen may produce a stoppage of growth before movement, and more especially protoplasmic streaming, have ceased.

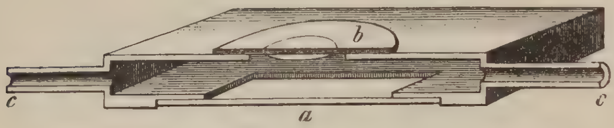

FIG. 57. Median section of gas-chamber (reduced).

The withdrawal of nutriment or even of a single essential constituent must sooner or later retard or stop movement, although streaming may continue in starving plants almost until death ensues[2]. This is the case in cells of *Chara* and *Nitella*, whereas in those of *Elodea* and *Vallisneria* a long period may elapse between the cessation of streaming and the permanent loss of vitality. On the other hand, cells packed with food-materials show no streaming, and the latter is not shown until the cells are partially emptied[3]. This in part arises from the decreased resistance coupled with the great activity of the cell during translocation, and naturally also the addition of food-materials accelerates streaming in starved cells.

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[1] Ritter, Flora, 1899, p. 329.

[2] Kühne, Zeitschr. f. Biologie, 1898, N. F., Bd. XVIII, p. 85; Ritter, l. c., p. 355; Ewart. Protoplasmic Streaming in Plants, 1903, p. 76; Wallengren, Zeitsch. f. allgem. Physiol., 1902, Bd. I, p. 67.

[3] Ewart, l. c.

Oxygen. Various forms of gas-chamber may be used to follow the influence of the withdrawal of oxygen upon streaming, and the partial pressure of oxygen may either be reduced by the aid of an air-pump attached to (*c*) Fig. 57, or by displacement with a neutral gas entering at the other tube. In the former case, the cover-slip (*b*), to which the hanging drop with the object is attached, must either be small or thick, and must be sealed on by vaseline stiffened with colophonium or wax. A still better attachment is given by melted shellac. To produce a complete absence of oxygen evacuation and the passage of hydrogen must be frequently repeated. A steady supply of pure oxygenless hydrogen can be obtained by the apparatus shown in Fig. 58, in which all the connexions are under water covered with liquid paraffin, and the gas, after passing through purifying tubes, is deoxygenated by pyrogallol and caustic potash [1].

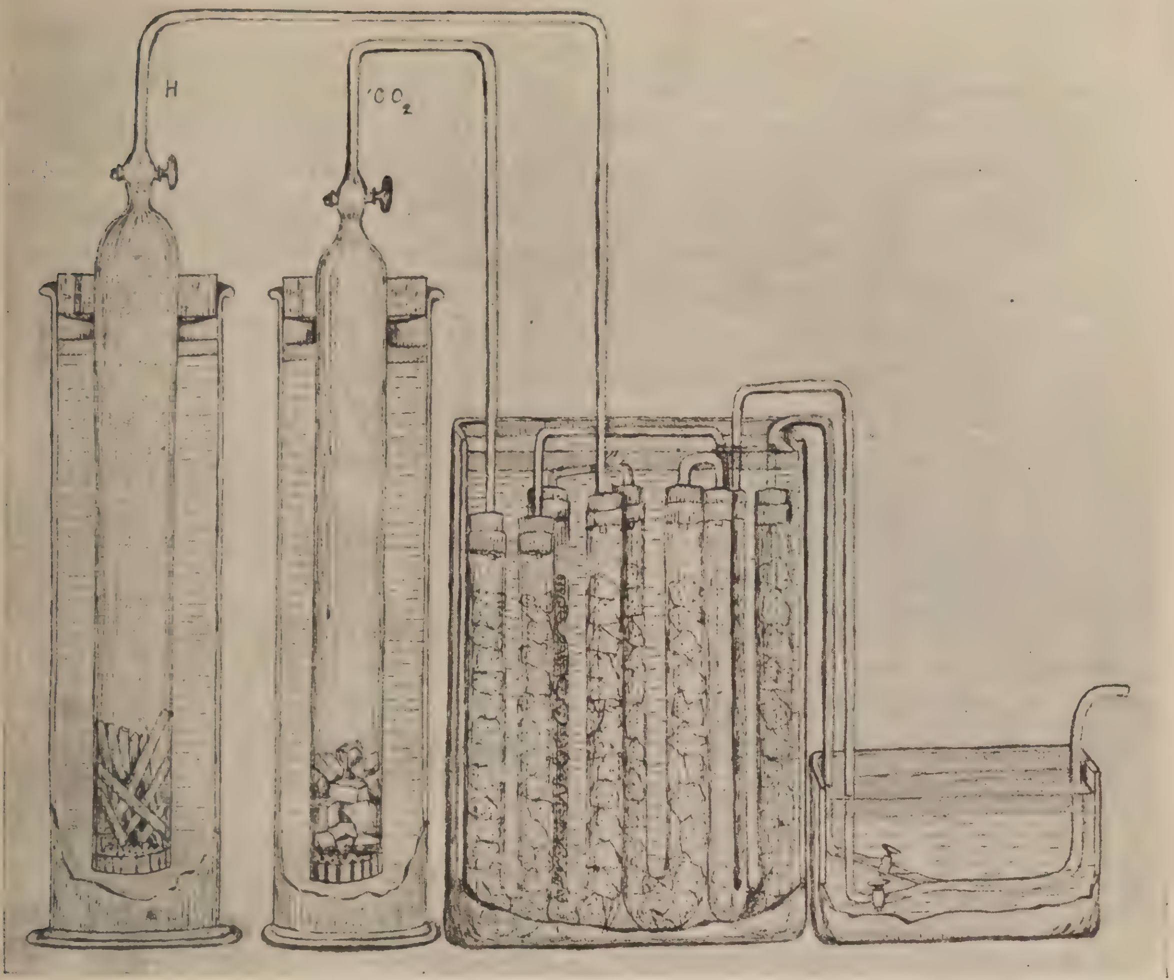

FIG. 58. Apparatus for obtaining pure hydrogen and pure carbon dioxide free from all oxygen. All the connexions are submerged in water, and all the liquids are covered with a layer of liquid paraffin. (The generators one-tenth and the remaining apparatus one-sixth natural size. After Ewart.)

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[1] A better form of gas-chamber is that figured on p. 315 (Fig. 52), by which the influence of

By adding a few motile aerobic bacteria to the hanging drop an additional test of the absence of oxygen is afforded. Under certain circumstances Recklinghausen's gas-chambers may be used, and the exit- and entry-tubes sealed after evacuation.

Facultatively anaerobic bacteria move for a longer time in the absence of oxygen when supplied with certain food-materials than with others. Thus Ritter[1] found that *Spirillum Finkler-Prior* continued to move for ten minutes in a solution of peptone, but for thirty-five to forty minutes in one to which sugar had been added. This may possibly be due to the sugar being a highly oxidized compound readily capable of yielding energy by anaerobic decomposition. On the other hand, obligate anaerobes cease to move within thirty minutes to an hour after the entry of oxygen[2].

In various chlorophyllous and non-chlorophyllous objects locomotion ceases rapidly in some cases, but in others not for a long time after all free oxygen has been removed[3]. Celakovsky found, for instance, that in darkness and in the absence of oxygen *Pandorina morum* ceased to move in eleven hours, *Euglena viridis* in forty-four, and *Pelomyxa palustris* in seventy-two hours.

The necessity of free oxygen for streaming was shown first by Corti[4], although streaming does not always cease when the cell is placed in oil[5], as in the experiments performed by Corti. Kühne and Hofmeister[6] showed the necessity of oxygen in all the cases examined by them, and Clark found that streaming usually ceased in plasmodia and in ordinary cells a few minutes after the oxygen had been removed, but in a few cases not until after four hours[7]. Ewart[8] found that preparations of *Chara* ringed with vaseline continued to show streaming for five weeks in darkness, but that when the preparations were submerged in deoxygenated water and

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oxygen and temperature, ether or electricity can be simultaneously investigated. See also Zimmermann, Das Mikroskop, 1895, pp. 220, 223; Bot. Ztg., 1887, p. 31; Clark, Ber. d. bot. Ges., 1888, p. 274.

[1] Ritter, Flora, 1899, p. 329.

[2] Beyerinck, Centralbl. f. Bact., 1893, Bd. XIV, p. 841; Ritter, l. c., p. 345.

[3] Clark, Ber. d. bot. Ges., 1888, p. 278; Celakovsky, Ueber d. Einfluss d. Sauerstoffmangels auf d. Bewegung einiger aëroben Organismen, 1898 (reprint from the Bull. internat. de l'Acad. de Bohême).

[4] Corti, 1772 (Meyen, Pflanzenphysiol., Bd. II, p. 224).

[5] Goebel, Ueber die Durchlässigkeit d. Cuticula, 1903, p. 14.

[6] Kühne, Unters. ü. d. Protoplasma, 1864, pp. 88, 105; Hofmeister, Pflanzenzelle, 1867, p. 49.

[7] Clark, l. c.; Kühne, Zeitschr. f. Biol., 1898, N. F., Bd. XVIII, p. 1; Lopriore, Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 571; Bot. Centralbl., 1902, Bd. LXXXIX, p. 118; Demoor, Contribut. à l'étude de la physiol. de la cellule, 1894 (reprint from the Arch. de Biologie, T. 13); Samassa, Ueber d. Einwirkung von Gasen auf Pflanzen, 1898 (reprint from the Verh. d. naturhist. Vereins zu Heidelberg, N. F., Bd. VI); Ritter, l. c., p. 347; Josing, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 221.

[8] Ewart, Linnean Society, 1897, Vol. XXXIII, p. 146. See also Farmer, Annals of Botany, 1896, Vol. X, p. 288.

kept in darkness, the streaming ceased in two or three days. This is, however, simply because of the accumulation of the injurious products of respiration, for Kühne and Ritter[1] found that streaming might continue for as long as nineteen days in the absence of oxygen, and by the aid of the apparatus shown in Fig. 59, which was sealed and kept under water, Ewart[2] was able to demonstrate the continuance of streaming in darkness, and in the absence of oxygen, for from six to eight weeks. This applies to *Chara foetida*, *Nitella translucens*, and *N. flexilis*, other species being less pronounced facultative anaerobes. In general, Clark found that streaming recommenced in aerobic plants under a pressure of from 1 to 7 mm. of oxygen, which is below the pressure required for normal aerobic respiration.

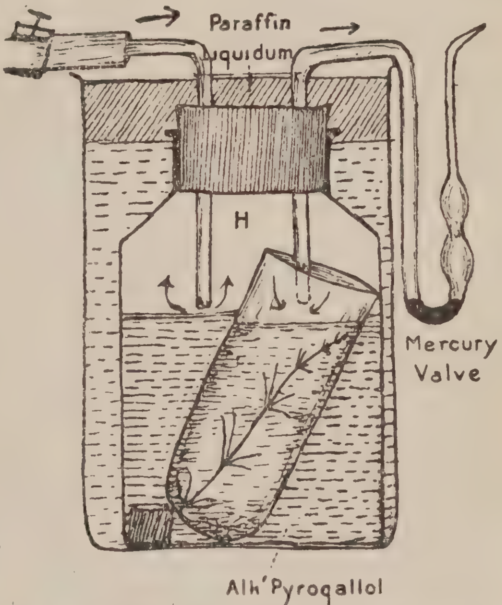

FIG. 59. Apparatus for testing the anaerobism of *Chara* and *Nitella* (two-thirds natural size).

The contradictory results of certain observers are partly due to the presence of oxygen or of poisonous impurities in the hydrogen employed, and partly to individual and cultural differences in the material used. Lopriore[3] stated that streaming never ceased in hairs of *Tradescantia* and of *Cucurbita* either in hydrogen or carbon dioxide, but this was undoubtedly due to the presence of oxygen in the gases used[4]. Lopriore[5] obtained different results in the morning to those yielded in the evening, possibly owing to changes of tone, and Josing[6] found that etherization causes streaming to cease sooner in the absence of oxygen. Carbon dioxide in all cases ultimately acts injuriously[7], but cuticularized hairs which seem to be naturally accommodated to high internal percentages of carbon dioxide may continue to show streaming in a mixture of 80 per cent. carbon dioxide and 20 per cent. oxygen. As in other cases, a temporary shock-stoppage may be produced by the sudden change from air to carbon dioxide[8]. In no case, except in the very doubtful one of *Pelomyxa*, does pure hydrogen exercise any direct injurious action, apart from that due to its displacing the oxygen required for respiration. The same applies to nitrogen and carbon monoxide in the case of plants, and as regards

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[1] Kühne, Zeitschr. f. Biol., 1898, N. F., Bd. XVIII, p. 30; Ritter, l. c., p. 351.

[2] Protoplasmic Streaming in Plants, 1903, p. 42.

[3] Lopriore, l. c., 1895, p. 28.

[4] Samassa, l. c., p. 2; Ewart, l. c., p. 38.

[5] Lopriore, l. c., 1902, p. 118.

[6] Josing, l. c., p. 221.

[7] Cf. Samassa, l. c., p. 2; Klemm, l. c., p. 36; Kühne, l. c., 1864, p. 106; Ewart, l. c., p. 78.

[8] Cf. Ewart, l. c., p. 79.

nitrous oxide, Demoor's[1] statement that aerobic plants continued to show streaming in this gas can be regarded as a proof that the gas used contained free oxygen[2].

Kühne[3] considered the long continuance of anaerobic streaming in Characeae to be due to the presence of a store of occluded oxygen, but Ewart[4] has shown that this is not the case.

Poisons. Every substance which influences metabolism may also influence streaming[5], either directly or as an after-effect, and apart from any retardation or stoppage produced as the effect of the shock of a sudden change. Many substances when dilute, such as alcohol, glycerine, and various poisons, may distinctly accelerate streaming, for a time at least, even when all shock-effect is avoided by gradual change. The effect of shock is commonly to produce a retardation or stoppage followed by a subsequent acceleration, but all these responses are manifestations of irritability and bear no relation to the changes of viscosity directly due to the presence of the exciting substance. Strong solutions of neutral substances, however, retard streaming largely owing to the rise of viscosity consequent on the withdrawal of water.

Transitory chloroforming[6], or treatment with solutions of poisonous or nutrient substances, may awaken streaming in quiescent cells, such as those of *Vallisneria*, and similarly all substances which act as chemical stimuli to the tentacles of *Drosera* also act as excitants to streaming in the responsive cells of this plant. Anaesthetics, such as ether, chloroform, and chloral hydrate, as well as such alkaloids as caffein, antipyrin, muscarin, atropin, eserin, veratrin, and curare readily retard and ultimately stop streaming and locomotory movement even when dilute. Muscarin, atropin, and veratrin, however, which are deadly poisons to higher animals, exercise relatively little effect upon plants[7], and may indeed be used as a food-material by such Fungi as *Penicillium*[8]. Anaesthetics appear commonly to stop

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[1] Demoor, Contrib. à l'étude de la Physiol. de la cellule, 1894, p. 35.

[2] Samassa, l. c., p. 2; Kauffman, Einwirkung der Anaesthetica auf Pflanzen, 1899, p. 16.

[3] Kühne, l. c., p. 92: cf. Ritter, l. c., p. 358.

[4] Ewart, l. c., p. 350. Ritter (l. c., p. 350) found that after the prolonged absence of oxygen this gas was immediately evolved on exposure to weak light, whereas the presence of absorbent substances should retard its appearance for some time. Pringsheim (Sitzungsb. d. Berl. Akad., 1887, p. 769) did actually find that *Chara* became incapable of evolving oxygen after remaining for a long time in darkness, but this was due to the induction of a condition of assimilatory inhibition in the chloroplastids. Cf. Ewart, Journ. Linn. Soc., 1896, p. 418.

[5] Demoor, l. c., p. 72; Lopriore, l. c., 1895, pp. 573, 621; Klemm, Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 680; Samassa, l. c., p. 2; Kühne, l. c., 1898, p. 36; Farmer u. Waller, Bot. Centralbl., 1898, Bd. LXXIV, p. 377; Kauffmann, l. c., p. 10; Josing, l. c., p. 223. For the detailed action of various chemicals see Ewart, Protoplasmic Streaming in Plants, 1903, p. 76.

[6] Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 220.

[7] Ewart, l. c., p. 86.

[8] Ewart, l. c., p. 81.

streaming in concentrations too dilute to cause a cessation of growth, whereas in many cases the chemotactic or phototactic irritability is suppressed before the power of movement [1].

Acids, even when in considerable dilution, such as from 0·01 to 0·05 per cent. in the case of most mineral acids, cause a rapid cessation of streaming [2]. The feebler organic acids are naturally less effective, but 1-per-cent. solutions of tartaric acid produce a stoppage of streaming within one or more hours in all the plants hitherto examined. Dutrochet [3] not only observed a similar retarding action in the case of alkalies, but also found that the repeated change from acid to alkali was more injurious than remaining for the same length of time in one medium. Both acids and alkalies induce protoplasmic deformation, which is evidenced by the pronounced vacuolation assumed as the result of treatment with alkali [4] (Fig. 60). Methyl violet, Bismarck brown [5], as well as caffein and other alkaloids [6], may produce pronounced deformation without causing streaming to cease. In all cases the timely removal of the reagent is followed by the recovery of the protoplasm, which reassumes its normal configuration, but poisonous reagents which combine with the protoplasm usually act fatally before they can be removed.

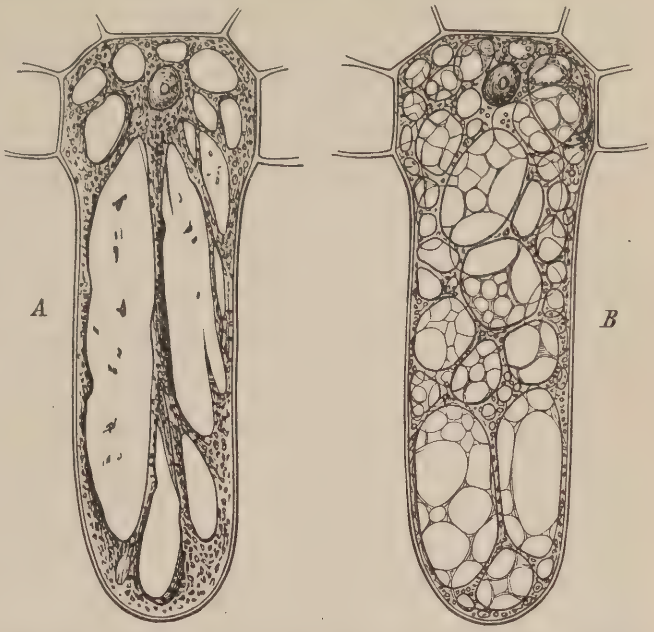

FIG. 60. Young root-hair of *Trianea bogotensis*. *A* before, and *B* one hour after, treatment with very dilute ammonia. (Magn. 1000.)

SECTION 74. **Chemotaxis and Osmotaxis.**

The usual method of showing chemotaxis is to place a capillary tube open at one end and containing a solution of the exciting substance in a drop of liquid containing the motile organisms. If the latter are positively

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[1] Rothert, Jahrb. f. wiss. Bot., 1903, Bd. XXXIX, p. 1, gives full details of actions of this character.

[2] Dutrochet, Ann. sci. nat., 1838, 2e sér., T. IX, p. 67; Klemm, Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 685.

[3] Dutrochet, l. c., p. 66: cf. also Ewart, l. c., p. 80; Jurgensen, Studien d. physiol. Inst. in Breslau, 1861, Bd. I, p. 107.

[4] Klemm, l. c., p. 658.

[5] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1886, Bd. II, pp. 250, 262, 264.

[6] Klemm, l. c., p. 665.

chemotactic they collect at the mouth of the tube, and in covered and ringed preparations aerobic organisms will ascend the tube in search of oxygen as the latter is exhausted outside (Fig. 61 *C*). If the organisms are negatively chemotactic or are osmotactic they will collect at some distance from the mouth of the capillary, and if they are positively chemotactic to dilute solutions they will gradually approach the tube as the substance diffuses from it. Convection currents due to differences of specific gravity may be avoided by placing the tube open end upwards on the tilted stage of the microscope[1].

Similar actions are exercised by the substances diffusing from a fragment of solid, or from a piece of meat or the leg of a fly. In addition, a drop of liquid may be tested in the manner shown in Fig. 60[2]. Plasmodia may be grown on wet filter-paper having one end in water and the other in the substance to be tested[3]. Currents of water must, however, be avoided, since these may excite a rheotropic response.

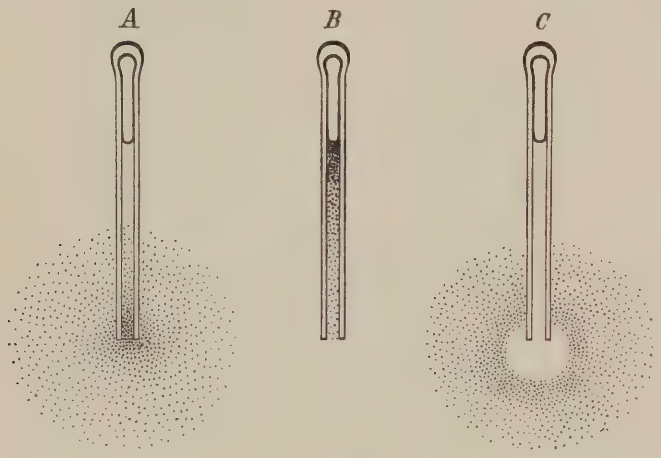

FIG. 61. Capillary tubes containing meat-extract and surrounded by bacteria. *A*, showing attraction; *B*, showing attraction exercised by the air-bubble in the tube; *C*, showing repulsion produced by acidified meat-extract. (Magn.)

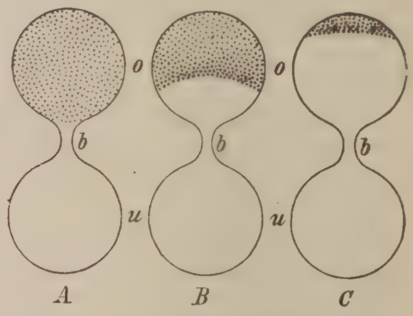

FIG. 62. Drops of distilled water (*u*) joined to drops of sea-water (*o*) containing *Spirillum* forms. The latter collect where the water is richest in salts, and hence appear to be repelled by the distilled water.

Antherozoids. The strongly chemotactic antherozoids of Ferns[4] escape in enormous numbers when small dry ripe prothallia are rapidly washed and placed in a drop of water. They are strongly attracted to a capillary containing 0·01 per cent. of sodium malate, and a feeble attraction is even exercised by solutions of 0·001 per cent. strength. Maleic acid is much less attractive[5], although more active and varied in its combin-

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[1] Pfeffer, Ber. d. bot. Ges., 1883, p. 524; Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, pp. 367, 451; 1888, Bd. II, pp. 585, 627.

[2] Jennings, Journal of Physiology, 1897, Bd. XXI, p. 264; Massart, Bull. de l'Acad. royale de Belgique, 1891, 3e sér., T. XXII, p. 152; Garrey, American Journal of Physiology, 1900, Vol. III, p. 295.

[3] Stahl, Bot. Ztg., 1884, p. 156.

[4] Pfeffer, Ber. d. bot. Ges., 1883, p. 524; Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 367; Voegler, Bot. Ztg., 1891, p. 641; Buller, Annals of Botany, 1900, Vol. XIV, p. 543.

[5] Pfeffer, l. c., 1884.

ing powers than malic acid. Potassium nitrate and ammonium phosphate exert a still feebler attractive action, which is easily overlooked, but Buller was unable to detect any chemotactic response to sodium chloride, ammonium nitrate, calcium chloride, sugars, asparagus, and glycerine[1].

Inactive malic acid acts similarly to the active form, while the free acid and its neutral salts seem to have the same excitatory value[2]. On the other hand, the diethylester of malic acid, in which the acid is not present as an ion, exercises no chemotactic action[3]. Malic acid exerts a repelling action when concentrated, but not its salts, and Buller[4] (l.c., p. 560) has shown that the chief attractive substance in the archegonium may be a salt of malic acid, possibly potassium malate, but cannot be free malic acid. Since the repulsion may be produced by citric and other acids, we have probably before us a reaction dependent upon the mere increase of acidity, i. e. upon the relative number of hydrogen ions[5]. Strong alkaline solutions, and sufficiently concentrated solutions in general, exercise a certain repulsion, which is often only shown at first, and which does not prevent the gradual entry of large numbers of the antherozoids into the capillary tubes, in which they soon become motionless and die[6]. They have, therefore, not the power of avoiding all injurious liquids, and are readily attracted to their death by introducing a tube containing malic acid mixed with a little mercuric chloride[7]. The chemotaxis of these antherozoids is the result of a typical tactic reaction[8], and the same appears to apply to the negative chemotaxis produced by free acids. It is, however, not yet certain whether the osmotactic repulsion produced by concentrated solutions is a tactic or a phobic reaction.

SPECIAL CASES. A salt of malic acid is probably also the chief attractive stimulus for the sperms of *Selaginella*, and possibly cane-sugar for those of Mosses, since the latter suffices to produce a perceptible attraction when diluted down to 0·001 per cent. strength[9]. The sperms of *Hepaticae*, of *Sphagnum*, and of *Marsilia* seem to be attracted into the archegonium in the same way, but the attractive substances have yet to be found[10].

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[1] Cf. Buller, Annals of Botany, 1900, Vol. XIV, pp. 548, 571.

[2] Pfeffer, l. c., Vol. II, pp. 381, 654; Voegler, l. c., p. 659.

[3] Pfeffer, l. c., p. 371.

[4] Buller, l. c., p. 560.

[5] Pfeffer, l. c., p. 387; Buller, l. c., p. 567.

[6] Pfeffer, l. c., p. 385. Buller (l. c., p. 555) observed only weak repulsion or none at all, and was unable to detect the transitory repulsion. Much depends upon the manner in which the experiment is performed.

[7] Pfeffer, l. c., p. 388.

[8] Cf. Rothert, Flora, 1901, p. 388.

[9] Pfeffer, l. c. 1884, pp. 422, 430. Other substances may also exert a slight action.

[10] Pfeffer, l. c., 1884, Bd. I, pp. 434, 435; 1888, Bd. II, p. 655. On the process of fertilization in Hepaticae cf. Strasburger, Jahrb. f. wiss. Bot., 1869-70, Bd. VII, p. 402; Leitgeb, Flora, 1885, p. 330.

It is not yet certain whether the antherozoids of Fucaceae adhere to the ovum simply as the result of a contact-stimulus, as Bordet supposes, or whether chemotactic influences come into play[1]. Further, it is questionable whether the sperms of *Chara* experience any chemotactic attraction, and the latter does not seem to be responsible for the conjugation of the zoospores of *Chlamydomonas* or of *Ulothrix zonata*[2], which seems to be left to chance. It is, however, hardly surprising that, as in the case of pollination, various modes should be used to bring motile sexual cells together[3]. In all cases, however, the ultimate fusion is determined by the properties of the protoplasts; so that, although the sperms of other species may be attracted into the archegonium and come into close contact with the ovum, no fusion occurs. The special attraction exerted by malic acid and its salts as well as their actual presence in the prothallus indicate their importance as agents for inducing fertilization in Ferns[4].

Bacteria. Motile Bacteria show all grades of sensibility, and both the chemotactic and osmotactic reactions are carried out in a phobotactic manner. Very sensitive forms react positively to most substances, but the less sensitive forms give little or no reaction when feebly stimulating substances are used[5]. Peptone and potassium salts are especially active, and are responsible for the high attractive power of meat extract. Sodium and calcium salts, asparagin and urea, are less active as stimuli, and while glycerine appears to produce no attraction at all, oxygen appears to influence all bacteria strongly.

Bacterium termo[6] and *Spirillum undula* appear to be especially sensitive, for a response is produced when the liquid in the capillary contains 0·001 per cent. of peptone, potassium chloride, or of meat-extract. *Spirillum serpens*, *S. volutans*, *Bacillus subtilis*, and especially *Spirillum Finkler-Prior*, are much less sensitive. Dextrin attracts *Bacterium termo* strongly, but *Spirillum undula* very feebly[7], while only a few bacteria are chemotactically affected by ether[8]. Sulphuretted hydrogen attracts *Chromatium Weissii*

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[1] Thuret, Ann. d. sci. nat., 1854, 4e sér., T. II, p. 17; Bordet, Bull. de l'Acad. royale de Belgique, 1894, 3e sér., T. XXVII, p. 889; Farmer and Williams, Phil. Trans., 1898, Vol. CXC, pp. 633, 643; Buller, Quarterly Journal of Microscopical Science, 1902, Vol. XLVI, p. 148.

[2] Pfeffer, l. c., 1884, pp. 438, 441.

[3] Cf. Pfeffer, l. c. 1884, p. 447. Chemotactic sensibility appears to be absent from the sperms of *Rana* (Massart, Bull. de l'Acad. royale de Belgique, 1888, 3e sér., T. XV, Nr. 5, und 1889, Nr. 8) and of *Echinodermata* (Buller, Quarterly Journal of Microscopical Science, 1902, Vol. XLVI, p. 151), but is shown by those of the rat (Otto Löw, Sitzungsb. d. Wien. Akad., 1902, Bd. CXI, Abth. iii, p. 118).

[4] Pfeffer, l. c., p. 884; Buller, l. c., 1900, p. 570.

[5] For details see Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. II, p. 582.

[6] Pfeffer (l. c., p. 590) mentions what is included under the term '*Bacterium termo*.'

[7] Pfeffer, l. c., p. 606.

[8] Rothert, Flora, 1901, p. 380.

and probably other sulphur-bacteria as well[1], while the comparatively insensitive typhus- and cholera-bacilli[2] are strongly attracted by potato-sap.

Increasing concentrations of neutral salts exert hardly any perceptible chemotactic or osmotactic repulsion[3] upon *Bacterium termo*, but a strong one upon *Spirillum undula*, while the action upon other forms lies between these extremes. Free acids produce repulsion in the case of *Spirillum undula* even when very dilute, but alkalies only when somewhat more concentrated. Ether and alcohol[4] may in certain cases produce repulsion, while the presence of oxygen dissolved at ordinary pressure from air is sufficient to repel *Spirillum undula* and *S. serpens*. Sulphur bacteria and other anaerobic bacteria react still more readily to oxygen, and in some cases are so sensitive that the merest trace of oxygen produces repulsion, although most bacteria are capable of positive chemotaxis in regard to oxygen[5].. Since *Bacterium termo* has hardly any negative osmotaxis or chemotaxis, motile forms penetrate concentrated solutions of sugar or potassium chloride in abundance, whereas a slight concentration exercises an osmotactic repulsion upon *Spirillum undula*.

Flagellatae and Volvocineae. Many colourless Flagellatae react chemotactically and osmotactically to various substances, and in general the reactions resemble those of Bacteria[6]. Thus *Bodo saltans*, *Trepomonas agilis*, and *Hexamitus rostratus* have about the same positively chemotactic sensitivity as the most sensitive bacteria, whereas *Hexamitus intestinalis* only reacts weakly, and *Astasia proteus* and *Tetramitus rostratus* not at all. So far as is known, the green Flagellatae show no positive chemotaxis, apart from their aerotaxis[7], whereas some of the Volvocineae are able to respond with moderate activity to the chemical substances already mentioned.

Many substances which produce a phobotactic action upon Bacteria induce a typical chemotactic reaction when presented to the above-named Flagellatae[8]. The zoospores of *Saprolegnia*[9] behave similarly

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[1] Miyoshi, Journal of the College of Science, University of Tokyo, 1897, Vol. x, p. 169.

[2] Pfeffer, l. c., p. 615; A. Cohen, Centralbl. f. Bact., 1890, Bd. VIII, p. 164.

[3] Pfeffer, l. c., p. 621.

[4] Rothert, l. c., p. 380.

[5] On 'Aerotaxis' or 'Oxygenotaxis,' cf. Bd. II, p. 582 footnote, and also Engelmann, Pflüger's Archiv, 1881, Bd. XXVI, p. 541; Beyerinck, Centralbl. f. Bact., 1893, Bd. XIV, p. 835; 1895, Abth. ii, Bd. I, p. 111; Rothert, l. c., p. 377. Oxygen exerts no chemotactic action on the sperms of Ferns (Pfeffer, l. c., 1884, p. 372) or upon the zoospores of *Saprolegnia* (Rothert, Cohn's Beiträge z. Biol., 1892, Bd. V, p. 341; Stange, Bot. Ztg., 1893, p. 139).

[6] Pfeffer, l. c., 1888, pp. 595, 615, 625.

[7] On the stimulating action of oxygen upon *Euglena viridis* see Aderhold, Jenaische Zeitschr. f. Naturwiss., 1888, Bd. XXII, p. 314.

[8] Cf. Rothert, Flora, 1901, p. 388.

[9] Rothert, l. c., p. 388. For substances acting as stimuli see Stange, Bot. Ztg., 1890, p. 124.

and for them phosphates are especially attractive. The hyphae of Fungi respond in general to the same substances as Bacteria and Flagellatae, and their positive and negative chemotropism has the character of a tropic movement. The different grades of repulsion exerted by weak acids on various Flagellatae as well as on fungal hyphae and on Bacteria are of similar character[1]. It remains, however, to be seen whether all Flagellatae are capable of a tropic reaction, and to what extent the osmotropic reactions[2], which are as well developed in these organisms as in Bacteria, are carried out in a tropic or a phobic manner. It may be mentioned that the Infusoria[3] are usually not chemotactically stimulated by the substances mentioned, but that certain species at least are capable of a positive phobotactic response towards dilute acids including carbonic acid, and of a negative one away from more concentrated solutions.

Myxomycetes. According to Stahl[4] the plasmodia show a positively chemotactic amoeboid movement towards an extract of tan, and Stange[5] has found that various substances act as stimuli. Stange has also shown that the zoospores of *Aethalium* and *Chondrioderma* are attracted by various substances, more especially by lactic, butyric, and malic acids. Concentrated solutions, or ones with a strong acid reaction, exert a repulsive action upon the zoospores as well as upon the plasmodia. It may incidentally be mentioned that the amoeboid leucocytes of animals are chemotactically stimulated by a variety of substances, and that by reactions of this kind various definite and physiologically important movements may be produced within the body[6].

THE USES OF CHEMOTAXIS AND ITS EXCITANTS.

By means of their chemotactic irritability organisms may be attracted to regions where food-material is abundant, or where their function is

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According to Rothert (l. c., p. 375) only the second zoospore stage responds chemotactically. The substances which attract the zoospores of Chytridiaceae are not known. Cf. Pfeffer, l. c., 1888, p. 643. According to W. Benecke (Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 554), Diatomaceae are capable of both chemotactic and aerotactic responses.

[1] Pfeffer, l. c., 1888, p. 625. According to Garrey (American Journal of Physiology, 1900, Vol. III, p. 291), *Chilomonas* exhibits a normal tactic reaction to dilute acids, and a phobic one to concentrated acids and other substances.

[2] Cf. Massart, Archives de Biologie, 1889, T. IX, p. 531; Bull. de l'Acad. royale de Belgique, 1891, 3e sér., T. XXII, p. 148.

[3] Jennings, Journal of Physiology, 1897, Vol. XXI, p. 320; American Journal of Physiology, 1900, Vol. III.

[4] Stahl, Bot. Ztg., 1884, p. 155. Olive (Proc. of the Boston Soc. of Natural History, 1902, Vol. XXX, p. 463) could detect no chemotaxis in Acraseae.

[5] Stange, Bot. Ztg., 1890, p. 155.

[6] Cf. Verworn, Allgem. Physiologie, 3. Aufl., 1901, p 451.

fulfilled, as when the sperm is attracted to the ovum[1]. This latter is better fulfilled by normal chemotaxis, although phobic reactions may also produce movement to particular points. It is not always readily possible to distinguish between osmotactic and chemotactic irritability, especially when repulsion only occurs with high concentration. If, however, an organism responds only to very few substances, or to those in very great dilution, the response is clearly due to the chemical properties of the exciting substance, and not to any osmotactic action. The attraction of the antherozoids of Ferns by malic acid, of Bacteria and flagellate Infusoria by peptone and potassium salts, is undoubtedly a positively chemotactic response.

Although many substances may stimulate a particular organism, a special substance may exert a preponderating action, and may overpower all others. In this sense malic acid or its salts may be regarded as the special stimulating substance for the antherozoids of Ferns, and probably cane-sugar for those of Mosses. The antherozoids of Hepaticae, Sphagnaceae and of *Marsilia* are either devoid of any chemotactic irritability or are only very feebly sensitive, since no certain attraction has as yet been observed with any substance or mixture of substances. It is worthy of note that if such reacting organisms as Bacteria, Flagellatae, Volvocineae, the zoospores of *Saprolegnia* and fungal hyphae are tabulated in descending order according to the stimulating action of a substance upon them, the order will on the whole follow approximately the same course when another substance of similar constitution is used.

The high sensitiveness to malic acid or to cane-sugar shown by the antherozoids of Ferns and Mosses respectively does not involve any special sensitiveness to peptone or potassium salts. These are in general the strongest stimulatory substances for Bacteria, which respond but feebly to malic acid and cane-sugar. Even in the case of Bacteria great differences are shown, for certain forms are attracted by sulphuretted hydrogen, and one species responds readily to dextrin which is usually but feebly chemotactic. Similarly the antherozoids of Ferns are neither attracted nor repelled, whereas very many bacteria, though not all, show pronounced chemotactic response to this gas. Infusoria and *Euglena* are also aerotactic, although they react but little (Infusoria) or not at all (*Euglena*) to other substances.

It seems unlikely that the mode of perception of different substances by a particular organism is in all cases the same; that, for instance, the primary reactions involved in a chemotactic response to acids or oxygen are the same as when the response is due to the presence of peptone or potassium salts. It may, however, with safety be concluded that the development of a chemotactic irritability adapted to the perception of

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[1] Since all nutrient materials do not act chemotropically, it is hardly advisable to follow Stahl (Bot. Ztg., 1884, p. 165) and use the terms 'trophotropism' and 'trophotaxis.'

a particular substance might unavoidably bring about a sensitivity to more or less closely allied substances. In this way we can understand how it is that, for instance, Bacteria are able to react to salts of rubidium or to aniline blue, and the spermatozoa of Ferns[1] to salts of rubidium and caesium, substances to which under natural conditions they are never called upon to respond.

The physiological action of a substance is of course dependent upon its chemical properties, but we are unfortunately unable to deduce from these chemical properties why one substance should be especially active but another less so. In the case of compounds which dissociate in watery solutions it needs to be determined how far the stimulation is due to the free ions, and how far to the undissociated molecules. The antherozoids of Ferns respond equally well to free malic acid and to its salts, whereas sodium and ammonium chlorides as well as the non-dissociating diethylester of malic acid are inactive. Hence the stimulating action is due to the malic acid ions. In the same way it can be determined that the repelling action of acids is due to the hydrogen ions, and that the intensity of action is proportional to the degree of dissociation[2].

SECTION 75. **Chemotactic and Osmotactic Repulsion.**

Chemotactic attraction is due to the chemical properties of the stimulating substance, but it is also possible that certain organisms may possess a power of positive osmotactic response to differences of osmotic concentration in the surrounding medium. Massart ascribes to this cause the passage of certain marine Bacteria and Flagellatae from very dilute solutions to sea-water, and similarly Stahl has observed that the plasmodia of Myxomycetes may creep from a dilute to a more concentrated solution of sugar[3].

Many organisms show negative osmotaxis with high concentrations, and hence whenever increasing concentration produces repulsion it needs to be determined whether this is due to negative osmotaxis or chemotaxis, or to their conjoint action. In some cases no repulsion appears to occur, as for example in the case of *Bacterium termo*[4], a marine *Spirillum*[5], *Polytoma uvella*, *Euglena viridis*, and various flagellate and ciliate Infusoria[6]. In all such cases the organisms swim without any check into

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[1] Buller, Annals of Botany, 1900, Vol. XIV, pp. 571 and 572.

[2] Cf. Buller, Annals of Botany, 1900, Vol. XIV, p. 543.

[3] Massart, Bull. de l'Acad. royale de Belgique, 1891, 3e sér., T. XXII, p. 152; Stahl, Bot. Ztg., 1884, p. 166. The proof of the absence of chemotaxis is by no means sure in either case.

[4] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. II, p. 626.

[5] Massart, l. c., p. 153.

[6] Massart, Archives de Biologie, 1889, T. IX, p. 560. The power of reaction is not always fully

the capillary filled with the chemotactic solution, however concentrated this may be. On the other hand, *Spirillum undula* and *Bodo saltans* are repelled by solutions of neutral salts having an osmotic concentration equivalent to from 0·5 to 1 per cent. of potassium nitrate. To produce the same repulsion in the case of *Trepomonas agilis* and *Spirillum volutans* requires a somewhat higher concentration, the organisms being less sensitive[1].

Repulsion produced by very dilute solutions, as for example by acids, can only be due to negative chemotaxis. Thus the presence of 0·1 per cent. of citric acid is sufficient to overcome the chemotactic attraction exerted by 0·19 per cent. of potassium chloride upon *Spirillum undula*, and 0·2 per cent. of citric acid neutralizes the attraction of 0·01 per cent. of malic acid upon the antherozoids of Ferns[2]. Similarly the repulsion exerted by dilute solutions of potassium cyanide, and of calcium nitrate are really chemotactic in character[3]. The attraction of *Spirillum* by low partial pressures of oxygen and its repulsion by high ones is obviously a chemotactic phenomenon, and also affords a good instance of a reversal of the reaction by increasing concentration[4].

A repulsion of Fern antherozoids is produced only by increasing concentrations of free malic acid, and not by its salts. The effect produced is, therefore, the resultant of the attraction exercised by the molecules of malic acid and the repulsion due to the free hydrogen ions. This is coupled with the fact that the full attraction of malic acid is produced by very dilute solutions, whereas that of the hydrogen ions increases progressively up to a high limit. It does not, however, follow that every chemotactic substance should produce repulsion when concentrated, or that every negatively chemotactic substance should produce attraction when sufficiently diluted. Thus free citric and hydrochloric acids always repel *Spirillum undula*, and the antherozoids of Ferns. Similarly, the smallest pressure of oxygen appears to produce repulsion in certain motile anaerobic Bacteria. On the other hand, even 15 per cent. solutions of cane-sugar do not repel the antherozoids of Mosses[5]. Presumably in cases where the positive chemotaxis persists, the repulsion is due to the fact that the negative osmotaxis increases more rapidly with rising concentration.

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developed. Thus cultures of *Spirillum undula* are sometimes found to be almost non-sensitive, and Pfeffer (l. c., p. 614) observed distinct repulsion in the case of *Polytoma uvella*, although Massart found this organism to be non-sensitive.

[1] Cf. Pfeffer, l. c., pp. 601, 614, 626; Massart, l. c.

[2] Pfeffer, l. c., 1888, p. 627; l. c., 1884, p. 387.

[3] Massart, l. c., 1889, p. 525.

[4] Cf. for this and the following, Pfeffer, l. c., 1888, p. 621 seq.

[5] Pfeffer, l. c., 1884, p. 432.

Positive chemotaxis may so delay the osmotactic repulsion that it can only become manifest with concentrated solutions, but when the substance induces negative chemotaxis when dilute, repulsion may be produced by solutions of less osmotic value than the cell-sap. Hence the actual result may differ considerably from that which would be produced by the osmotactic stimulus alone. It is, therefore, hardly surprising that the concentrations of various substances required to produce perceptible repulsion upon Bacteria and Flagellatae are not exactly isosmotic. That other factors may come into play is shown by the fact that glycerine usually exerts no action upon osmotactic organs[1]. Furthermore, the power of osmotic response may itself be influenced indirectly by chemotactic stimulation.

After Engelmann[2] had recognized the repulsion exerted by oxygen Pfeffer found that various substances were able to produce the same result[3], and concluded that the result was either due to negative chemotaxis or directly to the concentration. Massart[4] then observed that a variety of substances in isosmotic concentration produce about the same degree of repulsion. These results have only been obtained with *Spirillum undula* and *Bacillus megatherium*[5], but nevertheless they appear to apply to other motile forms. The stronger repulsion produced by potassium cyanide, calcium nitrate, &c., is due to their exerting in addition a strong negative chemotaxis. The lessened repulsion exercised by saccharose and dextrose, and the inefficiency of glycerine, are ascribed by Massart to their rapid penetration of the protoplasm preventing the depression of turgor which operates as the exciting stimulus[6]. Although several facts point to this conclusion, it remains to be seen whether all substances which rapidly penetrate the protoplast are unable to exert any repulsive action.

Experimental evidence is necessary to determine in what way the diminution or cessation of repulsion is produced. Phobotactic reactions may in fact be excited and

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[1] Pfeffer, l. c., 1888, p. 626; Massart, l. c., 1891, pp. 528, 559.

[2] Engelmann, Pflüger's Archiv f. Physiologie, 1881; Bd. XXVI, p. 541; Bot. Ztg., 1881, p. 442.

[3] Pfeffer, Ber. d. bot. Ges., 1883, p. 524; Unters. a. d. bot. Inst. zu Tübingen, 1884, pp. 385, 453; ibid., 1888, Bd. II, p. 621. Stahl (Bot. Ztg., 1884, p. 166) considers the repellent action of sugar-solution upon the plasmodium of *Aethalium* to be directly due to the withdrawal of water.

[4] Massart, Arch. de Biologie, 1889, Bd. IX, p. 529. The Bacteria used responded chemotactically to most of the substances used, and hence would have shown the antagonism between attraction and repulsion without the addition of the potassium carbonate used by Massart.

[5] Repulsion was attained by solutions isosmotic with a solution of from 0·005 to 0·006 of a gram-molecule ($\frac{1}{2}$ to $\frac{3}{5}$ of a gram) of KNO_3 per litre. The *Spirillum undula* used by Massart is apparently slightly different to that used by Pfeffer. Cf. Rothert, Flora, 1901, p. 413 footnote.

[6] Massart, l. c., p. 528; Rothert, Flora, 1901, p. 409. According to Miyoshi (Bot. Ztg., 1894, p. 17), glycerine appears to exert no repulsion upon the hyphae of Fungi. [Assuming that the ectoplasmic membrane were the percipient organ for osmotactic stimuli, it could only be stimulated when its inner and outer surfaces were exposed to differences of osmotic concentration, which could only be maintained by non-penetrating or slowly-penetrating substances. It is difficult to see how a general fall of turgor, operating equally on all sides could act as a directive stimulus. The neutral action of glycerine is certainly not due to its exerting a positive chemotaxis and negative osmotaxis which balance at all concentrations.]

also inhibited in various ways. Possibly the unequal distribution of the materials in the cell may act as a stimulus, which will be maintained so long as a difference of concentration exists on the two sides.

Many bacterial protoplasts re-expand rapidly or slowly in plasmolysing solutions, but others not at all[1]. These properties are not constant, however, and specific peculiarities are often shown in regard to particular substances. The two bacteria used by Massart behaved similarly on the whole, although asparagin repelled *Bacillus megatherium* as strongly as potassium nitrate, but *Spirillum undula* not at all in the concentrations used. This may be due to the especially rapid penetration of *Bacillus megatherium* by asparagin; but, for the reasons given, it is difficult to form a final judgement.

Many organisms show no negative osmotaxis when placed in solutions which strongly plasmolyse them[2]. On the other hand, Massart found that *Tetramitus rostratus* showed negative chemotaxis, although it has the power of rapidly accommodating itself to concentrated solutions without its power of movement being affected. Hence Fischer is hardly justified in concluding that the production or non-production of plasmolysis indicates the presence or absence of a capacity for osmotactic reaction. The causes which overcome or antagonize repulsion are not necessarily always the same, and repulsion, like chemotaxis, may often be produced by solutions in which the organism is capable of continued existence. It depends upon the properties and power of accommodation of the organism whether the transference to a concentrated solution hinders or inhibits the power of movement, and whether death ensues rapidly or gradually.

As the result of the attraction and repulsion, organisms of different sensibility collect in zones at variable distances around the mouth of the capillary tube from which the concentrated solution is diffusing. The gradual dilution caused by diffusion, together with the accommodation of the organisms and the consumption of oxygen, may cause the organisms in two zones to change places, or may induce the exit from the capillary of forms which had previously penetrated it[3]. Excreted products of metabolism may also produce attraction, and, according to Jennings[4], the crowding together of *Paramaecium* is due to the chemotaxis exerted by the excreted carbon dioxide.

Since these reactions may be produced either in a tropic or in a phobic manner, direct experiment is necessary to determine the detailed character of the reaction. The antherozoids of Ferns, Mosses, and *Selaginella*, certain Flagellatae, and the zoospores of *Saprolegnia*, show positive and apparently also negative chemotaxis; but it is not certain whether the

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[1] Cf. A. Fischer, Vorlesungen ü. Bacterien, 1903, 2nd Ed., pp. 24, 116. On the regulation of turgor see H. v. Mayenburg, Jahrb. f. wiss. Bot., 1901, Bd. XXXVI, p. 381.

[2] Fischer, l. c., p. 116.

[3] For details see Pfeffer, l. c., 1888, p. 639; 1884, p. 472. Also Massart, Bull. de l'Acad. royale de Belgique, 1891, 3e sér., T. XXII, p. 157; Beyerinck, Centralbl. f. Bact., 1893, Bd. XIV, p. 827; Abth. ii, 1895, Bd. I, p. 111; 1897, Bd. III, p. 1; Yegounow, Arch. d. sci. biol. de l'Inst. impér. de médecine de St. Pétersbourg, 1895, T. III, p. 381; Centralbl. f. Bacteriologie, 1898, Abth. ii, Bd. IV, p. 97.

[4] Jennings, Journal of Physiology, 1897, Vol. XXXI, p. 318. Cf. also Pfeffer, l. c., 1888, p. 619.

osmotactic reactions of these organisms are of phobic or tropic nature. The bacteria hitherto examined are stimulated by the same substances as the Flagellatae mentioned, but carry out phobic reactions alone. The curvatures of fungal hyphae have, however, a normal tropic character, and the same appears to apply to the positively chemotactic movements of Plasmodia, although the precise nature of their negatively chemotactic and osmotactic movements is doubtful.

It has been seen that it is often doubtful whether a substance exercises one or more stimulatory actions, and still less is known of the mode of perception and the conditions for it. The osmotropic and hydrotropic irritabilities might possibly be based upon similar sensibilities, although in some cases at least this does not appear to be the case. A few facts are, however, known concerning the minimal stimuli for response, the effect of the intensity of the stimulus, and the power of discrimination.

In the case of sensitive organisms a very small amount of a good stimulatory material suffices to produce a perceptible reaction. Antherozoids and Bacteria are attracted to a capillary tube containing a hundred-millionth of a milligram (0·00,000,000,001 gram) of malic acid or of peptone[1] respectively, and this although only a small fraction actually comes into contact with each excitable organism. These quantities are, however, not as small relatively as they appear, since an antherozoid is about 0·000,000,000,025, and a *Bacterium termo* 0·000,000,000,002 of a gram., i.e. the material in the tube weighs five times as much as the *Bacterium termo*, and has $\frac{1}{25}$ the weight of the antherozoid. Negative osmotaxis, on the other hand, is only exhibited in the presence of solutions whose concentrations are equivalent to at least 0·5 per cent. potassium nitrate solution.

It appears that the chemotactic and osmotactic sensitivities of certain micro-organisms are extremely changeable. Thus Massart[2] found that *Spirillum undula* after gradual accommodation to saline solutions required a salt solution of from five to eight times the previous concentration to produce perceptible repulsion.

The sensitivity may be lowered by unfavourable conditions, and Voegler[3] has shown that at low temperatures the antherozoids of Ferns require stronger solutions to produce a perceptible reaction than they do at ordinary temperatures. It remains, however, to be seen whether the sensitivity is lost sooner at low temperatures or in the absence of oxygen

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[1] Pfeffer, Unters. u. d. bot. Inst. zu Tübingen, 1884, p. 382; ibid., 1888, p. 628. [A trace of oxygen may suffice for the movement of aerobic bacteria without being able to produce any perceptible aerotaxis. This is well shown when the bacterium method is used to detect photosynthesis in isolated chloroplastids.]

[2] Massart, l. c., 1889, p. 548.

[3] Voegler, Bot. Ztg., 1891, p. 673. Cf. also Stange, Bot. Ztg., 1890, p. 139, in regard to the zoospores of *Saprolegnia*.

than the power of movement. Rothert[1] appears to have obtained this result by means of ether, which suppresses first the osmotactic and then the chemotactic reactions, when applied in increasing concentrations. The fact that a rise of concentration may convert attraction into repulsion is also an instance of change of tone produced by demand. If the repulsion is the result of the antagonism of positive chemotaxis and negative osmotaxis, or of two opposed chemotactic actions as when malic acid acts on Fern antherozoids, we have in both cases instances of the same substance exercising two different stimulatory actions, of which one increases more rapidly with concentration than the other.

The lessened effect of increasing stimuli follows in approximate accordance with the so-called Weber's law both in the case of the typical chemotactic and the phobo-chemotactic reactions of bacteria and of antherozoids. Probably also similar relationships will hold good for negative osmotaxis. Furthermore, in the presence of two chemotactic substances an organism may either be affected by each separately, or the two stimuli may fuse to a single perception.

SECTION 76. **The Influence of Water.**

GENERAL ACTIONS. The power of movement, like that of growth, is dependent upon the supply of water, and organisms become immotile or sluggish in concentrated solutions without necessarily being killed[2]. Thus Bacteria grow and form cilia in concentrated solutions, but these develop no power of movement[3]. Similarly there must be a certain optimal concentration for those forms which are unable to exist in dilute solutions[4]. Pure water is, indeed, injurious to many forms. On the other hand, streaming may continue in plasmolysed cells although more or less retarded[5].

Sudden transference from dilute to concentrated solutions usually causes disturbances of the power of movement, as for instance a temporary cessation of the motion of cilia, or a partial stoppage of amoeboid movement[6]. Sudden plasmolysis may produce a temporary stoppage of

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[1] Jahrb. f. wiss. Bot., 1903, Bd. XXXIX, p. 1.

[2] It has already been mentioned that salt-solutions repel *Paramaecium*.

[3] On ciliated epithelium see Engelmann, in Hermann's Handbuch für Physiologie, Bd. I, p. 398.

[4] The statements of Velten (Bot. Ztg., 1872, p. 649) and Dehnecke (Flora, 1881, p. 8) on the optimal turgor for streaming have no value, since the other factors at work were insufficiently considered.

[5] Dutrochet, Ann. d. sci. nat., 1838, 2e sér., T. IX, p. 73; A. Braun, Verhandlg. d. Berl. Akad., 1852, p. 225; Nägeli, Beiträge z. wiss. Bot., 1860, Heft ii, p. 75; M. Schultze, Protoplasma d. Rhizopoden u. Pflanzenzellen, 1863, p. 41; Hofmeister, Pflanzenzelle, 1867, p. 52; Ewart, Protoplasmic Streaming in Plants, 1903, pp. 8-9.

[6] Stahl, Bot. Ztg., 1884, p. 166.

streaming as the result of shock[1]; while, on the other hand, streaming may be excited or accelerated by a diminution in the percentage of water[2].

FIG. 63. Cell from a staminal hair of *Tradescantia virginica*: *A* fresh in water, *B* the same with ball and clumps of plasma *c*, in the zone *a–b* exposed to induction-shocks. Magn. 400. (After Kühne.)

TROPIC ACTIONS. A RHEOTACTIC IRRITABILITY[3] has only hitherto been detected in Myxomycetes, which creep on wet filter-paper or other media against the stream of water. To produce this movement a slow stream is sufficient, as when a plasmodium is developed upon a strip of filter-paper placed with one end in a beaker of water, and the other hanging over the edge of the beaker. Since freely motile organisms are carried along mechanically even by a feeble current, it is hardly likely that they should develop any special rheotactic irritability. Hence Roth's statement that certain Bacteria do actually swim against currents of water requires further proof[4].

HYDROTAXIS is also shown only by the plasmodia of Myxomycetes[5], and in virtue of this irritability the plasmodium creeps into a moist substratum. Towards the time of fruiting, however, the positive hydrotaxis becomes negative and the plasmodium creeps on to the surface of the substratum, and up the developing sporangial stalks away from the moisture.

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[1] Hofmeister, Pflanzenzelle, 1867, pp. 27, 53; Hörmann, Studien ü. d. Protoplasmaströmung bei Characeen, 1898, p. 48; M. Tswett, Bot. Centralbl., 1897, Bd. LXXII, p. 329.

[2] Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 214. [The evidence as to any such stimulating action of water on streaming is very unsatisfactory. On the physical action of the percentage of water cf. Ewart, l. c., p. 12.]

[3] B. Jönsson, Ber. d. bot. Ges., 1883, p. 515; Stahl, Bot. Ztg., 1884, p. 147; J. B. Clifford, Annals of Botany, 1897, Vol. XI, p. 180. According to Strasburger (Wirkung d. Lichts u. d. Wärme auf Schwärmsporen, 1878, p. 71) this action was first observed by Schleicher.

[4] Roth, Centralbl. f. Bact., 1893, Bd. XIII, p. 755. Aderhold (Jenaische Zeitschr. f. Naturwiss., 1888, N. F., Bd. XV, p. 314) could detect no rheotaxis in *Euglena viridis*.

[5] Stahl, l. c., p. 149. Whether the Myxamoebae of Acrasieae (cf. Fayod, Bot. Ztg., 1883, p. 172; Olive, Proceedings of the Boston Society of Natural History, 1902, Vol. XXX, p. 486), and also Diatoms and Oscillarias, react hydrotropically is uncertain.

SECTION 77. **Mechanical Actions.**

Pressure exercises in the first place a purely mechanical action, but if suddenly applied produces a certain shock-effect. As might be expected, the movement of swarm-spores is much retarded in viscous media such as solutions of gum-arabic or gelatine[1], and ceases like the movements of plasmodia[2] in solidified 2 to 5 per cent. gelatine, although *Oscillaria* is still able to move slowly in this medium.

Gravity and still more powerful centrifugal forces are able to produce accumulations of the denser constituents at one end of the cell in a purely mechanical manner. The protoplast, indeed, is able in virtue of its plasticity to undergo very pronounced deformation or may even be broken up into pieces without death ensuing. Deformations may result from rapid changes of temperature, from the action of certain chemicals, from severe pressure, as well as from the action of weak induction-shocks, which are especially well adapted to produce localized effects[3] (Fig. 63).

Streaming may continue in the internodal cells of *Nitella*, and in root-hairs of *Hydrocharis*[4] even when these are sharply bent, and similarly plants may be strongly shaken without any pronounced effect on streaming. In some cases, however, a transitory slowing or cessation of streaming[5] may result, and this may be followed by a temporary acceleration. Shaking and all mechanical shocks produce a distinct effect if sufficiently intense and suddenly applied, although all cells are not equally sensitive. Cells in which the streaming is permanent or has been a long time aroused (*Chara*, *Nitella*, *Elodea*) are always more sensitive than ones in which the streaming is only temporary and has been recently excited by stimuli (*Elodea*, *Vallisneria*)[6]. The plasmodia of Myxomycetes exhibit a tendency to assume a rounded shape when subjected to mechanical stimuli, and strong shaking as well as the action of electrical discharges causes a

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[1] See Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, pp. 390, 420.

[2] Pfeffer, Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, p. 277.

[3] Kühne, Unters. ü. das Protoplasma, 1864, pp. 74, 94; Klemm, Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 647, and the literature here given. On methods see these works and also Nägeli u. Schwendener, Mikroskop, 2. Aufl., 1877, p. 462; Zimmermann, Mikroskop, 1895, p. 231.

[4] Dutrochet, Ann. d. sci. nat., 1838, 2e sér., T. IX, p. 32; Meyen, Pflanzenphysiologie, 1838, Bd. II, p. 210; Hofmeister, Pflanzenzelle, 1867, p. 50. On the influence of injuries on the direction of streaming in *Caulerpa*, cf. Janse, Jahrb. f. wiss. Bot., 1890, Bd. XXI, p. 206, and in other plants, Ewart, Protoplasmic Streaming in Plants, 1903, p. 34 seq.

[5] Dutrochet, l. c., p. 32; Hofmeister, l. c., p. 50; Borsčow, Bull. de l'Acad. de St. Pétersbourg, 1868, T. XII, p. 213; Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 217; Hörmann, Studien ü. d. Protoplasmaströmung b. d. Characeen, 1898, p. 39; Rhumbler, Zeitschr. f. allgem. Physiol., 1902, Bd. I, p. 305.

[6] Ewart, l. c., 1903, p. 72. The detailed action of momentum, impact, and of pressure-waves is given here.

temporary retardation of the movement of swarm-spores of Diatoms and of *Oscillaria*[1].

Contact and other mechanical agencies produce a transitory stoppage of the cilia of *Chlamydomonas pulvisculus*[2], and the cilia of many locomotory organisms seem to possess a certain contact irritability, such as appears to be exhibited by *Stylonychia* and other Infusoria which run about over the substratum[3]. According to Bordet[4], the antherozoids of *Fucus* have a 'thigmotaxis' or 'haptotaxis' of this kind, and a similar but feeble irritability is supposed by Massart to be shown by *Spirillum undula*. Whether, as in the case of tendrils, the solid substratum directly exercises a contact-stimulus is not perfectly certain, since the Infusoria mentioned may also creep on the surface of the water[5]. The stoppage of movement in the cilia of *Chlamydomonas* produced by mechanical shocks is, however, comparable with the shock-movements of the leaves of *Mimosa pudica* in so far as both are irritable responses to stimuli, but whether still other special irritabilities may exist among these lower forms is an open question.

Wounding and injuries, however produced, always exert a certain influence on movement, and frequently an injury excites or causes an acceleration of protoplasmic streaming, and may also produce various traumatic aggregations of the cell-contents.

After a few observations by Frank and Velten, Keller and Hauptfleisch established the fact that the active streaming shown in sections often does not exist in the intact plant, but is produced, or accelerated when pre-existent, by the injury, and in part also by other stimuli[6]. Streaming is, for instance, absent from the intact leaves

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[1] Unger, Die Pflanze im Momente d. Thierwerdung, 1843, p. 67; Strasburger, Wirkung d. Lichts und d. Wärme auf Schwärmsporen, 1878, p. 6; Engelmann, Bot. Ztg., 1879, p. 55 footnote.

[2] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1884, Bd. I, p. 444; Massart, La sensibilité tactile chez les organismes inférieures, 1900 (extract from the Journal publié par la Soc. royale d. sci. méd. et nat. de Bruxelles).

[3] Pfeffer, Unters. a. d. bot. Inst. zu Tübingen, 1888, Bd. II, p. 618; Verworn, Psycho-physiolog. Protistenstudien, 1889, p. 90; Massart, l. c., 1900; Jennings, Journal of Physiology, 1897, Vol. XXI, p. 298; American Naturalist., 1901, Vol. XXXV, p. 372; Pütter, Archiv f. Anatomie u. Physiologie, physiolog. Abth., Supplement, 1900, p. 243.

[4] Bordet, Bull. de l'Acad. royale de Belgique, 1894, 3e sér., T. XXVII, p. 889. On the thigmotaxis of certain animal spermatozoids see Dewitz, Pflüger's Archiv f. Physiologie, 1886, Bd. XXXVIII, p. 358; Centralbl. f. Physiol., 1903, Bd. XVII, p. 89; Massart, Bull. de l'Acad. royale de Belgique, 1888, 3e sér., T. XV, Nr. 5; Buller, Quarterly Journal of Microscopical Science, 1902, Vol. XLVI, p. 145.

[5] Massart, l. c., p. 7. Massart concludes that the surface-tension film may act as a solid, and considers the accumulation of *Chromulina Woroniniana* at the surface to be the result of tactic stimulation. Even a very slight accumulation of minute solid or liquid floating particles at the surface would be able to exercise tactic stimulation.

[6] Frank, Jahrb. f. wiss. Bot., 1872, Bd. VIII, pp. 220, 292; Velten, Bot. Ztg., 1872, p. 672; I. Keller, Ueber Protoplasmaströmung im Pflanzenreich, 1890; P. Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 190; De Vries (Bot. Ztg., 1885, p. 1) from his observations on sections concluded that streaming was a much more common and normal occurrence than it actually is. The act

of *Vallisneria spiralis*, but soon appears in the leaf-cells when a section is watched under the microscope. It appears first near the point injured, and spreads for a short distance through the parenchyma, but for a longer distance when the vascular bundle is also affected. In such cases it may spread over the entire leaf, or even over all the leaves on the plant[1]. The leaf of *Elodea canadensis* responds similarly, except that streaming is often present in the intact leaf in the cells along the midrib, and here the streaming may be so accelerated that the chloroplastids are drawn into it and circulate round the cells. Usually the effect of the stimulus gradually passes away and the plant returns to its original condition. The same applies to the increased respiration and production of heat which, together with streaming, are all signs of the increased activity produced by an injury. Streaming is absent from certain cells under all conditions and whatever stimuli be applied, while in other cases streaming begins without any special external stimulus being required, and may then continue as in *Chara* and *Nitella* for the whole life of the cell[2].

Frank observed that even in the absence of streaming an injury might cause a marked change in the position of the chlorophyll bodies, and Tangl, Nestler, Němec, and Miehe[3] have shown that a cut or puncture causes, in a great variety of plants, a more or less pronounced movement and collection of the protoplasm and nucleus on the wall facing the injury. The time of reaction depends upon the plant and on the external conditions, but in roots it may, according to Němec, be shown in from a quarter to several hours, and spreads with decreasing intensity from 0·5 to 0·7 mm., according to Nestler, and even up to 1·3 mm., according to Němec, from the point of injury.

After the maximum reaction has been reached in a few hours or a few days, the aggregation is gradually redistributed. According to Němec, this takes place so rapidly in roots that the reaction has already ceased near to the injury by the time it has reached its maximum in the furthermost zones affected. A secondary change, consisting of the enlarging and fusion of the vacuoles, was then observed by Němec, but this spreads to a less distance than the primary reaction. Interesting as these movements are, however, they simply form another indication of the wound reaction, and do not give any insight into the causes of it.

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of preparation usually does not inhibit streaming or does so only temporarily. Kienitz-Gerloff's discussions (Bot. Ztg., 1893, p. 36) show an ignorance of the nature of irritability, and the same applies to I. Keller (l. c., p. 8), who considers streaming to be a purely pathological phenomenon.

[1] Hauptfleisch, l. c., p. 196; Kretschmar, Jahrb. f. wiss. Bot., 1903, Bd. XXXIX, p. 275; Ewart, Protoplasmic Streaming in Plants, 1903, p. 104. [All three authors observed a more rapid propagation longitudinally than transversely. Kretschmar observed a maximal rate of propagation in *Vallisneria* of 3 cm. per minute, whereas the average rate of propagation observed by Ewart (l.c., p. 105) in the leaf of *Elodea* was 1–3 mm. per minute at 30° C., and was barely more rapid in *Vallisneria*.]

[2] [On the reasons for the absence of streaming in certain cells, cf. Ewart, l. c., p. 29 seq. In small plant-cells diffusion from end to end is more rapid than streaming, whereas in large cells like those of *Chara and Nitella* in which streaming is an essential factor in continued life the protoplasm may stream several times round the cell during the time required for complete diffusion. Hence the importance of streaming in large cells: cf. Ewart, On the Ascent of Sap in Trees, Phil. Trans. of the Royal Society, 1905, p. 40.]

[3] Tangl, Sitzungsb. d. Wien. Akad., 1884, Bd. XC, Abth. i, p. 10; Nestler, Sitzungsb. d. Wien. Akad., 1898, Bd. CVII, Abth. i, p. 708; Němec, Die Reizleitung u. d. reizleitenden Structuren, 1901, p. 8; Miehe, Flora, 1901, p. 127.

SECTION 78. **Galvanotaxis.**

Electrical currents of no greater strength than those which normally circulate through plants do not influence streaming or locomotory movements. Since, however, strong currents act injuriously or even fatally, ones of moderate intensity might be expected to produce some physiological effect, such as the galvanotropic reaction of many motile organisms. Furthermore, a sudden increase or decrease in intensity, as on making or breaking the current, acts as a shock-stimulus, like a blow or sudden pressure. A single make or break shock is sufficient to stimulate the pulvinus of *Mimosa pudica*, whereas a series of successive shocks are required to produce a complete reaction in tendrils or in the leaflets of *Oxalis*. Electrical shocks produce the same effect in the plasmodia of Myxomycetes, and in cell-protoplasts, as do mechanical ones[1]. According to the properties of the organism and the intensity, frequency, and character of the stimulus, either an acceleration of retardation of movement, or a slight change of shape, or pronounced deformation may ensue. Furthermore, either electrical or mechanical shocks may cause cilia to contract or may decrease or accelerate their movement.

Electrical stimuli are especially of value in that their intensity and duration can be exactly measured, and in that they can be locally applied[2]. Since, however, their action in plants is merely that of shock-stimuli, no special detailed description of their mode of action is required[3]. Certain peculiarities, as compared with mechanical stimuli, are due to the fact that the action is strongly polar, and that local electrolytic actions due to the separation, sorting, or interaction of ions, may arise at every point where the current passes from one medium to a dissimilar one[4]. The physical differences between the make and break shocks naturally induce differences in their physiological action[5]. It is, however, possible that induction-shocks may exercise some special electrical influence in addition to their more mechanical action.

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[1] This similarity has been recently pointed out by E. Roesele (Zeitschrift f. allgem. Physiologie, 1902, Bd. II, p. 162) and by Ewart (On the Physics and Physiology of Protoplasmic Streaming in Plants, 1903, p. 88). For facts see Kühne, Untersuch. ü. d. Protoplasma, 1864, 1874, 1894; Engelmann, Handbuch d. Physiologie von Hermann, 1879, Bd. I, pp. 366, 403; Verworn, Psychophysiologische Protistenstudien, 1889, p. 110; Allgem. Physiologie, 3. Aufl., 1901, p. 431; Klemm, Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 647; G. Hörmann, Studien ü. d. Protoplasmaströmung bei d. Characeen, 1898, p. 60; and the literature quoted in these works.

[2] For methods see Nägeli u. Schwendener, Mikroskop, 2. Aufl., 1877, p. 462; Zimmermann, Mikroskop, 1895, p. 231; Roesele, l. c., p. 143. Also Biedermann, Elektrophysiologie, 1895; L. Hermann, Physiolog. Practicum, 1898.

[3] [The existence of a power of galvanotropic response to constant currents in plants hardly coincides with this assumption.]

[4] Cf. Ewart, l. c., pp. 95, 99, 123; Ewart and Bayliss, Proc. of Royal Society, Nov., 1905, p. 63.

[5] Cf. Verworn, Allgem. Physiologie, 3. Aufl., 1901, p. 431; Fr. Schenck, Pflüger's Archiv f. Physiologie, 1897, Bd. LXVI, pp. 257, &c. The action of make and break shocks is given here, as well as their relation to Pflüger's law, and the deviations from it.

The influence of constant currents on streaming shows no features of especial importance, apart from the fact that the direction of the current in no wise influences the direction of streaming, and produces no effect upon the relative velocity of opposed streams[1]. There is, however, a special physiological reaction, galvanotaxis, which may be termed positive or anodic, and negative or kathodic, according to whether the responding motile organisms wander towards the negative or positive electrodes. Galvanotaxis appears to be shown chiefly by Infusoria, Flagellatae, and Bacteria[2], and negative galvanotaxis appears to be commoner than positive. In some cases, a rise in the intensity of the currents converts a positive galvanotaxis into a negative one, while some forms exhibit transverse galvanotaxis.

Negative galvanotaxis is shown by *Paramaecium aurelia*, *P. bursaria*, *Coleps hirtus*, and all the ciliate Infusoria examined, with the exception of *Opalina ranarum*, which shows positive galvanotaxis with weak currents, but negative with stronger ones, according to Wallengren. Among the Flagellatae, Verworn found *Trachelomonas hispida*, *Peridinium tabulatum* to show negative, and *Polytoma uvella*, *Cryptomonas ovata* positive galvanotaxis, while *Chilomonas paramaecium* behaves like *Opalina ranarum*[3]. *Volvox aureus* shows negative galvanotaxis, according to Carlgren[4], and possibly other Volvocineae as well, although Verworn could detect no such irritability in *Euglena viridis*[5]. Certain bacteria do, however, appear to have a power of galvanotactic response[6], and, according to Verworn[7], Amoebae show negative galvanotaxis at about 25° C., while Schenck[8] has shown that at lower and higher temperatures the galvanotaxis becomes positive.

Transversal galvanotaxis is shown by the Infusorian *Spirostomum ambiguum*[9] and by *Oxytrichia* and *Stylonychia* while creeping on the substratum, whereas free-swimming individuals show negative galvanotaxis[10].

The chamber shown in Fig. 64 may be used to contain the organisms to be

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[1] Cf. Ewart, Protoplasmic Streaming in Plants, 1903, p. 100, and the works mentioned there.

[2] L. Hermann (Pflüger's Archiv f. Physiologie, 1885, Bd. XXXVII, p. 457; 1886, Bd. XXXIX, p. 414) first observed galvanotaxis in tadpoles, and the same irritability was detected in Infusoria and Flagellata by Verworn (Pflüger's Archiv f. Physiologie, 1889, Bd. XLV, p. 27; 1889, Bd. XLVI, p. 268; Psycho-physiologische Protistenstudien, 1889, p. 115; Allgemeine Physiologie, 3. Aufl., 1901, p. 476). See also V. Ludloff, Pflüger's Archiv f. Physiologie, 1895, Bd. LIX, p. 525; J. J. Loeb, ibid., 1896, Bd. LXV, p. 518; Jennings, Journal of Physiology, 1897, Vol. XXI, p. 305; Pütter, Archiv f. Anatom. u. Physiologie, physiol. Abth., Supplementband, 1900, p. 243; Wallengren, Zeitsch. f. allgem. Physiol., 1902, Bd. II, p. 341; 1903, Bd. III, p. 22.

[3] Cf. also Wallengren, l. c., p. 377.

[4] Carlgren, Centralbl. f. Physiol., 1900, Bd. XIV, p. 35.

[5] Verworn, l. c., 1889, p. 290. Diatoms have not yet been investigated.

[6] Verworn, l. c., 1889, p. 291; Chauveau, Compt. rend., 1896, T. CXXI, p. 892.

[7] Verworn, l. c., 1889, p. 272; Pflüger's Archiv f. Physiol., 1896, Bd. LXV, p. 47.

[8] Fr. Schenck, Pflüger's Archiv f. Physiol., 1897, Bd. LXVI, p. 253.

[9] Verworn, l. c., 1901, p. 480; Pflüger's Archiv, 1896, Bd. LXII.

[10] Pütter, l. c., p. 275.

tested. The current should be led in by non-polarizable electrodes[1], the brushes soaked in normal saline solution touching the porous sides of the cell. By reversing the commutator and changing the direction of the current, the reacting organisms will be caused to collect at the opposite electrode, and this may be repeated many times. The striking reaction shown by *Paramaecium* may be made visible to a large audience by means of a projection lantern[2]. If a current of from five to twenty volts is used, the best current strength is readily reached by adjusting the resistance. According to Ludloff, this lies between 0·1 to 0·6 of a milliampère in the case of *Paramaecium*, whereas with 0·06 of a milliampère the reaction is barely perceptible[3].

Little doubt can exist that we are here dealing with a physiological movement due to stimulation, and that the movement is not the direct result of the kataphoric action of the electrical current. That strong currents may exercise such an action is certain, but nevertheless, it is not possible to agree with Birukoff and Pearl in ascribing the movements to the direct action of the current[4]. For instance, using a mixture of species, the positively galvanotactic forms will move towards the anode, the negatively galvanotactic forms towards the kathode, while dead individuals do not move at all.

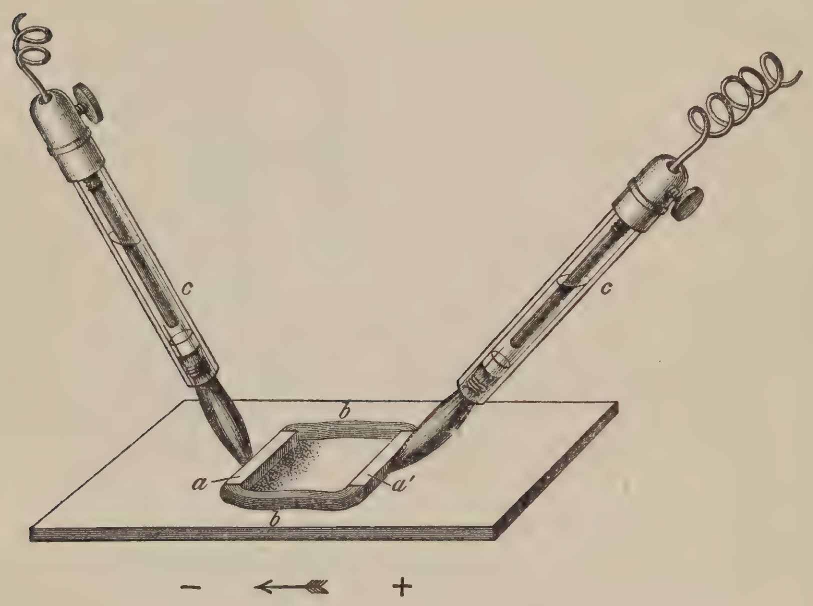

FIG. 64. Apparatus to show galvanotaxis. The non-polarizable electrodes *c* are applied to the bars of porous porcelain ('biscuit'). These are joined at *b b* by bars of wax-colophonium mixture. The water in the cell contains the negatively galvanotactic *Paramaecium aurelia* which moves towards the kathode.

Infusoria and Flagellatae show a typical tactic reaction, that is, they orient themselves in regard to the direction of the current by presenting the front end towards either the kathode or anode, and always swimming with the same end first. At the same time, the movement may either be

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[1] On non-polarizable electrodes cf. Biedermann, l. c., p. 150; Hermann, l. c., p. 29; Cyon, Methoden d. physiolog. Experimente, 1876, p. 386.

[2] Pfeffer, Jahrb. f. wiss. Bot., 1900, Bd. XXXV, p. 719.

[3] [The current density within the cell, which in the case of a uniform conductor depends upon the area of cross-section and upon the current strength, requires consideration.]

[4] Birukoff, Pflüger's Archiv f. Physiologie, 1899, Bd. LXXVII, p. 555; Pearl, American Journal of Physiology, 1900, Vol. IV, p. 96. See also Pütter, Archiv f. Anatomie u. Physiologie, 1900, Supplementband, p. 299.

accelerated or retarded by a direct or indirect action of the electric current[1]. Since the orientation is unaltered so long as the current remains constant, it is evidently due to the stimulus exercised by the current, and not to any transitory shock-effect. Possibly, however, organisms may be found to show orienting movements under the action of induction-shocks, and it has still to be determined whether certain Bacteria and other organisms can show a phobo-galvanic response.

The conversion of positive into negative galvanotaxis produced by an increase in the strength of the current is due to a reversal of the polar orientation, just as in the reversal of phototaxis by increasing intensity of light. In both cases the tropic stimulus so modifies the movement of the cilia as to cause the organisms to turn in a particular direction, and then to swim continually in this direction. This applies whether the organism has a single flagellum, or a tuft of cilia at one end, or whether it is covered all over by numerous similar or dissimilar cilia. According to Ludloff[2], the galvanotactic orientation of *Paramaecium* is correlated with a dissimilar action upon the ciliary movement at the two ends. Similarly, Wallengren[3] concludes that it is owing to the cilia on different regions of the body being unequally affected that *Opalina ranarum* shows negative instead of positive galvanotaxis when the current increases beyond a certain intensity. *Paramaecium aurelia* swims hinder end first in a 0·4 to 0·7 per cent. solution of sodium chloride; and, according to Loeb, this causes the organism to show positive instead of negative galvanotaxis, although the body is oriented in the same way as in water[4].

These observations leave it uncertain whether the cilia are directly or indirectly affected[5], nor do they give any insight of the mode of perception. Separate ciliated fragments of Infusoria move in the same way as the intact organism, and in the case of *Bursaria truncatella*, show the same galvanotactic responses[6]. Hence it appears that individual cilia and groups of cilia have a considerable degree of independence, and are in themselves individually responsive to galvanotropic stimuli. It is not, however, certain whether the galvanotactic movement of Amoebae carried out by the protrusion and retraction of pseudopodia is a physiological reaction or is

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[1] Verworn, Pflüger's Archiv f. Physiologie, 1889, Bd. XLVI, p. 280; Ludloff, l. c., p. 544; Wallengren, l. c., p. 369.

[2] Ludloff, l. c., p. 552.

[3] H. Wallengren, l. c., pp. 375, 381. More varied results may be obtained when the organism possesses dissimilar cilia which react differently.

[4] J. J. Loeb, Pflüger's Archiv f. Physiologie, 1897, Bd. LXVI, p. 352. Pütter (l. c., p. 297) finds that the backward movement ceases as the organisms become accommodated to the salt-solution.

[5] On the unequal sensitivity of dissimilar cilia cf. Verworn, Pütter, and Wallengren. E. Roesele (Zeitschr. f. allgem. Physiologie, 1902, Bd. II, p. 164) states that the mouth opening near to the basis of the cilia possesses the greatest sensitivity to induction-shocks and to mechanical stimuli in *Stentor* and *Vorticella*.

[6] Verworn, 1889, l. c., p. 293.

merely due to the fact that the polar electrolytic action of the electrical current causes the surface-tension to be lowered on the side towards which movement occurs, or raises it on the opposite side[1].

Theoretical. It seems probable that the first stage in perception is due to the electrolytic decomposition, and the sorting of the ions set up by the electrical current. If the organisms are in *pure* water[2], changes of this kind can only go on internally, whereas in saline media all the conditions for chemotropic stimulation will be produced. The protoplast may possibly not be permeable to all ions, so that local accumulations of them might be produced[3]. It is not, however, possible to say whether the separated anions and kations may act like externally applied chemicals[4], or whether the partial or unequal dissociation at different points in the protoplast may act as a tropic stimulus.

Loeb[5] concludes that the galvanotropic stimulus is directly due to the impact of the negative and positive ions on the organism as they travel to anode and kathode. Loeb finds that the local action of acids and alkalies produces similar deformations to those caused by electric currents, but forgets that the stimulating action of a reagent does not necessarily remain the same when it is applied in concentrated form. Furthermore, Pütter[6] has shown that the action of a strong galvanic current is not the same as that of acids and alkalies.

SECTION 79. **Cytotaxis.**

By negative cytotaxis is denoted the tendency of organisms or parts of organisms to separate from each other, by positive cytotaxis their tendency to approach[7], but the terms give no direct indication of the ways and means by which such phenomena are brought about. In some cases tropic stimuli come into play, as when an excreted substance exerts a chemotropic action, such as is shown during the attraction of certain antherozoids to the ova. Individuals of the same species of Infusoria and also of Bacteria may exert tropic stimuli on each other by means of their excreta. The attraction of aerotactic Bacteria to an assimilating algal cell

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[1] Cf. Verworn, Pflüger's Archiv f. Physiol., 1889, Bd. XLVI; Schenck, ibid., 1897, Bd. LXVI.

[2] [Practically an impossibility owing to exudation from the organisms. The resistance of pure water is so high ($3{\cdot}4 \times 10^5$ ohms. per c.c. at 11° C.) that a considerable increase of voltage would be necessary, and the water would rapidly become overheated.]

[3] That electrolysis may cause the culture-fluid to become poisonous is well known.

[4] Cf. Nernst, Nachricht. d. Ges. d. Wiss. zu Göttingen, 1899, p. 104; Ewart and Bayliss, Proc. of the Royal Society, 1905, p. 63.

[5] Loeb, Pflüger's Archiv f. Physiol., 1897, Bd. LXV, p. 518. See also H. H. Dale, Centralbl. f. Physiol., 1901, Bd. XV, p. 303.

[6] Pütter, Archiv f. Anat. u. Physiol., Supplementband, 1900, p. 294.

[7] Roux, Archiv f. Entwickelungsmechanik, 1894, Bd. I, pp. 57, 200; Programm und Forschungsmethoden d. Entwickelungsmechanik, 1897, p. 10.

is also an instance of chemotropic cytotaxis, and if sensitive *Spirillum* forms are used these collect a little distance away from the cell. Chemotropic cytotaxis is probably also involved in the attraction of the pollen-tube to the embryo-sac, as well as in the penetration of a host by the hyphae of a parasitic fungus, and in the formation of Lichens.

In some cases osmotropic, thigmotropic, and even also hydrotropic stimuli may be used for purposes of physiological interaction, whereas thermal, galvanic and photic stimuli are of little or no value in this respect [1]. Thus few plants are luminous, and the electric currents and differences of temperature due to vital activity are so trifling as to be unable to exert any appreciable tropic stimulation. Reflected rays, or local heating due to external radiation, may, of course, exercise some effect, but these are not within the control of the plant. Thigmotropic reactions, on the other hand, are responsible for the attraction and fusion of the sperm and ovum of *Fucus*, as well as for the coiling of tendrils round each other.

The stimuli may either act across short distances, or only when the cells are in contact—in the former case attraction being ensured, while in the latter case accidental contact is made permanent. Small objects may be brought together by surface-tension forces, and also repelled from one another without their possessing any special motile organs. In such cases we have a purely physical movement produced in the same way as when an oil-drop comes into contact with a soap-solution on one side. The movement is only physiological in the sense that metabolism causes the production of the substances responsible for the modifications of surface-tension. According to Roux [2], it is by a physiochemical action of this kind that the separated fragments of a frog's egg creep together again. The plasmodial aggregation of the Myxamoebae of Acrasieae may be brought about in the same way; but, since the Myxamoebae have a power of independent movement, it seems more probable that we have here another instance of physiological chemotaxis. The fact that the aggregation ceases under certain conditions shows nothing, for it might be due to a cessation of the secretory activity on which the changes of surface-tension and the chemotaxis might alike be dependent.

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[1] A regular arrangement may also arise from purely mechanical causes.

[2] Roux, Archiv f. Entwickelungsmechanik, 1894, p. 43; Rhumbler, Biolog. Centralbl., 1898, Bd. XVIII, p. 22; Ergebnisse d. Anat. u. Entwick. von Merkel und Bonnet, 1898, Bd. VIII, p. 587.

CHAPTER V

THE PRODUCTION OF HEAT, LIGHT, AND ELECTRICITY

PART I

THE PRODUCTION OF HEAT

SECTION 80. **General.**

PLANTS are poikilothermic organisms which assume approximately the temperature of the surrounding medium owing to their relatively feeble powers of heat-production and their excessive loss of heat by radiation and transpiration. According to whether the former or latter preponderate, the temperature will be slightly above or slightly below that of the surrounding medium.

Since the heat is produced by respiration, less will be formed by the more feeble intramolecular respiration than by normal aerobic respiration. In the case of anaerobes, however, the pronounced decompositions they excite may be accompanied by a considerable liberation of chemical energy in the form of heat. Many plants respire actively, and Fungi and Bacteria have four to one hundred times the respiratory activity of mammals, so that such organisms may produce relatively more heat even than birds. Owing to their extensive surface area, and the usual presence of so much dead tissue, most plants, even when transpiration is reduced to a minimum, become hardly at all or only 0·3° C. warmer than the surrounding saturated air. In dry air the transpiration usually keeps the temperature of the plant slightly below that of the air. In fleshy actively transpiring bodies such as the spadix of Aroids a pronounced rise of temperature is shown, whereas in tubers, in the trunks of trees and in most thick organs respiration is relatively feeble and the rise of temperature is usually less than in thinner but more actively respiring organs. Most Fungi and Bacteria expose a large surface to the air, and if grown under water the heat produced is naturally conveyed away still more rapidly[1].

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[1] [The sporophores of *Agaricus*, *Boletus*, and *Lycoperdon* (*Scleroderma*) also form good material, the thermometer being placed in a hole bored in the sporophore while young, and the whole as well as the control thermometer being enclosed in cotton-wool. Similarly, vigorous broth-cultures of bacteria, if aerated and then corked after the introduction of a thermometer, show a temperature from 0·1 to 0·4 C. higher than that registered by a similar thermometer placed in a corresponding tube containing sterile broth, both tubes being surrounded by cotton-wool. Since the specific heat of water is high, this slight rise of temperature represents a considerable production of heat.]

Although metabolism may involve exothermal as well as endothermal chemical changes, these appear to balance approximately, the heat produced being derived almost solely from respiration. The swelling of dry seeds does, however, produce a distinct temporary rise of temperature, and the rapid commencement of respiration in the moistened seeds produces a secondary rise[1].

Even when the living cells respire actively, organs containing a large amount of dead tissue can never be much warmed. In the cell itself only the protoplasm is active, and the production of heat in it must often be great enough to produce an injurious or even fatal rise of temperature, were it not for the rapid removal of heat by the surrounding water[2]. Similarly the temperature of the most actively respiring Bacteria cannot be appreciably higher than that of a fluid medium in which it is growing.

The curves of respiration and heat-production are approximately parallel when plants are exposed to varying conditions in saturated air. For instance, after an injury respiration and heat-production attain a maximum at about the same time. Changes of temperature affect respiration and heat-production in corresponding degree, and as far as is known continued rises of temperature produce increasing differences between the temperature of the plant and that of the surrounding medium until the fatal limit is reached. Otherwise the temperature of the plant closely follows that of the surrounding medium, and hence plants appear to have no power of regulating their temperature like mammals by either increasing the production of heat or diminishing the loss of it. The cooling effect of transpiration may prevent the plant from being excessively heated by insolation, but this is a purely accessory physical effect, and as far as any physiological regulation comes into play this is concerned solely in preventing a fatal loss of water. Hence the transpiration from an exposed leaf may be checked just when its cooling effect is most needed, the plant sacrificing the exposed organ rather than risk its whole existence. The protective movements of certain leaves do actually involve a temporary increase of transpiration, but usually the movement is such as to reduce not only the transpiration but also the exposure to the radiant energy of the sun[3].

Poikilotherms have this advantage over homoiotherms, that their body temperature may vary within wide limits without danger to life. On the other hand, homoiotherms, if well nourished, may remain active at low temperatures which suppress the activity of poikilotherms more or less completely. The latter, however, avoid the waste of energy involved in maintaining a high body-temperature.

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[1] Wiesner, Versuchsstationen, 1872, Bd. XV, p. 138.

[2] Engelmann, Bot. Ztg., 1888, p. 713.

[3] Cf. Ewart, The Effects of Tropical Insolation, Annals of Botany, Vol. II, 1897, pp. 450, 457, 459.

Plants are able to grow when their temperature is, owing to transpiration, kept permanently below that of the surrounding medium, and their growth is not appreciably affected by their own production of heat. The latter is therefore merely an accessory result of metabolism, and has no special economic value, but merely indicates a more or less pronounced preponderance of exothermic chemical changes. The heat-vibrations produced in this way in the interior of the protoplast may, however, have quite a different value and importance to the heat derived from without.

In certain cases a rise of temperature may be of definite advantage to the plant. For instance, the warmth of the spadix of an Aroid may aid in the rapid development of the pollen, and also in attracting pollen-carrying insects[1]. Furthermore, the production of heat enables feeble transpiration to continue in air saturated with moisture, and hence may aid in preventing the injection of the intercellular spaces with sap. No protection against frost is possible, however, since respiration and the production of heat entirely or almost entirely cease as the temperature sinks below zero centigrade[2]. On the other hand, the increasing production of heat with rising temperature instead of being advantageous may cause the plant to be more rapidly fatally affected.

Owing to their relatively less surface, fleshy or bulky organs are appreciably warmed by a smaller production of heat than thin membranous ones. The aggregation of different parts as well as the provision of hairy or non-conducting coverings by lessening the loss of heat will cause the temperature to rise. In fact a heap of living respiring plants in saturated air will always show a temperature appreciably higher than that of the surrounding air. Furthermore, the rise of temperature in the interior will excite more active respiration if the aeration is sufficiently rapid. The heating of the heaped grass cut from a lawn, as well as of imperfectly dried hay in hay-ricks, is in the first instance due to the plants' own warmth, although the subsequent more pronounced heating is largely due to the rapid development of micro-organisms at the raised temperature.

The actual amount of heat produced by a plant can only be determined by calorimetric measurement, but such estimations give no idea as to the exothermic and endothermic chemical changes which may go in the plant[3]. Even when such substances as starch or sugar form the main material con-

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[1] Cf. Ludwig, Biologie, 1896, p. 261; G. Kraus, Die Blüthenwärme bei *Arum italicum*, 1882, p. 20 (reprint from Abhandlg. d. naturf. Ges. zu Halle, Bd. 16); Ann. d. Jard. bot. de Buitenzorg, 1896, T. XIII, p. 271).

[2] Seignette (Revue générale de Bot., 1889, T. I, p. 614) observed in the case of bulbs and tubers a greater difference of temperature at −6° C. than at 3° C. and 11° C., but this was probably due to special causes. Cf. H. Dixon, Transact. of the Irish Academy, 1903, T. XXXII, Part III, p. 145.

[3] Cf. Pfeffer, Studien zur Energetik, 1892, p. 189; Ostwald, Lehrb. d. allgem. Chemie, 2. Aufl., 1893, Bd. II, p. 1.

sumed in respiration other substances may also be oxidized, and in addition to carbonic dioxide and water other substances may be formed in variable amount with different or in some cases unknown caloric equivalents. The production of carbon dioxide and absorption of oxygen does not, therefore, form a sure guide as to the amount of chemical energy liberated, and hence we are unable to decide how much of this energy is set free in the form of heat and how much appears as mechanical work.

Rodewald[1] found that in such resting organs as ripe apples and the swollen stems of the cabbage turnip (Kohlrabi) the amount of heat produced represented practically the whole of the energy of respiration, as determined from the production of carbon dioxide and absorption of oxygen, and assuming that these represented so much completely oxidized carbohydrate material. According to Bonnier[2], however, seedlings of the Pea liberate more heat than is represented by their respiratory activity. During later stages of development the difference is lessened, and during flowering the actual liberation of heat becomes less than the theoretical values.

Bonnier suggests that during germination, in addition to respiration, other chemical changes and dissociations of exothermic character occur in abundance, while at a later date, especially during the storage of reserve-materials, endothermic condensations and polymerizations take place which involve an absorption and storage of heat. The respiratory quotient $\left(\frac{CO_2}{O_2}\right)$ is actually less than unity during germination, especially in the case of oily seeds, but the subject is worthy of further investigation. In any case the difference between the actual and estimated production of heat is not due to the work done during growth, since the excess of the actual production of heat over the theoretical amount is greatest during the period when growth is most active. Furthermore the mechanical equivalent of heat is very high, so that a small absorption of heat would represent an enormous amount of work. Ewart has, for instance, shown that the work done in maintaining streaming in a large cell of *Nitella* for a year represents the heat produced by the complete combustion of $\frac{1}{200000}$ of a gram of cane-sugar, the work done being 252 ergs per day. In smaller cells more energy is consumed in streaming, but even then the work done is insignificant compared with the heat produced by respiration[3].

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[1] Rodewald, Jahrb. f. wiss. Bot., 1888, Bd. XIX, p. 291; 1887, Bd. XVIII, p. 342.

[2] Bonnier, Ann. d. sci. nat., 1893, 7e sér., T. XVIII, p. 1; Bull. de la Soc. bot. de France, 1880, T. XXVII, p. 141.

[3] Ewart, Protoplasmic Streaming in Plants, 1903, p. 27. [1 gram-calorie is the amount of heat required to raise a gram of water 1° C. in temperature, a kilogram-calorie the amount needed to raise a kilogram 1° C. If the expansion of water were uniform the value of the calorie would be the same at all temperatures, and this is practically the case between 4° C. and 100° C. As regards the mechanical equivalent of heat 1 gram-calorie represents 42,350 gram-centimetres, or $4{\cdot}17 \times 10^7$ ergs

In an experiment with germinating Barley carried out at 16°C., each kilogram weight produced per hour 3·72 kilogram-calories[1]. The respiratory quotient was 0·65, and the heat-production estimated from the liberation of carbon dioxide was 1·74 kg.-cal., from the absorption of oxygen 2·7 kg.-cal. For the ripening ears the respiratory quotient was 1·05, the heat produced 0·24 kg.-cal., and the estimated amount both from the consumption of oxygen and the evolution of carbon dioxide 0·3 kg.-cal.

Both the respiratory activity and the production of heat attain a maximum during germination, and subsequently gradually fall. An adult man produces per kilogram per hour about 1·4 kg.-cal., but a puppy as much as 6·4—so that the production of heat in seedling plants is quite comparable with that in animals.

Few experimental researches on heat-production have been performed, but these suffice to show its dependence upon the respiratory activity, and in fact the more readily followed changes in the heat-production can be used to trace the wound-reaction in place of the respiratory changes. Under constant conditions as regards the external loss of heat a change of temperature must always indicate an alteration in the vital activity, involving an increase or decrease in the exothermic or endothermic metabolism.

Methods. The warmth of the spadix of certain Aroids can either be felt or shown by pressing a thermometer with a small bulb against the object. Germinating seeds, or flowers of Rhubarb or Chamomile, may be placed in a vessel as in Fig. 65, through which a stream of air or of hydrogen saturated with moisture can be drawn[2]. In the absence of oxygen the rise of temperature decreases to a minimum[3]. For comparison a similar vessel should be used containing seeds killed by steaming. If a large mass of germinating seeds is merely placed in a large beaker and covered with a bell-jar, a rise of temperature of a few degrees may be shown, and if the experiment is carried on in a large calorimeter, or if the whole vessel is surrounded by cotton-wool, the temperature may be over 10°C. higher than that of the control. In some cases the rise is so high as to kill the seedlings, and if in that case *Aspergillus fumigatus* or other thermophile organisms develop the temperature may rise to over 60° C.[4]

To detect the slight warming of single organs thermo-electric methods were employed by van Beek and Bergsma, by Dutrochet, and by various subsequent authors[5].

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of work. The heat of combustion of fats is greater than that of carbo-hydrates. Thus 1 gram of glycerine produces 4,200 gram-calories; starch and cellulose, 4,100; cane-sugar, 4,000; lactose, 3,900; dextrose, 3,700; albumen, 5,000 to 6,000; fat, about 9,000 calories, when burnt into carbon dioxide and water. Cf. Landolt and Börnstein, Physikalisch-chemische Tabellen.]

[1] Bonnier's results are given in terms of one hour.

[2] This method of heaping seedlings, &c., together to show the evolution of heat was first used by Göppert, Ueber Wärmeentwickelung in den lebenden Pflanzen, 1832, p. 10.

[3] See Eriksson, Unters. a. d. bot. Inst. zu Tübingen, 1881, Bd. 1, p. 105.

[4] Cohn, Schlesische Ges. für vaterländ. Cultur, 1888, p. 150; Ber. d. bot. Ges., 1893, General-vers., p. 66.

[5] Van Beek und Bergsma, Observations thermo-électriques s. l'élévation de la température des fleurs de *Colocasia*, 1838; Dutrochet, Ann. d. sci. nat., 1839, 2^e^ sér., T. XII, p. 77; 1840, 2^e^ sér.,

A copper or German-silver wire (*e*, Fig. 66) is smelted to two iron wires (*m*, *n*). The tips, covered with shellac, are embedded, one in the living shoots, the other in a dead one (*d*) held up by a thread (*s*). The whole is covered with a bell-jar, and the current measured by means of a reflecting galvanometer. In this way a difference of temperature of $\frac{1}{500}$°C. can be detected and the temperature at different points on the same plant can be compared.

For quantitative experiments various forms of calorimeters may be used, of which several have been especially adapted for animal physiology[1]. Rodewald determined the absolute temperature thermo-electrically, and then estimated from this the amount of heat required to balance radiation and transpiration. This method is, however, liable to lead to serious error owing to the difficulty of control.

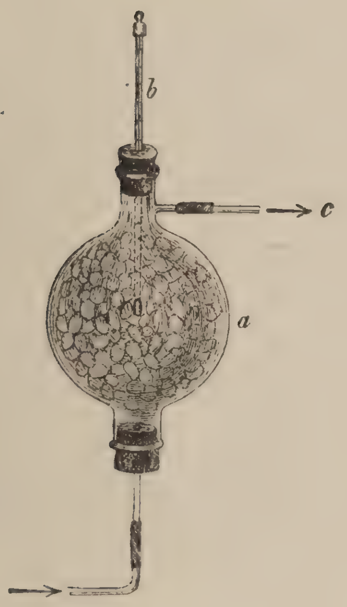

FIG. 65. Apparatus for showing the influence of oxygen upon the production of heat: (*a*) contains the germinating seeds; (*b*) thermometer; gases can be drawn through at (*c*).

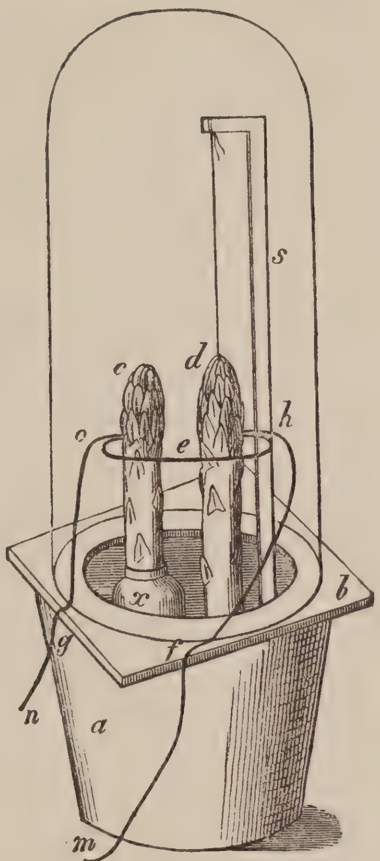

FIG. 66. Apparatus for thermo-electric measurement of temperature: (*c*) living, (*d*) dead shoot; (*e*) German-silver wire; (*m* and *n*) iron wire; at *o* and *e* the thermo-electric junctions are inserted in the shoots.

The difference between the heat of combustion of the seed and of the dried seedling grown in darkness gives approximately the amount of heat liberated during

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T. XIII, p. 5; Rodewald, l. c., 1887, p. 276; 1888, p. 221; Seignette, Rev. gén. de Bot., 1889, T. I, p. 574; Richards, Annals of Botany, 1897, Vol. XI, p. 31. On methods see also Cyon, Methoden der physiologischen Experimente, 1876, p. 484; Hermann, Handbuch d. Physiologie, 1882, Bd. IV, T. II, p. 305. The bolometric method has not yet been used for determining temperature in plant physiology.

[1] See Rubner, Die calorimetrische Methodik, 1891; Traité de physique biologique, publié p d'Arsonval, &c., 1901, p. 804.

development[1], but the method is naturally not a particularly accurate one even for comparative experiments. The amount of transpiration in saturated air forms a still more unsatisfactory measure of the production of heat.

SECTION 81. **The Evolution of Heat by Aerobes.**

Lamarck was the first to observe the production of heat by the spadix of *Arum italicum*[2], and in the case of this plant as well as in that of *Arum maculatum* a delicate thermometer may show a temperature 6° or 10° C. above the surrounding air when applied to the upper free sterile portion of the spadix. A difference of 17·6° C. has even been observed in the case of *Arum italicum*, and G. Kraus[3] obtained a rise of temperature of 27° C. by grouping five spadices around a thermometer, and a rise of 35·9° C., when the whole was covered by a cloth. In the last case the temperature of the air was 15·4° C., and of the spadix 51·3° C., a temperature which could hardly be sustained for any length of time without injury. A similar rise of temperature was observed long ago by Huber[4] in the spadix of *Arum cordifolium* (*Colocasia odora*), and apparently all spadices are able to raise their temperatures to a greater or less extent.

Apparently this specially active production of heat is shown only during flowering. In the case of *Arum italicum* and *A. maculatum* it begins during the opening of the spathe, increases for three or four hours, remains constant for the next one or two hours, and then decreases to a minimum in the course of a few hours. In other plants and aroids the rise of temperature is repeated at intervals, and the single period of the two plants mentioned may begin at any time of the day, but usually attains a maximum between 6 and 9 p.m., since the spathe commonly opens in the afternoon or early evening.

Dutrochet observed a rise of temperature in the sterile portion of 8·20° C., in the region of the male flowers of 4·9° C., and in the zone of female flowers of 1·4° C.[5]

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[1] Cf. Wilsing, Jahresb. d. Agrikulturchemie, 1884, p. 118.

[2] Lamarck, Flore française, 1778, T. III, p. 538; Senebier, Physiol. végétale, 1800, T. III, p. 314; Huber, Journal de physique, 1804, T. LIX, p. 281; Göppert, Ueber Wärmeentwickelung i. d. lebenden Pflanzen, 1832, p. 25; Vrolik and de Vriese, Ann. d. sci. nat., 1836, 2^e sér., T. V, p. 142; 1839, 2^e sér., T. XI, p. 77; van Beek and Bergsma, Observations thermo-électriques sur l'élévation de la tempér. des fleurs de *Colocasia odora*, 1838; Dutrochet, Ann. d. sci. nat., 1840, 2^e sér., T. XIII, p. 65; Brongniart, Nouv. Ann. du Musée d'histoire nat., 1843, T. III, p. 153; Garreau, Ann. de sci. nat., 1851, 3^e sér., T. XVI, p. 255; Romer, Mittheil. d. naturwiss. Vereins von Neu-Vorpommern u. Rügen, 1870, p. 51; Hoppe, Nova Acta d. Leopold. Carol. Akad., 1879–80, Bd. XLI, p. 199; G. Kraus, Ueber die Blüthenwärme bei *Arum italicum*, Bd. I, 1882; Bd. II, 1884 (reprint from Abhandl. d. naturf. Ges. zu Halle, Bd. XVI); Ann. du Jard. bot. de Buitenzorg, 1896, T. XIII, p. 217; Passerini, Nuov. giornale bot. italiano, 1901, T. VIII, p. 64.

[3] G. Kraus, l. c., 1882, p. 12; 1884, p. 79.

[4] Huber, l. c. Cf. G. Kraus, l. c., 1882, p. 12.

[5] Kraus could detect no rise of temperature in the female flowers by means of a thermometer, but Dutrochet succeeded in this by using a thermo-electric needle. Kraus denies the recurrence of warming observed in *Arum italicum* by a few observers, and also shows that there is no evidence to indicate whether the central or peripheral tissues produce most heat.

Other aroids may show differences, and the fact that the maximum temperature is not attained in all parts at the same time makes certain divergences in the observations of different workers comprehensible.

A rise of temperature of 5° or even of 10° C. has been observed in open air on the inflorescences of a few Cycads[1] and Palms[2], as well as in the flowers of *Nelumbo nucifera*[3] and *Victoria regia*[4]. This applies more especially to the stamens in the latter case, which in general appear to become warmer than the carpels. Thus Saussure[5] observed a rise of temperature of from 4° to 5° C. in the male flowers of *Cucurbita*, but of only 3° C. in the female ones. In open slender flowers and inflorescences the rise of temperature is usually trifling, but is often more pronounced than in the foliage-leaves. Flowers commonly respire relatively more actively than foliage-leaves, and at the period of opening both the respiration and the production of heat increase[6].

Vegetative organs rarely show any pronounced production of heat. Thus Dutrochet[7] observed a maximal rise of temperature of 0·34° C. (shoots of *Euphorbia lathyris*) under the most favourable conditions, while the rise was usually below 0·1° C. In many shoots, rhizomes, ripe fruits, and other organs no rise of temperature at all could be directly detected[8]. The fact that when heaped together all plant organs show a rise of temperature shows that all living parts are able to produce heat. When transpiration was allowed Dutrochet often observed a fall of temperature of 0·5° C. below that of the surrounding air, while when the shoot was killed the fall was at first still more pronounced, owing to the fact that the immediate effect of death upon a suddenly-killed turgid organ is to hasten the rate of transpiration.

In aerobes almost the whole of the heat is derived from aerobic

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[1] G. Kraus, Abhandl. der naturf. Ges. zu Halle, 1896, p. 218. The earlier observations are quoted here.

[2] G. Kraus, l. c., 1896, p. 251.

[3] K. Miyake, Physiological observations on *Nelumbo nucifera*, 1898, p. 18 (reprint from the Botanical Magazine, Tokyo, Vol. XII).

[4] Caspary, Flora, 1856, p. 218; E. Knoch, Bibliotheca botanica, 1899, Heft lxxvii, p. 44. Bory de St. Vincent (Journal de physique, 1804, p. 289) states that the flowers of *Pandanus utilis* and of Cannaceae become in some cases warm enough to melt cocoa-butter.

[5] Saussure, Ann. de chim. et de phys., 1822, Bd. XXI, p. 296. The temperature of these and other flowers was measured by a kind of air-thermometer. A few observations on the flowers of *Cactus* and *Pancratium* are given by C. H. Schulz, Die Natur d. lebendigen Pflanze, 1828, p. 185.

[6] Dutrochet (l. c., 1840, p. 81) observed a rise of temperature when the thermo-electric needle was plunged in the ovary of the Rose, *Papaver somniferum* and *Paeonia officinalis*, when flower-buds were examined in saturated air.

[7] Dutrochet, Ann. d. sci. nat., 1840, 2^e sér., T. XIII, p. 44. Dutrochet and MacNab (Bot. Ztg., 1873, p. 560) give observations on *Agaricus*, *Boletus*, and *Lycoperdon*.

[8] A slight rise of temperature was observed in tubers by Seignette, Rev. gén. de Bot., 1889, T. I, p. 573. See also Dixon, Trans. of the Irish Academy, 1903, Vol. XXXII, iii, p. 145.

respiration, and Vrolik and de Vries, as well as other authors[1], state that it ceased when the plants were placed in nitrogen or hydrogen. The intramolecular respiration of aerobes sets free so little heat that special methods are required to detect it[2]. Saussure[3] indeed observed that the spadix of an aroid absorbs oxygen most rapidly when it is producing most heat, and that the spathe which barely warms at all consumes but little oxygen. Saussure[4], Dutrochet, and Wiesner[5] have also shown that in general the most active respiration occurs during the period of most active heat-production, and Bonnier's[6] quantitative estimations of the respiration and heat-production of seedlings lead to the same conclusion. An exact correspondence between the curves showing the respiratory activity and the production of heat is hardly to be expected, and the divergences will be still greater between the respiratory curve and that showing the excess of temperature above the surrounding medium, since the amount of excess is influenced by various factors.

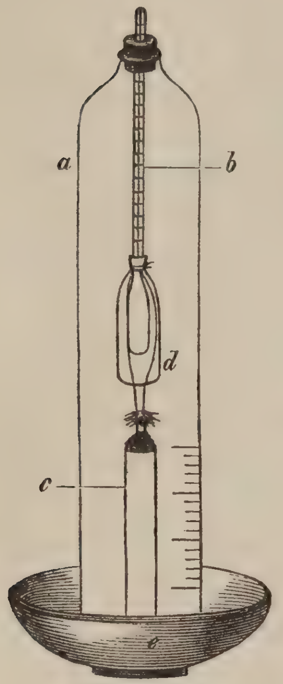

FIG. 67. Garreau's apparatus to show the relation between the respiration and the production of heat by the spadix of *Arum italicum*: (*a*) bell-jar, (*b*) thermometer, (*c*) support for spadix.

The table given on p. 375 was compiled by Garreau from observations upon *Arum italicum*. The spadix was enclosed in a narrow graduated cylinder, and the thermometer laid against it surrounded by muslin (*d*). The inner walls of the bell-jar were smeared with potash, the rise of water in the bell-jar giving the consumption of oxygen. During the first six hours, with an air temperature of 16°C., 470 c.c. of oxygen were consumed, but only 300 during the following eighteen hours, when the spadix was producing but little heat. Kraus[7] has shown that during this period of active respiration the dry-weight may decrease by seventy-five per cent. in a few hours.

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[1] Vrolik u. de Vries, Ann. d. sci. nat., 1839, 2e sér., T. XI, p. 79. A cessation of the production of heat by the inflorescence of *Colocasia odora* was observed by Huber (Journal de physique, 1804, T. LIX, p. 284) after smearing it with oil, and similar observations were made by G. Kraus, l. c., 1884, p. 60.

[2] J. Eriksson, Unters. a. d. bot. Inst. zu Tübingen, 1881, Bd. I, p. 105; G. Kraus, l. c., 1884, p. 61.

[3] Saussure, Ann. de chim. et de phys., 1822, T. XXI, p. 283. Dutrochet (l. c., 1840, p. 6) also considered the heat to be produced by respiration. See also Garreau, Ann. d. sci. nat., 1851, 3e sér., T. XVI, p. 250.

[4] Saussure, Mémoires de Genève, 1833, T. VI, pp. 251, 558.

[5] Wiesner, Versuchsstationen, 1872, Bd. XV, p. 155.

[6] Bonnier, Ann. d. sci. nat., 1893, 7e sér., T. XVIII, p. 33.

[7] G. Kraus, Abhandl. der naturf. Ges. zu Halle, 1884, pp. 9, 67; l. c., 1896, p. 271. See also Knoch, l. c., 1899, p. 52.

Time.	Excess of temperature of spadix.	Average excess per hour.	Oxygen consumed in c.cm.	Oxygen consumed, measured in volumes of the spadix.
4 p.m.	2·5°C.			
		3·5°C.	45	10·0
5 p.m.	4·5 "			
		6·1 "	70	15·5
6 p.m.	7·7 "			
		8·6 "	95	21·1
7 p.m.	9·5 "			
		10·5 "	140	31·1
8 p.m.	11·5 "			
		10·0 "	85	18·9
9 p.m.	8·5 "			
		5·7 "	35	7·7
10 p.m.	3·0 "			

Presumably every influence acting on respiration will be reflected in the production of heat, and it has in fact been observed that at lower temperatures the excess of temperature over that of the surrounding air decreases[1]. Bonnier also found that seedlings of *Triticum* produced per kilogram per hour 2·1 kilogram-calories at 15·8° C., and 0·18 kilogram-calorie at 5·7° C. It appears further that the production of heat, like the respiratory activity, rises with increasing temperature until death ensues; and in fact the spadices of Aroids as well as masses of other plants may heat themselves up to the fatal limit when heaped together and supplied with air[2].

No detailed research on the influence of the pressure of oxygen has been carried out. Vrolik and de Vries, however, state that the temperature of the inflorescence of *Colocasia odora* rises, and J. Schmitz that that of the buds of *Aesculus hippocastanum* does the same when the surrounding air is replaced by oxygen[3]. This is probably the result of an increase in the activity of respiration.

Injuries increase the activity of respiration and also the production of heat. Richards[4] was able to show this by means of a thermometer in plants massed together, and in single organs by thermo-electric means. The feverish rise of temperature in the potato spread not more than 20 mm. from the injury and in a particular case amounted to 0·05° C. 15 mm. away, and to 0·21° C. immediately beneath the cut surface. An onion, on the other hand, showed a rise of 0·28° C. beneath the cut surface and as much as 0·17° C. at a distance of 45 mm. Injured onions when heaped together showed a temperature higher by one or more degrees centigrade than uninjured ones.

Richards inserted thermo-electric needles into sound potatoes, and when the

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[1] Cf. Saussure, Mémoires de Genève, 1833, T. VI, p. 251; J. Schmitz, Ueber die Eigenwärme d. Pflanze, 187, p. 220.

[2] Saussure (l. c., 1822, p. 298) stated that the production of heat in the flower of *Cucurbita* decreases above 15 to 20° C., while Vrolik and de Vries (l. c., 1836, p. 140, cf. also Caspary, Flora, 1856, p. 219) observed that above 30° C. the spadix of *Colocasia* produces less heat. Possibly this was partly due to a rise in the rate of transpiration and partly to some indirect action on respiration.

[3] Vrolik and de Vries, l. c., p. 77; J. Schmitz, l. c., p. 51.

[4] Richards, Annals of Botany, 1897, Vol. XI, p. 29.

temperature became constant made an incision near one of the needles. In a particular case the temperature near to the fresh injury was higher than that at the point of insertion of the other needle by 0·09° C. after 2 hours, 0·19° C. after 4½ hours, 0·31° C. after 8½ hours, 0·21° C. after 12½ hours, and 0·02° C. after 40 hours, while towards the end of the fourth day the difference of temperature was imperceptible. The curves of respiration and heat-production are in this case very similar, the flatter character of the latter curve being due to the rapid loss of heat by conduction and radiation. The uninjured potato was 0·16° C. warmer than the surrounding air, so that the temperature in the injured region underwent a twofold increase. The production of heat depends upon the respiration, and hence on cutting an average potato into quarters the production of heat increases approximately tenfold. The whole increase takes place in the tissues immediately bordering the injury, so that these must respire with remarkable activity.

Little is known as to the detailed course of the grand period of heat-production and whether it exhibits secondary maxima or oscillations is unknown. Daily variations of the excess of temperature do occur in plants showing a marked production of heat, and Dutrochet observed slight oscillations in shoots and fruits[1].

The existence of a daily periodicity in the warming of the spadix of Aroids has been shown by Kraus and by the authors already quoted. Kraus has shown that the same applies to the inflorescences of Cycads and Palms, and Knock to the flowers of *Victoria regia*[2].

Observations in the open seem to show a periodicity in the production of heat independently of the air-temperature, and the same was shown under fairly constant conditions by a plant of *Colocasia odora* (*Arum cordifolium*) kept in a room at 17° C. by van Beek and Bergsma[3]. Thus in the selected zone of sterile male flowers the rise of temperature above the surrounding air was 10·6° C. at 2 p.m., 14·7° C. at 5 p.m. of the next day, 20·2° C. at 2.30 p.m. of the third day, and 11·1° C. at 2 p.m. on the fourth day. Each morning the excess-temperature lay between 1·30 C. and 5° C., it rose to a maximum during the day and fell to the morning temperature at evening.

The maximum may be earlier or later on some days than on others, and although it usually occurs during the daytime may also appear early in the morning or during the evening hours. The spadices of *Arum maculatum* and *A. italicum* show only a single pronounced period of heat-production, but, according to Dutrochet[4], both before and after this a feebler daily periodicity is shown. Here, as in the case of most of the shoots and fruits used by Dutrochet, the excess temperature observed was usually less than 0·3° C.[5] The maximal excess temperature observed in air saturated

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[1] Dutrochet, Ann. de sci. nat., 1840, 2^e^ sér., T. XIII, p. 41.

[2] G. Kraus, Ann. du Jard. bot. de Buitenzorg, 1896, T. XIII, p. 217; Knoch, ibid.

[3] The irregularities observed by Hoppe (l. c., p. 239) in the rise of temperature in the spadix of *Arum* were due to changes of temperature in the surrounding air. These may also exercise a stimulating action, for Kraus (l. c., 1884, p. 52) found that the spadix is very sensitive to external agencies.

[4] Dutrochet, l. c., 1840, p. 66. G. Kraus (l. c., 1884, p. 81; 1882, p. 1) used an ordinary thermometer, and hence was unable to detect any of these small oscillations.

[5] According to J. Schmitz (Ueber die Eigenwärme der Pflanze, 1870, p. 20) the buds of *Aesculu hippocastanum* show a daily periodicity of heat-production.

with moisture was shown between 10 a.m. and 3 p.m., and usually became imperceptible towards evening and remained so until morning.

Dutrochet has shown that the daily periodicity continues for a few days in darkness with decreasing amplitude, and is reinduced on re-exposure to periodic illumination, the other conditions remaining constant. This periodicity, therefore, closely corresponds to the periodicity of growth and movement induced by the intermittent daily illumination. It is, however, uncertain whether the periodicity of heat-production in the spadices of Aroids is produced in this way or not, nor has it been determined whether the rise of temperature may not be due to a decreased loss of heat as well as to an increased production of heat. No daily periodicity in respiration has yet been determined[1], although in fleshy plants the daily accumulation of organic acids in the tissues indicates a periodic diurnal alteration of respiration.

The spadices of Aroids have but little chlorophyll, and Hymenomycetes have none, so that the daily periodicity of heat-production in these forms can hardly be dependent upon photo-synthesis. Nor is it due to the fact that the lessened growth in the daytime consumes less of the energy of respiration, for the spadices of Aroids have ceased to grow when the production of heat is most active; and a daily periodicity of heat-production is shown, according to Dutrochet, by adult Cactus stems[2]. The rise of temperature is certainly not the direct result of the absorption of heat from the radiant light-rays, although the latter by favouring transpiration may cause an increased loss of heat, and hence lower the temperature. A periodicity of temperature is also shown by man, the maximum at evening being about 1·2°C. higher than in the morning.

SECTION 82. **The Production of Heat by Anaerobic Metabolism.**

Anaerobic metabolism probably always involves a liberation of heat, and alcoholic fermentation, in the absence of free oxygen, always produces a distinct rise of temperature. No detailed researches on the production of heat by anaerobic metabolism have been performed[3]; and although the heating of dung and of fermenting fluids is mainly due to anaerobic metabolism, it is not impossible that anaerobic organisms may exist whose normal metabolism involves an absorption of heat, just as that of green plants involves an absorption of light. In such cases the temperature of the plant will be continually below that of the surrounding medium. An absorption and extinction of the dark heat-rays does actually occur in the purple bacteria, the energy of these rays being used in photo-synthesis; but in this case the supply of energy precedes the endothermic chemical change, whereas in the other the endothermic chemical change is supposed to take place first, the subsequent inflow of heat from without following as a natural consequence of the fall of temperature[4]. It

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[1] Cf. Kolkwitz, Jahrb. f. wiss. Bot., 1898, Bd. XXXIII, p. 128.

[2] G. Kraus, l. c., 1884, p. 17.

[3] Popoff (Bot. Jahrb., 1875, p. 286) observed a slight warming during marsh-gas fermentation; Rubner, Hygienische Rundschau, 1903, Bd. XIII, p. 753.

[4] Cf. Pfeffer, Studien zur Energetik, 1892, p. 189.

is worthy of note that certain anaerobes are able to work with the utmost economy. The anaerobic respiration of obligate aerobes is too feeble to maintain life, but nevertheless it produces sufficient heat to raise the temperature of plants massed together from 0·1 to 0·3° C. above that of similar masses of dead plants, whereas in the presence of oxygen a difference of temperature of from 5° to 16° C. would be shown.

Eriksson[1] in obtaining these results took ample precautions to ensure the absence of all free oxygen, and also the absence of micro-organisms, by washing and by rapid observation[2]. During alcoholic fermentation the fermenting liquid may rise 10° C. in temperature[3]. The decomposition of a gram-molecule (160 grams) of dextrose into alcohol and carbon dioxide yields 33 kilogram-calories, i.e. sufficient heat to warm a litre of water from 4° C. to 37° C.[4] The complete combustion of dextrose yields, however, twenty times more heat, namely 673·7 kg.-calories. During alcoholic fermentation traces of other substances are formed in addition to alcohol and carbon dioxide. Hence the theoretical and the observed amount of heat produced will not necessarily correspond. Bouffard found that 180 grams of dextrose when fermented only produced 23·3 kg.-calories instead of the estimated 32·07, but this may possibly have been due to the difficulty of preventing the loss of heat by radiation and conduction.

Alcohol and carbon dioxide are also produced during the intramolecular respiration of aerobes; but, since other decompositions occur simultaneously, no theoretical calculation can be made of the amount of heat produced from the quantity of alcohol and of carbon dioxide formed. It is possible, however, that investigations of this kind may throw light upon the phenomena of intramolecular respiration. The liberation of carbon dioxide from an oxidized compound may be an endothermic change (decomposition of carbonates) or only a feebly exothermic one (fermentation of alcohol), so that even when equal quantities of carbon dioxide were produced the anaerobic production of heat would be considerably less than the aerobic one, in which the process is practically one of complete combustion, and the respiratory materials contain relatively little or no combined oxygen.

The decomposition of 1 gram-molecule of dextrose into 2 gram-molecules of lactic acid liberates 14·7 kg.-calories, and its splitting into 1 gram-molecule of butyric acid and 2 gram-molecules of hydrogen sets free 10·9 kg.-calories[5].

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[1] Eriksson, Unters. a. d. bot. Inst. zu Tübingen, 1881, Bd. I, p. 105.

[2] Pasteur (Compt. rend., 1872, Bd. LXXV, p. 1056, Étude s. la bière, 1876, p. 261) observed a marked rise of temperature in fruits and fleshy roots in the absence of oxygen, but this was probably due to the development of anaerobic bacteria.

[3] Cf. Dubrunfaut, Journ. f. pract. Chemie, 1856, Bd. LXIX, p. 444; Fitz, Ber. d. chem. Ges., 1873, p. 57; Brefeld, Landw. Jahrb., 1876, Bd. V, p. 300; Eriksson, l. c.; Nägeli, Theorie d. Gährung, 1879, p. 58; Bouffard, Compt. rend., 1895, T. CXXI, p. 136.

[4] Cf. Bouffard, l. c.; E. Duclaux, Traité de Microbiologie, 1898, Bd. II, pp. 77, 739. The heats of solution are allowed for in the above value, but otherwise it would be reduced to 22·3 kg.-calories, the difference between the heat of combustion of dextrose (1 gram-molecule = 673·7 kg.-cal.) and of alcohol (2 gram-molecules = 651·4 kg.-cal.).

[5] Cf. R. O. Hertzog, Zeitschr. f. physiol. Chemie, 1903, Bd. XXXVII, p. 383, and textbooks of Physical Chemistry.

Hence the lactic and butyric fermentations yield heat, although the observed amount is less than that theoretically calculated unless the heats of solution are taken into account. In addition the by-products of fermentation will influence the liberation of heat according to their character and properties. Most metabolic processes are attended by a trifling production of heat, and in fact it is even possible that metabolism may in some cases be attended by an absorption of heat[1].

SECTION 83. **The Temperature of the Plant under Normal Conditions.**

External and internal radiation, the conduction and production of heat, the temperature of the surrounding medium, and the activity of transpiration are among the factors regulating the temperature of the plant, and they do not affect the different organs of the plant alike. Hence the temperature of a root or of a shaded organ is usually different to that of the stem or of an insolated organ. In such cases a slow transference of heat may occur from the hotter to the colder organ by conduction, or by convection or transpiration currents of water.

Small or slender organs rapidly assume the temperature of the surrounding medium, but hours may elapse before the full effect of a change of temperature in the external medium is shown at the centre of a tree-trunk or of a large tuber. Neighbouring regions may indeed be at widely different temperatures, if one part is insolated but the other not, or if one part projects above water but the other is submerged. Plants are able to grow in spite of these local and general variations of temperature, if they are not too pronounced.

It must be remembered that under constant external conditions the activity of transpiration may undergo autogenic modification, and that its cooling effect will alter correspondingly. Gaseous exchanges may be modified in the same way, but these have a much feebler influence upon the body-temperature. Fleshy objects often become hotter in sunlight than the exposed bulb of a thermometer. Thus Askenasy[2] observed a temperature of 52° C. when the thermometer-bulb was inserted between the rosetted leaves of *Sempervivum alpinum* (shade temperature = 28·1° C.), whereas a thermometer pressed against the thinner leaves of *Gentiana cruciata* or between the tufted leaves of *Aubrietia deltoidea* showed a temperature

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[1] Cf. Pfeffer, Studien zur Energetik, 1892, p. 189. Nägeli incorrectly supposed that all enzyme action was accompanied by an absorption of heat, and proposed to make this a distinction from 'vital' fermentation accompanied by a production of heat. Cf. Hertzog, l. c.

[2] Askenasy, Bot. Ztg., 1875, p. 441. Cf. also Haberlandt, Sitzungsb. d. Wiener Akad., 1892, Bd. CI, Abth. i, p. 787; Passerini, Nuovo giornale bot. italiano, 1901, vol. VIII, p. 69. Rameaux (Ann. sci. nat., 1843, 2^{e} sér., T. XIX, p. 21) observed 33° C. registered by a thermometer whose bulb was inserted in a thin insolated branch, whereas with the bulb in sunlight 24° C. was shown. Becquerel (Compt. rend., 1858, T. XLVII, p. 717) observed 37° C. at the centre of a thick stem exposed to sunlight. For the older literature see Göppert, Die Wärmeentwickelung i. d. Pflanze, 1830.

of 35° C. In the tropics fleshy leaves are quite commonly raised above 50° C. by prolonged insolation, and may be injuriously or even fatally affected, for the cooling effect of the attendant rise of transpiration is limited by the supply of water. Hence arises the common practice in tropical plantations, especially when young (Coffee, Cocoa, &c.), of planting rapidly growing shade-trees at intervals to ward off the midday sun; and the same effect is produced by the usual mode of planting *Vanilla*, whose fleshy leaves are still more sensitive than those of such a plant as *Hoya carnosa*[1]. Thin leaves, on the other hand, have relatively more surface for radiation and transpiration, and in addition their gaseous exchanges are much more rapid than those of fleshy leaves.

Colour, hairiness, and position are all factors of considerable importance in determining the rise of temperature due to insolation. Green and other coloured leaves may absorb from fifty to ninety per cent. of the sun's rays falling upon them, while when a leaf places its lamina at right angles to the incident rays the absorption of heat is naturally greatly increased. A thick covering of hairs largely intercepts the incident rays, and only a small fraction of the heat absorbed by the hairs is transferred by conduction to the body of the leaf. The excretion of ethereal oils by lowering the diathermanicity of the surrounding air may help to cut off the heating effect of the sun's rays to a certain extent, but the amounts excreted even by the most active plant are not sufficient to have much effect, in spite of the extreme efficiency of these vapours for that purpose[2].

Cork and bark are bad conductors of heat, but a thin layer of cork can be penetrated by sufficient radiant rays to raise the temperature of a young branch considerably. Even when a thick layer of cork is present the heat conducted inwards may make the sunny side of a tree 20° C. warmer than the shaded one, and the centre of a tree exposed for some time may rise to over 40° C. in temperature[3].

Contact with cold water naturally removes heat more rapidly than contact with equally cold air, and in both cases the movement of the medium accelerates the loss of heat, to which the effect of air-currents in accelerating transpiration is to be added. Similarly, during cold clear nights the uninterrupted radiation makes the plant colder than when the sky is covered by clouds which hinder radiation. The temperature among the grass of a meadow may be 6° or 8° C. lower than that of the air above during night-time[4], and in fact it is even possible for plants to be killed by

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[1] Cf. Ewart, On the Effects of Tropical Insolation, Annals of Botany, 1897, Vol. XI, p. 444.

[2] Detto, Flora, 1903, p. 161; Volkens, Sitzungsb. d. Berlin. Akad., 1886, p. 78.

[3] Cf. Ihne, Bot. Centralbl., 1883, Bd. XV, p. 231; Müller-Thurgau, Landw. Jahrb., 1886, Bd. XV, p. 531; R. Hartig, Forstl. naturwiss. Zeitschrift, 1892, Heft iii, pp. 10, 12; Prinz, Bot. Jahresb., 1894, Bd. I, p. 226; Büsgen, Bau und Leben d. Waldbäume, 1897.

[4] Boussingault, Agronom., Chim. agricole et Physiol., 1861, T. II, p. 380; Tyndall, Fragments of Science, 1879, Vol. I, p. 90; Müller-Thurgau, l. c., 1886, p. 557; Th. Hormén, Bot. Ztg., 1894, p. 277.

frost when a thermometer in air does not sink below zero. This fall of temperature induces the deposition of dew upon the plant, the latent heat of the condensed vapour exercising a pronounced warming action[1].

The water ascending the trunk of a tree usually exercises a more or less pronounced cooling effect, according to the rate of ascent and the coldness of the water. Rameaux[2] found that the centre of a transpiring tree-trunk was 10° C. colder than that of a non-transpiring dead tree when both were exposed to the sun, but when the branches were cut off the living tree the temperature in both trunks became approximately the same.

Convection currents within the cells will aid in transferring heat upwards in elongated cells, but not downwards, and it is owing to the conduction through the elongated wood-elements that heat is able to pass more rapidly longitudinally than transversely through wood[3]. During winter the centre of a stem is usually warmer than the surrounding air, owing to the upward conduction of heat from the warmer water in the soil, coupled with the action of the cork jacket in retaining heat, and the absence of transpiration. In the higher portions of the stem this heating effect is slight owing to the poor conduction of heat by the wood, while in the smaller branches it is negligible. It is partly owing to the slow inward conduction of heat that Hartig[4] observed that the maximal temperature was reached 4 cm. deep in an oak stem at 6 p.m., and 20 cms. deep not until towards midnight after a day's insolation.

The thinner plant-organs are subjected to greater extremes of temperature than the centre of a thick stem, which responds but slowly to changes of temperature; but the latter is subject to greater daily and yearly variations of temperature than the root-system, owing to the more constant temperature of the soil[5]. Hartig found, for instance, that the interior of a tree-trunk sank to −13° C. during a winter when the air was frequently at −15° C. to −22° C., in spite of the upward flow of heat from the warmer roots.

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[1] Cf. Jamin, Naturforscher, 1879, p. 140; Wollny, Forschung. a. d. Gebiete d. Agriculturphysik, 1892, Bd. XV.

[2] Rameaux, l. c., p. 23. Hartig observed (Bot. Jahresb., 1874, p. 760) that the temperature in the interior of a stem sinks when the buds unfold and transpiration becomes active.

[3] Researches on the conductivity of wood to heat were carried out by de Candolle, Ann. d. Physik u. Chemie, 1828, Bd. XIV, p. 590; Knoblauch (ibid., 1858, Bd. CV, p. 623); Wiesner, Die Rohstoffe des Pflanzenreichs, 1873, p. 292; Sowinsky, Bot. Jahresb., 1875, p. 773. Sowinsky found the ratios between the transverse and longitudinal conductivities of wood to be as 1 : 1·15 (*Quercus robur*) and 1 : 1·43 (*Carpinus betulus*). Sowinsky found that some woods conducted better when dry, others when moist.

[4] Hartig, Bot. Jahresb., 1873, p. 508. See also Göppert, Die Wärmeentwickelung i. d. Pflanzen, 1830, p. 160. Cf. also Müller-Thurgau, l. c.; Ihne, l. c.

[5] On the temperature of subterranean tubers see Seignette, Rev. gén. de Bot., 1889, T. I, p. 573.

PART II

THE PRODUCTION OF LIGHT

SECTION 84. **Instances and Causes of Luminosity.**

Like many animals[1], certain plants are self-luminous, such as many Bacteria, Fungi, and the chlorophyllous *Ceratium tripos*[2]. Among Fungi, it is usually the fruit body of Hymenomycetes or Ascomycetes that is luminous, but the mycelium may also be luminous and cause, for instance, the luminosity of wood attacked by Fungi. The so-called phosphorescence of fish and of meat is due to the activity of Bacteria.

The glow is usually feeble like that of moist phosphorus in darkness, but Gardner states that in Brazil a few specimens of *Agaricus Gardneri* gave out sufficient light to read print[3]. The rays from luminous Bacteria are able to produce heliotropic curvatures or even the production of chlorophyll[4], and to enable the organisms to photograph themselves on a sensitive plate[5].

Bacteria. Pflüger showed that the phosphorescence of meat was due to Bacteria, and *Bacterium phosphorescens*, *B. Pflügeri*, *B. indicum*, and *B. luminosum* are all strongly luminous species[6]. Certain forms are always present in sea-water, and hence the readiness with which moist fish, or moistened smoked haddock, becomes luminous when hung up in a fairly cool room. In the same way a piece of flesh partially immersed in a saline solution will usually become luminous owing to the

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[1] Cf. Dubois, Leçons de Physiol., 1898, p. 301; Verworn, Allgem. Physiol., 3. Aufl., 1901, p. 263: de Kerville, Die leuchtenden Thiere u. Pflanzen, German translation by Marshall, 1893.

[2] J. Reinke, Wiss. Meeresunters. d. deutschen Meere, 1898, N. F., Bd. III, p. 39.

[3] Gardner, Flora, 1847, p. 756. Good cultures of phosphorescent bacteria give out sufficient light to enable one to tell the time by a watch at night.

[4] Molisch, Sitzungsb. d. Wiener Akad., 1902, Bd. CXI, Abth. i, p. 141; Isatschenko, Chlorophyllbildung im Bacterienlicht, Centralbl. f. Bact., 1903, Abth. ii, Bd. X, p. 498.

[5] Forster, Centralbl. f. Bact., 1887, Bd. II, p. 338; B. Fischer, ibid., 1888, Bd. III, p. 140; Molisch, Sitzungsb. d. Wiener Akad., 1903, Abth. i, Bd. CXII, p. 297.

[6] Pflüger, Archiv f. Physiol., 1875, Bd. X, p. 275; Bd. XI, p. 223. Cf. Molisch, Bot. Ztg., Orig., 1903, p. 1. For nomenclature see Migula, System d. Bacterien, 1897, Bd. I, p. 336; B. Fischer, Zeitschr. f. Hygiene, 1887, Bd. II, p. 54; Centralbl. f. Bact., 1888, Bd. III, pp. 105, 137; 1888, Bd. IV, p. 89; Beyerinck, Archives Néerlandaises, 1889, T. XXIII, pp. 104, 367, 416: 1891, Bd. XXIV, p. 369; Koninklijke Akad. v. Wetenschappen te Amsterdam, Proceedings of the Meeting, 27. Oktob., 1900, p. 359; Lehmann, Centralbl. f. Bact., 1889, Bd. V, p. 785; Kutscher, ibid., 1890, Bd. VIII, p. 124; Katz, ibid., 1891, Bd. IX, p. 157; C. Eijkmann, ibid., 1892, Bd. XII, p. 656; Suchsland, ibid., 2. Abth., 1898, Bd. IV, p. 713; Tarchanoff, Compt. rend., 1900, T. CXXXI, p. 246; McKenney, Obs. on the cond. of light production in Bacteria, 1902, reprint from Proc. of the Biol. Soc. of Washington, Vol. XV, p. 213; Barnard and Macfadyen, Annals of Botany, 1902, Vol. XVI, p. 387. A summary is given by Migula, System der Bacterien, 1897, Bd. I, p. 336; Flügge, Mikroorganismen, 3. Aufl., 1896, Bd. I, p. 166.

wide distribution of the germs[1]. The germs grow well in a decoction of fish to which one or two per cent. of peptone, of sodium and magnesium chlorides, and if necessary of glucose, have been added. By the addition of gelatine or agar solid media may be produced.

Meyen observed luminous masses containing numerous colourless *Oscillaria* filaments in the Atlantic, and Ehrenberg states that the Diatoms *Chaetoceras* and *Discoplea* are self-luminous[2], but it is possible that the light was produced by adherent Bacteria[3].

Fungi. Retzius and von Humboldt[4] showed that the long-known luminosity of wood was due to parasitic Fungi. The sclerotium (*Rhizomorpha*) of *Agaricus melleus*, and the finer mycelium of *Xylaria hypoxylon* are commonly responsible for the peculiarity. It is usually sufficient to keep wood destroyed by Fungi, especially that of the root, in a damp chamber for it to become luminous[5]. The mycelium of *Agaricus melleus* when grown in a fluid nutrient medium gives out a considerable amount of light[6], and the mycelia and fruit bodies of both Ascomycetes and of Hymenomycetes may become luminous when grown on artificial media.

The gill lamellae of *Agaricus olearius*[7] which grow on old olives in S. Europe, phosphoresce strongly, as does also the remainder of the sporophore, but less strongly. In the tropics many forms seem to be strongly luminous, such as *Agaricus Gardneri*[8] (Brazil), *A. igneus*[9] (Amboina), *A. noctilucens*[10] (Manila).

The older observations upon the production of flashes of light by leaves, flowers, and so forth are probably the result of optical illusions[11], but the St. Elmo's fire produced by electrical radiation may occur on plants. According to Mornay and Martius, certain Euphorbias have luminous latex, the latter possibly undergoing oxidatory photo-chemical changes on exposure to air, or becoming impregnated with

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[1] Molisch, Bot. Ztg., 1903, p. 17, always found *Micrococcus phosphoreus* (Syn. = *Bact. phosphorescens* Beyerinck).

[2] Meyen, Physiol., 1838, Bd. II, p. 202. Cf. Ludwig, Centralbl. f. Bact., 1887, Bd. II, p. 402; Ehrenberg, Die das Funkeln u. Aufblitzen des Mittelmeeres bewirkenden kleinen Lebensformen, 1874, p. 3 (reprint from Festschr. d. Ges. naturf. Freunde zu Berlin).

[3] Dubois (Leçons de Physiologie, 1898, p. 451) has given up his earlier statement that the phosphorescence of *Pholas dactylus* (the rock-boring mollusc) was due to a symbiotic Bacterium.

[4] See Agardh, Allgem. Biol. d. Pflanzen, 1832, p. 179; de Candolle, Pflanzenphysiologie, 1835, Bd. II, p. 680, footnote; P. Heinrich, Phosphorescenz der Körper, 1811.

[5] For literature and facts see Ludwig, Ueber d. Phosphorescenz d. Pilze u. d. Holzes, 1874; Lehrbuch d. niederen Cryptogamen, 1892, p. 525. Hitherto no luminous bacteria have been found to cause the luminosity of wood.

[6] Brefeld, Bot. Unters. ü. Schimmelpilze, 1877, Heft iii, p. 170.

[7] Fabre, Ann. sci. nat., 1855, 4e sér., T. IV, p. 179; Tulasne, ibid., 1848, 3e sér., T. IX, p. 541. Cf. also Ludwig, l. c., 1874, p. 9. The light is evolved before the development of the hymenium, and it ceases before the collapse of the tissues. Cut surfaces may also be luminous.

[8] Gardner, quoted by Ludwig, l. c., 1874, p. 9.

[9] Rumph, Herbarium amboinense, 1750, Bd. VI, p. 130.

[10] Gaudichaud, quoted by Ludwig, l.c., 1874, p. 9.

[11] For literature see Fries, Flora, 1859, p. 178; Meyen, Pflanzenphysiologie, 1838, Bd. II, p. 200; Ludwig, l.c., 1874, p. 5; Crié, Compt. rend., 1881, Bd. XCIII, p. 853; Ascherson, Naturwiss. Wochenschrift, 1901, p. 106. Senebier (Physiol. végétal., 1800, T. III, p. 315) states that the spadix of *Arum maculatum* phosphoresces when placed in oxygen.

luminous Bacteria[1]. There is also always a possibility that the phenomenon is one of fluorescence, light rays absorbed during the daytime being emitted at night. The glimmering of the protonema of *Schizostega*, on the other hand, is simply due to the collection of the feeble rays of light by the lens-shaped cells of the protonema [2].

Uses. Although it is possible that the luminous sporophore of a Fungus may attract night-flying insects, and so aid in the dissemination of the spores, it is not easy to see what use the luminosity of Bacteria or of a mycelium in wood could have. The presence of luminous Bacteria on a dead fish may attract fishes which swallow the Copepoda and other forms which devour the Bacteria, and in the dark depths of the ocean the luminous properties of an organism acquire greater importance.

The production of light is a physiological process dependent upon respiration, and, like the latter, it continues in darkness [3]. We are dealing, therefore, with a chemical production of light [4], and not with a fluorescent emission of light rays previously absorbed. The production of light usually begins in Fungi at a certain stage of development and then spreads to all parts. Similarly, McKenney states that Bacteria become luminous only at the end of the period of active locomotion. Under unfavourable conditions the luminosity vanishes and it attains an optimum under definite conditions as regards temperature, concentration, and food-supply. Luminosity, like growth, decreases above the optimum temperature, and does not like respiration and the production of heat increase up to the maximum temperature.

Luminosity, like locomotion and the production of pigments or poisons, may be suppressed without fatal injury to the organism. Many luminous forms have been grown at temperatures at which they produce no light, and Beyerinck [5] has in fact found that certain forms appear to become temporarily luminous under special conditions.

When the conditions are favourable the light is emitted continuously,

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[1] For literature see Meyen, l. c., p. 203.

[2] Unger, Flora, 1834, p. 33; Noll, Arbeit. d. bot. Inst. in Würzburg, 1888, Bd. III, p. 477. Ingenhousz (Versuche mit Pflanzen, German ed. by Scherer, 1786, Bd. I, p. 191) observed that the vapours of ethereal oil excreted by the inflorescence of *Dictamnus albus* burst into flame when a lighted match was brought near.

[3] Moderate light appears to exercise no effect upon the luminosity of *Rhizomorpha*. Cf. Ludwig, l. c., 1874, p. 26. Pflüger and also McKenney (l. c., p. 222) obtained similar results with Bacteria, but strong light, owing to its germicidal action, retards or inhibits the appearance of luminosity. Cf. Tarchanoff, Compt. rend., 1900, T. CXXXI, p. 247; Suchsland, Centralbl. f. Bact., 2. Abth., 1898, Bd. IV, p. 714.

[4] Wiedemann, Ann. d. Physik u. Chem., 1889, N. F., Bd. XXXVII, p. 180; 1889, N. F., Bd. XXXVIII, p. 485; Wiedemann und Schmidt, Zeitschr. f. physik. Chemie, 1895, Bd. XVIII, p. 528; Roloff, ibid., 1898, Bd. XXVI, p. 354; Winkelmann, Handbuch d. Physik, 1894, Bd. II, Abth. i, p. 486. [Sudden crystallization may cause a liquid to glow with light, as, for instance, when salt is precipitated in darkness by adding alcohol or concentrated hydrochloric acid to strong brine. This is, however, hardly likely to be responsible for any appreciable production of light in the living plant.]

[5] Beyerinck, Koninklijke Akad. v. Wetenschappen te Amsterdam, Oct. 1900, p. 359.

no special stimulation being necessary as it is in the case of *Noctiluca*[1]. In this organism and in *Ceratium tripos* the luminosity appears as the result of a shock-stimulus. It is possible that sudden changes of temperature or of concentration may temporarily increase or diminish the production of light in Fungi and Bacteria. These changes are usually but slight in amount, the organism rapidly adjusting itself to the new conditions. In some cases spontaneous increases and decreases in the intensity of the illumination are shown, but the causes of these are unknown.

Certain resistant organisms may continue to produce light at temperatures or in concentrations which ultimately cause a cessation of the luminosity or even death. In some cases gradual accommodation is possible, so that the organism or its descendants become luminous at temperatures which at first inhibited the production of light. Since variations in the production of light are readily perceptible, they may be used as indications of the vital activity upon which they are dependent. Beyerinck has in fact used luminous Bacteria as a test for the evolution of oxygen, and by means of his auxanographic method has determined the value of different nutrient materials or of metabolic products for the production of light. Owing to the after-effects already mentioned and to other physiological peculiarities care is, however, needed in interpreting the results.

The influence of temperature. All observers agree as to the existence of an optimum temperature for luminosity. The optimum lies between 25° and 30° C. in the case of *Rhizomorpha*[2], the minimum between 1° and 3° C. Similarly only approximate values have been obtained for Bacteria, and the divergences between the results of different authors are due partly to incorrect naming, and partly to the influence of dissimilar nutrient and cultural conditions[3]. Various Bacteria are still luminous at 0° C. to 5° C., whereas McKenney found that *Photobacterium indicum* (Beyerinck), the *Bacillus phosphorescens* of B. Fischer, ceases to emit light at 15° C., the optimum lying between 22° to 28° C., the maximum between 30° and 35° C. In the case of *Photobacterium* (*Microspira*) *luminosum* the cardinal temperatures are 10° C., 15° C., and 22° C. respectively. Here and in other cases also the maximum temperature for the production of light lay 5° to 10° C. below that for growth. McKenney found that the minimum temperatures for growth and for luminosity were the same, but the results of other observers show that this is not always the case.

Various workers have observed that light continues to be given off for a certain time after the luminous organism has been cooled below zero or even to −12° C.[4]

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[1] Bütschli, Protozoen, 1883–7, 2. Abth., p. 1088; Kruckenberg, Centralbl. f. Physiologie, 1887, Bd. 1, p. 689; Massart, Bull. scientifique de la France et de la Belgique, 1893, T. XXV, p. 76.

[2] Ludwig, l. c., p. 35; Brefeld, l. c., p. 4. Wood has been observed to emit light at 0° C. by the older observers. Cf. Ludwig, l. c., p. 25. Fabre (l. c., p. 187) finds that *Agaricus olearius* emits light only above 3° or 4° C.

[3] B. Fischer, l. c., 1887, p. 78; 1888, pp. 89, 139; Lehmann, l. c., 1889, p. 789; Beyerinck, l. c., 1891, pp. 8, 66; Eijkmann, l. c., 1892, p. 656; McKenney, l. c., p. 219.

[4] B. Fischer, l. c.; Lehmann, l. c.; Tarchanoff, l. c., p. 247. Suchsland (l. c., p. 80) found that after cooling to − 80° C. the luminosity of certain resistant Bacteria returned on warming.

McKenney, however, observed that the luminosity rapidly disappeared below the minimum temperature and above the maximum, while the continued cultivation of *Photobacterium indicum* at the highest possible temperature raised the maximum for the production of light from 30° to 35° C. According to the same author sudden changes produce a shock-effect on the luminosity, whereas other authors have observed slight transitory disturbances of the luminosity to result, especially in bacteria. According to Ludwig[1], *Rhizomorpha* becomes temporarily non-luminous when suddenly cooled from 40° to 10° C.

Chemical effects. Insufficient nutriment naturally produces a cessation of the luminosity more or less rapidly, but the presence of ether or alcohol, as well as changes of composition or concentration of the medium, may allow the Bacteria to grow but not become luminous[2]. Thus in all forms examined hitherto, not only must organic food be supplied, but also inorganic salts. Thus McKenney[3] found that when sodium chloride, sodium nitrate or other salts of sodium, or magnesium chloride formed the only salt present, growth and luminosity were both shown, but that both were suppressed when only a single salt of potassium, rubidium, lithium, ammonium, or calcium was present. The addition of magnesium chloride to the sodium chloride seems to favour luminosity, and hence the ready growth of these organisms in sea-water. The amount of salt may vary between 1 and 4 per cent. without growth and the evolution of light being perceptibly affected.

All luminous Bacteria appear to require peptone, while *Photobacterium phosphorescens* and *P. Pflügeri* seem also to need a suitable carbohydrate, although for *Photobacterium luminosum* and *P. indicum* peptone alone suffices. The presence of a large amount of glucose diminishes the luminosity, and *Photobacterium luminosum* is so sensitive that it ceases to be luminous in the presence of 1 per cent., and to grow in the presence of 3 to 5 per cent. of glucose.

Beyerinck worked largely by the auxanographic method, and the slight divergences between his results and those of McKenney are probably the result of dissimilar cultural conditions. In all cases a slight acidity or a somewhat stronger alkalinity is sufficient to inhibit luminosity, and subsequently growth also. Hence at the electrodes in an electrolysed medium containing luminous Bacteria no luminosity is shown if the acid and alkali are set free at the anode and kathode in sufficient amount[4]. Since McKenney found that the luminosity is only shown after movement has ceased, and since it is possible by maintaining the original composition of the medium to keep the organisms permanently motile, it would presumably be possible to grow them as non-luminous forms[5].

The production of light is dependent upon aerobic respiration and ceases in the absence of oxygen. This applies not only to aerobic fungi[6] and

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[1] Ludwig, l. c., p. 25.

[2] McKenney, l. c., p. 223; Tarchanoff, l. c., p. 247. Cf. also the works quoted of B. Fischer, Beyerinck, Lehmann, and Katz.

[3] McKenney, l. c., p. 226. [4] Suchsland, l. c., 1898, p. 715. [5] Cf. McKenney, l. c., p. 229.

[6] Fabre, Ann. sci. nat., 1855, 4e sér., T. IV, p. 190; Nees von Esenbeck, Nöggerath u. Bischoff, Nova Acta d. Leopold. Acad., 1823, Bd. XI, Th. ii, pp. 667, 694. Boyle showed that oxygen was necessary for the luminescence of wood. Cf. Dessaignes, Journ. de physique et de chimie, 1809, T. LIX, p. 29, and Heinrich, Die Phosphorescenz d. Körper, 1811, p. 334.

Bacteria[1] but also to the facultatively anaerobic *Bacterium phosphorescens*, Beyerinck, which is able to develop but not to luminesce in the absence of oxygen. It is, however, quite possible that facultative anaerobes may exist which are capable of emitting light in the absence of oxygen.

The luminescence is decreased or suppressed when the partial pressure of the oxygen is much increased or diminished, but no definite numerical results have been obtained. According to Lehmann[2], however, compressed air under a pressure of six atmospheres, or pure oxygen under a pressure of an atmosphere, exerts no perceptible effect upon the luminescence of meat or wood, whereas Fabre[3] finds that the emission of light by *Agaricus olearius* increases in pure oxygen. The fact that the luminescence of certain Bacteria only gradually disappears in the absence of oxygen does not afford satisfactory evidence that these organisms store up occluded oxygen.

The emission of light is not the result of intense respiration, for the latter continually increases up to the maximal temperature, whereas the former rapidly ceases above a rather lower optimum temperature. In addition the luminous Fungi and Bacteria do not respire with especial activity[4], while the spadix of an Aroid evolves no light during its most active period of respiration and heat-production. Luminous organisms may indeed evolve light when their production of heat is so slight that their temperature is below that of the surrounding medium.

Certain substances evolve light during slow oxidation without any perceptible production of heat[5], and hence it is possible that during either the metabolism, or more especially the respiratory katabolism of luminous organisms, materials may be produced whose slow oxidation gives rise to light. According to Dubois[6], two substances, *luciferin* and *luciferase*, may be isolated from *Pholas dactylus*. These evolve light when brought into contact and therefore presumably are responsible for the emission of light by

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[1] Pflüger, l. c., p. 223; B. Fischer, l. c., 1887, p. 37; Lehmann, l. c., 1889, p. 788; Beyerinck, l. c., 1889; Katz, l. c., 1891, p. 314; Eijkmann, l. c., 1892, p. 657.

[2] K. B. Lehmann, Einfluss des comprimirten Sauerstoffs auf d. Lebensprocesse, Zürich, 1883, p. 87. [Dessaignes (l. c., p. 29) also observed no increased luminosity of wood in pure oxygen, whereas Nees, Nöggerath, and Bischoff (l. c., p. 693) state that it increased; and Heinrich (l. c., p. 332) found that it increased in air at a pressure of two atmospheres, but not in pure oxygen. These varying results are probably due to the influence of fatigue and of accommodation upon the visual judgement of the intensity of a feeble source of illumination, a striking instance of which is afforded by the statements of different observers in regard to Blondhlot's '*n* rays.']

[3] Fabre, l. c., p. 191.

[4] Fabre (l. c., p. 193) found that *Agaricus olearius* respired most actively during the luminous condition.

[5] Radziszewski (Ann. d. Chemie, 1880, Bd. CCIII, p. 330; Ber. d. chem. Ges., 1877, p. 321; 1883, p. 597) states that lophin dissolved in alkali, and liver oil dissolved in toluol containing a few drops of cholin or neurin solution, emits light at as low a temperature as 10° C. Dubois (Compt. rend., 1901, T. CXXXII, p. 431) has shown that aesculin dissolved in alcoholic potash phosphoresces.

[6] Dubois, Leçons de Physiologie, 1898, p. 524; Compt. rend., 1896, T. CXXIII, p. 653. Dubois formerly had expressed the opinion that the emission of light was produced by the conversion of colloids into crystalloids.

this organism. Even in this case the production, interaction, and oxidation of these substances are processes of which the former is more especially under physiological control, and so long as the substances in question are kept separate no light would be produced. According to whether the contact took place inside or outside the cell, we should have an intracellular or extracellular production of light [1]. It is uncertain to what degree the latter occurs, and it must be remembered that the emission of light by excreted slime or mucilage may be due to the presence of luminous Bacteria.

Whatever the physiological action may be, we have in each case a production of light by a transformation of chemical energy not involving any appreciable production of heat [2]. Hence light is produced here much more economically than when a body is heated to incandescence by physical or chemical action [3]. The actual expenditure of energy by the organism in producing the luminous substance is uncertain, but it is of interest to note that energy may be radiated from a cold body to a warmer one which absorbs the emitted light [4].

The composition [5] of the light is often that of white light, but in many cases the light has a bluish or greenish tinge. The composition appears, however, to vary according to the cultural conditions, as is shown by spectroscopic examination. No rays resembling the Röntgen or Becquerel rays appear to be present [6].

PART III

THE PRODUCTION OF ELECTRICAL TENSIONS IN THE PLANT

SECTION 85. **The Origin and Detection of Electro-motive Changes.**

No plants are able like electrical fishes to give perceptible electrical shocks, but nevertheless slight differences of potential capable of maintaining

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[1] *Noctiluca* phosphoresces internally, especially at certain points, and this continues for a little time after the organism has been crushed. Bütschli, Protozoen, 1883–7, Abth. ii, p. 1092. Whether the luminescence of wood is produced in the fungal hyphae or outside of them is uncertain. Cf. Ludwig, Lehrb. d. niederen Cryptogamen, 1892, p. 530. Lehmann (l. c., 1889, p. 789) and Beyerinck (l. c., 1891, p. 52) are wrong in supposing that the cessation of the light on death disproves the existence of a special luminous substance. Beyerinck's supposition that the production of light is connected with the assimilation of peptone has no sure foundation.

[2] [The light might still have a purely physical origin in certain cases without involving any production of special luminous substances. When present these might undergo radiatory atomic disintegration, or might shorten the wave-length of the heat vibrations due to respiration sufficiently to produce visible light rays.]

[3] Langley u. Very, Beibl. z. d. Ann. d. Physik u. Chemie, 1890, Bd. XIV, p. 1096; Dubois, l. c., 1898, p. 376.

[4] Wiedemann, Ann. d. Physik u. Chem., 1889, N. F., Bd. XXXVIII, p. 485.

[5] Ludwig, Zeitschr. f. wiss. Mikroskopie, 1884, Bd. I, p. 181; l. c., 1892, pp. 78, 537; Lehmann, Centralbl. f. Bact., 1889, Bd. V, p. 787; Dubois, l. c., 1898, p. 510.

[6] Suchsland, l. c., 1898, p. 715; Barnard and Macfadyen, Annals of Botany, 1902, Vol. XVI, p. 587; Molisch, Sitzungsb. d. Wiener Akad., 1903, Bd. CXII, Abth. i, pp. 305, 310.

currents are of common occurrence, although to detect them delicate measurements are usually required. These are usually made by laying two non-polarizable electrodes on the regions to be examined, and placing them in circuit with a galvanometer whose deflection indicates the passage of a current from the region of higher potential to that of lower potential. A positive result gives, however, no indication as to how the potential differences are produced.

The continuance of the current in the external circuit shown by the permanent deflection of the galvanometer indicates that the difference is continually maintained, and that a return current flows in the plant in such a direction as to form a complete internal and external circuit. A break in the external circuit must exert some influence upon the internal circuit, but the internal currents are hardly likely to cease as when a battery circuit is broken, for a difference of potential between two points must always produce a current of electricity if the resistance of the intervening medium is not too high. The direction and intensity of these currents will largely depend upon the shape, arrangement, and conductivity of the intervening tissues, which may be such as to permit of the continual circulation of electrical currents in plants. The only evidence at our disposal is, however, derived from observations made upon the currents led off and measured in circuits external to the plant.

A variety of factors may induce variations of electrical potential in plants, and if the sum of the processes producing a rise of potential is equal to that of those tending to diminish the potential no external modification will be made manifest. In general the visible differences of potential appear to result directly or indirectly from metabolism, and to a very much less degree from the imbibition of water and its passage through capillary tubes.

All chemical changes in which ions take part involve also electrical changes. In a galvanic cell, for instance, the electrical charges imparted to the plates maintain the difference of potential, which induces flow in the external circuit. When oxidation or reduction takes place in tissues separated by an intervening conducting space, it is usually possible to lead off an external current, and the same is even possible when two reacting substances are brought into contact by diffusion[1]. In plants, therefore, we have all the conditions for the production of electrical currents.

It is possible that the protoplasmic membranes may allow some ions to pass but not others, and in this way, or even by retarding the speed of certain ions, a difference of potential may be produced capable of giving rise

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[1] Haake (Flora, 1892, p. 465) observed a pronounced deflection of a galvanometer connected with the ends of a strip of filter-paper at the moment when copper sulphate and ferrocyanide of potassium met by diffusion and interacted. Cf. also Dubois, Centralbl. f. Physiol., 1901, Bd. XIV, p. 32.

to an external current[1]. The processes of diosmosis and of diffusion may, therefore, give rise to electrical currents, which may indeed be produced in various ways by differences of concentration. All these are factors within the control of the organism, and capable of alteration by appropriate metabolic activity.

In all cases it depends upon circumstances whether any current perceptible externally is produced. For instance if a zinc-copper couple is completely immersed in dilute sulphuric acid, the whole of the liberated chemical energy is ultimately transformed into heat, no external current being perceptible. In the same way no differences of potential need exist on the surface of a cell when internal electrical currents circulate in the cytoplasm or cell-sap, and these are impossible to demonstrate in small plant-cells. It is, however, possible to demonstrate the existence of differences of electrical potential between the different parts of the internodal cells of Nitella.

Bernstein[2] considers that in muscle-tissue the differences of electrical potential are produced by the action of temperature, and not by chemical changes, a rise of temperature increasing the electro-motive force in a chain of rising concentration. In the case of plants, however, other factors may come into play, and most animal physiologists regard the electro-motive force as being directly derived from chemical changes[3].

The occasional existence of externally perceptible electrical currents in dead organs is hardly surprising when we consider that the metabolic products may be at first unequally distributed and that by their diffusion and chemical interaction differences of potential may be produced[4]. Naturally also, such currents gradually diminish and disappear, and the disappearance may be so rapid that in the dead organ no currents can be detected. These post-mortem currents may in part represent actions which go on during life, but in all cases the cessation of metabolism immediately influences the

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[1] Cf. Ostwald, Zeitschr. f. physik. Chem., 1890, Bd. VI, p. 69; Walden, ibid., 1892, Bd. X, p. 718; Oker-Blom, Pflüger's Archiv f. Physiol., 1901, Bd. LXXXIV, p. 191. On concentration chains cf. Ostwald, Lehrb. d. allgem. Chemie, l. c., p. 824; Grundriss, l. c., p. 442.

[2] Bernstein, Pflüger's Archiv f. Physiologie, 1902, Bd. XCII, p. 521. Here and in Winkelmann's Handbuch d. Physik, 1903, p. 420, full details are given as to the required temperatures.

[3] Biedermann (Elektrophysiologie, 1895, p. 300), L. Hermann, and E. Hering (Lotos, 1889, N. F., Bd. IX, p. 56) all ascribe animal electricity to chemical processes. Du Bois-Reymond considered the phenomena to result from the special arrangements of bipolar molecules, but left the sources of energy an open question.

[4] Ranke (Sitzungsb. d. Bayrischen Akad., 1892, p. 181) and Munk (Die elektrischen u. Bewegungserscheinungen im Blatte von Dionaea, 1876, p. 43) observed a gradual disappearance of the electrical currents from dead organs. B. Velten (Bot. Ztg., 1876, p. 296) and O. Haake (Flora, 1892, p. 467, footnote) found that currents persisted for a time after sudden killing by steam or hot water. Haake states that the current disappears rapidly from a dead stem of *Pisum* in moist air, but reappears on laying in water, probably because of the differences of concentration produced by the outward diffusion. According to Waller (Centralbl. f. Physiol., 1901, Bd. XV, p. 480) death by cold is accompanied by a sudden 'explosive' production of electricity.

electrical conditions. On the other hand, it requires a special arrangement of the parts to enable the chemical actions involved in metabolism to produce differences of potential sufficient to maintain perceptible external currents. Changes of metabolic activity will naturally affect these currents[1], but might conceivably take place in such fashion as to leave the difference of potential unaffected. The absence of oxygen, changes of temperature, the action of chloroform and ether all produce a distinct effect upon the external currents led off from a plant, not only because of their general action on metabolism, but also when locally applied. The local application of anaesthetics or of poisons, as well as local injuries, may not only influence a pre-existent electrical current, but may also cause difference of electrical potential to appear in regions which were previously isoelectric[2].

Similar phenomena are shown by adult organs in which, when kept under otherwise constant conditions and in air saturated with moisture, the removal of oxygen or a change of temperature mainly affects the metabolic activity. When, however, movement takes place, as in a stimulated leaf of *Dionaea*, the resulting movements of water and of the tissues as a whole may produce a certain amount of electricity. Under similar conditions symmetric points on a leaf or stem are usually isoelectric, and the same may even apply to organs which are morphologically and functionally dissimilar. The reversal of the normal current of action during life or under special conditions shows that the polarity of the organ does not involve any fixed electrical polarity. Currents can usually be obtained between any two points after appropriate treatment, provided that the surfaces are not covered by non-conducting cork layers. Hence the production of electricity, like the production of heat, is a property common to all living organisms, and not one possessed by a few, as is for instance the property of luminosity.

The difference of potential between different surfaces on an intact or injured organ is usually less than 0·1 to 0·14 of a volt[3], which is the same as exists in resting muscle between the longitudinal and transverse surfaces. The total amount of electricity produced is quite uncertain, and even when the conductivity of the different tissues and of the different parts of the

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[1] The relationships here are the same as when growth and movement are affected by external stimuli, and hence no sharp distinction can be drawn between currents of rest and currents of action. Cf. Biedermann, l. c., p. 331.

[2] [Waller (Journ. Linn. Soc., 1904, Vol. XXXVII, p. 32) finds that as the result of electrical stimulation a 'blaze' current, lasting a few minutes or longer, is produced in the adult tissues of most plants. The direction of this current may be the same or opposite to that of the exciting current, and it is in some cases of quite appreciable intensity, the difference of potential produced amounting to $\frac{1}{50}$ volt. In some cases where a compensating current was used to balance the action current or injury current of the object tested, the 'blaze' current obtained was simply due to a decrease of resistance allowing the compensating current to produce a deflection of the galvanometer.]

[3] Cf., in addition to the works already quoted, Biedermann, Elektrophysiologie, 1895, p. 441.

cells are better known, we shall still be unable to accurately determine the magnitude and current-density of the internal streams of electricity. The tissues of plants have in general, like the tissues of animals, a very low electrical conductivity, their resistance being often one or two million times greater than that of mercury[1]. The resistance will naturally depend upon the substances present in the cell, upon the arrangement of the cells, upon the nature of the imbibed solutions, upon secretory activity, and upon the presence of air or of sap in the intercellular spaces. Hence it is hardly surprising to find that the transitory passage of a strong electrical current through a tissue may cause a diminution of its electrical resistance[2]. A fall of resistance between two points will tend to lower the difference of potential between them, for if the resistance between them was *nil* no perceptible difference of potential could be maintained.

Ewart[3] has shown that in plant-cells the protoplasm offers a greater resistance to the passage of an electrical current than the cell-sap, or even than the cell-wall when the latter is saturated with sap. The resistance decreases considerably as the temperature rises, and in egg-albumin, which appears to conduct in much the same way that protoplasm does, the resistance of 501 ohms per centimetre cube at 16° C. sinks to one of 188 ohms at 85° C., the coagulation of the albumin exercising no effect upon its conductivity. Young highly protoplasmic organs have a very low conductivity, which is presumably due to their deficiency in electrolytes[3].

Apart from the electrical fishes which use their special powers for attack and defence, we know of no definite cases in which the production of electricity is of use to the organism. Very possibly the production of electricity is largely an accidental accompaniment of metabolism, although the weak currents circulating in plants may exert stimulating or orienting actions[4] on the protoplast, or may aid by the transport of ions in the conveyance of food and other materials from one part to another. No conclusions can, however, be drawn from the galvanotactic responses of certain organisms, and the facts known as to the influence of external

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[1] Cf. Biedermann, Electrophysiologie, 1895, p. 704; Kunkel, Arb. d. bot. Inst. in Würzburg, 1879, Bd. II, p. 333; Wjasemsky, Ueber den Einfluss d. elektrischen Ströme auf d. Leitungswiderstand der Pflanzengewebe, 1901; Galeotti, Zeitschr. f. Biologie, 1902, Bd. XLIII, p. 289. On the conductivity of wet and dry wood cf. Villari, Ann. d. Physik u. Chemie, 1868, Bd. CXXXIII, p. 418; Mazotto, Bot. Jahresb., 1897, p. 92.

[2] Wjasemsky (l. c., p. 20) concludes that the fall of resistance is due to the passage of water inwards from the moist electrodes, through the cuticle. Waller has shown, however (Journ. Linn. Soc., Vol. XXXVII, 1904, p. 46), that the same fall of resistance is shown in peas after the skin has been removed, and suggests that the action of the original current is to cause an increase in the number of conducting electrolytes, which appear to be deficient in young highly protoplasmic organs. Ewart (On Protoplasmic Streaming in Plants, 1903, pp. 96, 123) observed a fall of resistance in the protoplasm on death, and ascribes this to the same cause, since coagulation exercises no effect on conductivity (l. c., p. 124).

[3] Ewart, l. c.

[4] Cf. Ewart, l. c., p. 116.

currents upon vital activity afford no safe guide as to the action of the weak internal currents[1]. These may, however, exert a distinct stimulating action, and if prolonged may represent a considerable total expenditure of energy.

Variations of the electrical current in an external circuit indicate autogenic or aitiogenic changes within the plant, but unfortunately the origin of the change of potential or of the altered resistance producing the modified current is usually unknown and is in all cases difficult to determine. Nevertheless the ease and exactness with which the external currents can be measured render them of great value as indicators of internal changes. Even in animal physiology, however, where much work has been done in this direction, but little is known as to the function of the electrical currents observed[2]. Hence we need only discuss the electrical currents and changes of potential so far as is necessary to show their general character and their relationship with other vital processes. The action of stimuli upon the production of electricity agrees as regards the influence of summation, intensity, and conjoint action with that of stimuli in general. Variations of the strength of the current due to polarization effects or to changes of resistance are naturally of less importance than those produced by an increased difference of potential due to greater electrical activity.

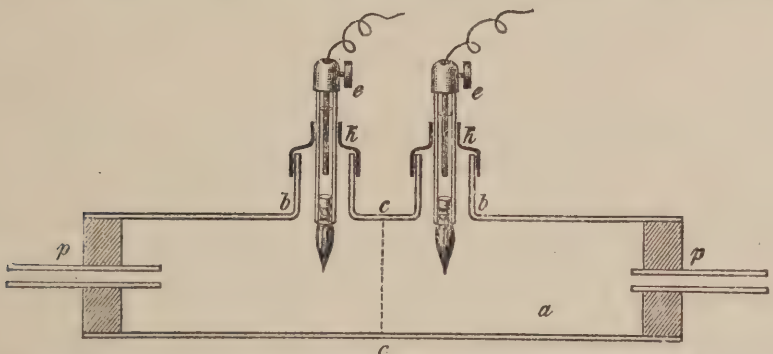

FIG. 68. Testing-apparatus for electrical currents. The glass tube (*a*) can be separated into two halves at (*c*). Gases can be led into and out of the two halves by the tube at (*p*). The electrodes (*e*) are attached by air-tight india-rubber caps (*k*) to the side tubes (*b*, *b*).

Methods. These have already been developed very fully in animal physiology[3]. The brushes of the non-polarizable electrodes (Fig. 68) are moistened with a dilute solution (0·05 per cent.) of sodium chloride, or with spring-water, care being taken to wash away any traces of zinc sulphate that may diffuse through from the tube containing the carbon electrode. Haake[4] used a tube (Fig. 68) which could be separated

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[1] Cf. Euler, Meddelanden från Stockholms Högskolas Botaniska Institut, 1899, Bd. II; Lemström, Electricity in Agriculture, 1904; Ewart, l. c., pp. 88–93.

[2] Biedermann, l. c., p. 273.

[3] See Hermann, Physiolog. Practicum, 1898, p. 75; Biedermann, Elektrophysiologie, 1895; Burdon-Sanderson, Kunkel, and Haake, l. c. The addition of a drop of water, or the mere application of the electrode may produce a transitory current. Hence careful control is required.

[4] Haake, Flora, 1892, p. 461.

into two halves by an air-tight partition at *c*, so that one-half of the plant might be in hydrogen, the other in air, or if the plant was surrounded by cotton-wool at *c*, one-half could be kept at a higher temperature than the other. At the same time the whole plant, or stem, can be kept in air saturated with moisture.

To measure the current in the external circuit either a sensitive reflecting galvanometer or a Lippmann's capillary electrometer may be used. The latter instrument consists of a capillary tube containing mercury, whose open end is immersed in dilute sulphuric acid which also fills the tube up to the mercury. On passing a current from the mercury to the sulphuric acid the capillary constant alters and a corresponding movement of the mercury ensues, which when read off by means of a horizontal microscope may enable changes of potential of less than 0·0005 of a volt to be detected by means of a delicate instrument[1]. Rapid changes in the intensity of the current may be detected and measured by causing the thread of mercury to throw a strong shadow upon a slowly-moving photographic plate[2]. The electrical potential may be determined either by means of a compensator which is adjusted until the mercury regains its original position, or by determining the actual pressure required to drive the mercury back to its original position while the current is still passing.

SECTION 86. **The Influence of External Agencies on the Production of Electricity.**

The existence of externally perceptible electrical currents was discovered by Becquerel[3] on injured plants, and on the uninjured leaves of *Dionaea* by Burdon-Sanderson and Munk, while Kunkel, Müller-Hetlingen, Haake, and others subsequently extended these observations to a variety of uninjured plants[4]. In fact there does not appear to be a single plant of any size in which differences of potential cannot be detected between points on its

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[1] See Hermann, Physiol. Practicum, 1898, p. 93; Ostwald, Hand- u. Hilfsbuch f. physiko-chemische Messungen, 1893, p. 247; Hermann and Gildemeister, Pflüger's Archiv f. Physiologie, 1900, Bd. LXXXI, p. 491.

[2] See Langendorff, Physiol. Graphik, 1891, p. 90; Garten, Abhandl. d. math.-physisch. Klasse d. Sächs. Ges. d. Wiss., 1901, Bd. XXVI, and textbooks of animal physiology.

[3] Becquerel, Ann. de chim. et de physique, 1851, 3^{e} sér., T. XXXI, p. 40; Wartmann, Bot. Ztg., 1851, p. 308; Buff, Ann. d. Chem. u. Pharm., 1854, Bd. LXXXIX, p. 76; Heidenhain, Studien d. physiol. Inst. zu Breslau, 1861, Heft i, p. 104; Hermann, Pflüger's Archiv f. Physiologie, 1871, Bd. IV, p. 155; Ranke, Sitzungsb. d. bayrisch. Akad., 1872, p. 181; Velten, Bot. Ztg., 1876, p. 273.

[4] Burdon-Sanderson, Proc. of the Royal Soc., 1876–7, Vol. XXV, p. 411; Phil. Trans., 1882, Part i; 1888, Vol. CLXXIX, p. 417; Biol. Centralbl., 1882, Bd. II, p. 481; 1889, Bd. IX, p. 1; Munk, Die elektrischen u. Bewegungserscheinungen am Blatte von *Dionaea*, 1876; Kunkel, Pflüger's Archiv f. Physiol., 1881, Bd. XXV, p. 342; Arb. d. bot. Inst. in Würzburg, 1878, Bd. II, pp. 1, 333; Müller-Hettlingen, Pflüger's Archiv f. Physiol., 1883, Bd. XXXI, p. 193; Haake, Flora, 1892, p. 455; B. Klein, Ber. d. bot. Ges., 1898, p. 335; Dubois, Centralbl. f. Physiol., 1899, Bd. XIII, p. 699; Waller, Proc. of the Physiol. Soc., 30. Juni, 1900, und 9. Nov., 1901; Proc. of the Royal Soc., 1900, Vol. LXVII, p. 129; Centralbl. f. Physiol., 1901, Bd. XV, p. 480; Tompa, Beihefte z. Bot. Centralbl., 1902, Bd. XII, p. 99; Querton, Institut Solvay, Travaux du Laboratoire d. Physiol., 1902, T. V, Fasc. 2, p. 81; Bot. Centralbl., 1903, Bd. XCII, p. 145; Plowmann, Bot. Centralbl., 1903, Bd. XCIII, p. 61. The rather fantastic discussions of R. Keller (Reibungselektrische Untersuch. an pflanzlichen Geschlechtsorganen, 1902) hardly need comment.

surface. Haake even found this to be the case in the internodal cells of *Nitella* and the same may apply to large non-cellular Algae like *Caulerpa*, although, to judge from the absence of 'blaze' currents from most Algae, they are comparatively incapable of electrical response[1].

There is, however, no constant rule for the distribution of the surface potential even under homogenous and regular external conditions. Symmetric points on a leaf or stem are usually isopotential[2], while judging from the direction of the current in the external circuit the midrib is positive to the lamina. Nevertheless exceptions occur[3], as is also the case when the potentials of old and growing zones are contrasted, while in the latter case changes commonly occur during development. Although electrical disturbances were known to occur during the rapid closure of the leaf-lobes of *Dionaea*, and as the result of injury and of changes of temperature, Haake was the first to show that they always take place when the metabolism is sufficiently modified by changes in the external conditions.

The removal of oxygen[4] always causes a certain electrical disturbance. When the entire object is in hydrogen the galvanometer deflection is usually lessened and is sometimes reversed, whereas the local absence of oxygen produces an increased deflection, independently of whether the negative or positive region is placed in the hydrogen. Although deviations are often shown[5], the results indicate the prominent part played by aerobic respiration in the production of electricity, although the latter can still be formed by the intramolecular respiration occurring when oxygen is absent. No definite causal relationships are revealed by these facts, and the complicated nature of respiration in general renders it hardly surprising that on the return of a still living plant to air, the original distribution of potential may not be restored, and that in the continued absence of oxygen the galvanometer may show a varying deflection. In both cases the transition to the new conditions produces pronounced temporary deflections of the galvanometer.

Temperature. The changes of current produced by rises or falls of temperature in objects kept in air saturated with moisture are, in part at least, due to quantitative and possibly qualitative alterations of respiration and metabolism, although alterations of resistance and other factors

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[1] Waller, Journ. of Linn. Soc., 1904, Vol. XXXVII, pp. 32, 40.

[2] On the isopotentials of leaves cf. Kunkel, l. c.; Haake, l. c., p. 483; Munk, l. c., p. 37.

[3] Cf. Kunkel, l. c., 1878, p. 2; Haake, l. c., p. 458; Klein, l. c., p. 336.

[4] Haake, l. c., p. 467. On some researches on the effect of the removal of oxygen on animals cf. Biedermann, l. c., p. 402. The changes of potential are not due to the gaseous movements due to production and consumption.

[5] Haake (l. c., p. 470) observed an increased deflection when the seedling of *Vicia Faba* was placed in hydrogen, possibly because during the intramolecular respiration of this plant as much, or in the case of the cotyledons even more, carbon dioxide is produced than during normal oxygen respiration.

may come into play. Haake[1] found that in general the warmer half of a shoot or leaf experienced an increase of positive potential, which caused either an increased or a decreased deflection according to whether the previous difference of potential was increased or diminished thereby.

Photosynthesis. The assimilation of carbon dioxide involves alterations of potential, which hence become perceptible when a leaf is exposed to changes of illumination, as was first shown by Haake and by Klein. Waller and also Querton have shown that the current in the external circuit moves from the shaded to the illuminated half of a leaf, but *Tropaeolum* and *Matthiola* show exceptions to this rule. The most pronounced effect is produced behind a solution of potassium bichromate which lets through mainly the rays most effective in photosynthesis.

Anaesthetics such as chloroform and ether[2] also produce changes of potential, probably largely owing to their influence upon metabolism.

The movements of water in the cell-membranes and in capillary spaces exert a purely physical electromotive action in both living and dead objects[3], but in the living plant the electricity produced in this way is but slight in amount. Haake[4] could detect no difference in the galvanometric deflection obtained from a leaf or stem on permitting and then preventing transpiration with its attendant movement of water. Even when a flaccid plant was suddenly made turgid by forcing in water under pressure, only a slight variation of the current in the external circuit was shown.

Since the normal differences of potential on plants are shown also in air saturated with moisture, Kunkel's supposition[5] can hardly be correct, for according to this author all the electrical currents in plants are derived from the mechanical energy of the movements of water. Kunkel attaches especial importance to the fact, corroborated by Haake, that the current passing from the midrib to the mesophyll of a leaf undergoes a transitory reversal when a drop of water is placed upon the mesophyll. The same result is, however, produced when the leaf is saturated with water so that no absorption occurs, and it remains an open question whether the variations in the electrical currents produced by rapidly bending a shoot are due to movements of water as Kunkel supposes, or are produced in other ways[6]. Since the effect is produced at once it cannot be the result

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[1] Haake, Flora, 1892, p. 476.

[2] Waller, Proc. of Royal Soc., 1900, p. 134; Querton, l. c., p. 110.

[3] Querton, l. c., 1902, p. 119; Haake, l. c., p. 480. For a few observations on the influence of chemical agents upon the production of electricity by animals cf. Biedermann, l. c., pp. 302, 408.

[4] On stream currents, and on electrical endosmosis, cf. Winkelmann, Handbuch d. Physik, 1893, Bd. III, i, pp. 493, 504; G. Bredig, Zeitschr. f. Elektrochemie, 1903, Bd. IX, p. 738.

[5] Kunkel, l. c., 1878, 1881; cf. Haake, l. c., p. 457.

[6] Whether changes of concentration or of resistance take part in the phenomenon is uncertain. Protoplasmic streaming may be inhibited without the production of electricity being appreciably

of an internal injury, for the wound-reaction is only manifested after a certain latent period. It is not impossible that the sudden bending might modify metabolism, although in the case of the leaf of *Dionaea* the variations in the current produced by excitation begin before the leaf closes. The resulting movements of water may, however, then aid in maintaining differences of potential[1].

Dionaea muscipula. The leaf of this plant shows in the resting condition a similar distribution of potential to that of an ordinary leaf, whereas after stimulation pronounced disturbances occur according to Burdon-Sanderson and to Munk. The former, using extremely delicate modes of investigation, found that a variation of the current in the external circuit took place 0·04 of a second after the application of a single weak induction-shock, whereas the resulting movement began only after a latent period of a second, the closure of the leaf-lobes requiring 5 to 6 seconds for completion at 20° C. If the shock is extremely weak, the electrical variation may be produced without any movement resulting. Presumably the electrical response is an indication of the commencement of chemical or other changes which, when completed, lead to a movement. That this stimulatory action spreads rapidly is shown by the speed of propagation of the electrical variation, for this occurs only 0·05 of a second later at a point 10 mm. away, the velocity of propagation being therefore 200 mm. per second. The progress and character of the electrical variation strongly resembles that shown on animal objects[2].

A pulvinar thorn on the leaf of *Mimosa pudica* is strongly positive to the upper surface of the pulvinus, and according to Kunkel[3] a marked electrical variation ensues when the leaf is stimulated.

Injuries produce pronounced electrical variations, and these possibly initiate or at least indicate the commencement of the disturbances leading to the wound-reaction. According to Hermann, Ranke, Velten, and Kunkel the injured region usually becomes negative or more negative towards the uninjured part. Hence an injured stem may yield a current although none was shown when intact[4]. Indeed the current of injury was the first one observed, for a considerable difference of potential often exists between the injured and uninjured surfaces[5].

Not only is the injured surface of a previously quiescent stem negative to uninjured regions, but also points on the latter near to the injury are negative

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affected. Cf. Velten, l. c., p. 295; Haake, l. c., p. 480; Hörmann, Studien ü. d. Protoplasmaströmung bei den Characeen, 1898, p. 72.

[1] A. Tompa (l. c., p. 116) denies Waller's statement (Proc. of the Physiol. Soc., 9. Nov., 1901; Centralbl. f. Physiol., 1901, Bd. XV, p. 480) that local blows produce current-variations, but his experiments are not conclusive. Cf. also Bose, Journ. of Linn. Soc. Botany, 1902, Vol. XXXV, p. 275.

[2] A complete summary is given by Biedermann, l. c., p. 455.

[3] Kunkel, l. c., 1878, p. 11; Dubois, Centralbl. f. Physiol., 1899, Bd. XIII, p. 699.

[4] According to Tompa (Beiheft z. bot. Centralbl., 1902, Bd. XII, p. 117) a current of injury is perceptible on injured air-dried seeds.

[5] Internal currents may be present in a plant-organ although no external current can be led off, whereas a resting muscle shows no internal currents. Cf. Biedermann, l. c., p. 288.

to those further away. The reaction extends for a limited distance, for Kunkel[1] could observe no difference of potential on a previously isoelectric stem when the electrodes were placed 5 and 6 cms. away from the injury. When a piece is cut out of a stem, the two cut surfaces are isopotential and the greatest difference of potential exists between the median point of the stem and either cut surface. Right and left of the median line isopotential zones exist, the connexion of which, by an external circuit, produces no current. The distribution of potential is therefore exactly the same as on an isolated cylindrical muscle, in which it has been more deeply studied[2].

If the epidermis is removed from the segment of the stem, the current is immediately reversed according to Ranke and Velten[3], flowing from the transverse section to the longitudinal surface in the external circuit. A similar reversal may take place, according to Hermann, on pieces of stem in which the epidermis remains uninjured, and which showed at first similar currents to those in muscle.

There are exceptions to these rules, and possibly more will be found in the future. Thus Ranke[4] found that on the petiole and peduncle of *Nymphaea alba* the current passed from the transverse surface to the longitudinal epidermal one both before and after the epidermis had been removed, while Velten[5] found that the current directed from the longitudinal surface to the transverse one persisted after the removal of the epidermis.

The current of injury is produced instantly, so that if the electrodes are laid on the stem and an incision made near to one of them, an immediate deflection is produced in the galvanometer. It is, however, uncertain whether the reaction is purely one of physical chemistry or is due to a vital action such as that which leads to the closure of the leaflets of *Dionaea*. In ordinary tissues the electrical changes might form the first indication of the physiological reaction leading to an increased activity of respiration and an enhanced production of heat. It is also unknown to what extent the electrical changes are connected with the gradual progress and development of the wound-reaction. The electrical variations are produced when neither electrode touches the cut surface, as well as when it is at once washed with water. Kunkel[6] found that local bending also produced a negative variation at the part affected, and it has yet to be determined whether this variation and the variation due to injury are produced in the same way. If so, then the injury and death of cells would not form an essential condition for the production of the 'injury' current. In all cases it must be remembered that the removal of the epidermis decreases the previous electrical resistance, and furthermore that electrical stimulation may considerably increase the conductivity more especially of young and highly protoplasmic tissues such as the cambium and apical meristem.

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[1] Kunkel, Arb. d. bot. Inst. in Würzburg, 1878, Bd. II, p. 6.

[2] Cf. Biedermann, l. c., p. 275.

[3] Ranke (l. c.) calls the current led off from an uninjured epidermal surface the false, and that from the injured epidermal surface the true plant-current.

[4] L. c., p. 197.

[5] L. c., p. 291.

[6] L. c., 1878, p. 7.

CHAPTER VI

THE SOURCES AND TRANSFORMATIONS OF ENERGY IN THE PLANT

SECTION 87. **General View.**

THE fact that all vital activity is bound up with a liberation of chemical energy by respiration gives no indication of the mode in which the energy is utilized, nor does this energy necessarily become immediately manifested externally as movement, heat, light, or electricity. It may be stored as potential energy in the form of food-materials, or as osmotic energy which, together with surface-tension energy, form two physical factors of the utmost importance to plants.

During photosynthesis the plant stores up food-materials and energy for future or immediate use, and the energy thus obtained may never enter directly into metabolism. For instance, many substances present in the plant exert a considerable osmotic action without ever being drawn into metabolism, being absorbed directly from the soil and accumulated in the cells by a purely physical process of selective absorption and passive secretion. Transpiration affords another instance of the creation of a difference of potential which aids the ascent of water in trees, and hence is of considerable importance in the vital economy without being a purely vital function.

The action of any form of energy in the plant is largely dependent upon the structural arrangement and physical properties of the cells and tissues, so that the same form of energy may produce widely different results in different plants, or in different parts of the same plant, or in the same part at different times. Every physiological action is coupled with a transformation of energy, and for a complete causal explanation of any such action not only must the sources and transformations of energy be known, but also the metabolic changes connected with them. Locomotion, growth, translocation, the production of heat, light and electricity, and constructive and destructive metabolism in general, all involve transformations of energy which may become perceptible internally or externally, and which are to be regarded as manifestations of vital activity.

Apart from the locomotory movements which are absent from most plants, as many external manifestations of energy are shown in the vegetable kingdom as among animals. A growing plant, for instance, may exert considerable pressure against a resistance. The internal manifestations of energy during growth are probably very similar in both animals and plants, but must acquire much greater intensity in an actively vegetating bacterium than in a slowly growing animal. The respiratory activity and the production of heat are in fact much greater in rapidly growing Fungi and Bacteria even than in warm-blooded animals. The luminescence of a few plants and animals, as well as the feeble production of electricity, represent relatively little energy. As compared with ordinary animals and Fungi, chlorophyllous plants and animals have the advantage of being able to convert a portion of the radiant energy of the sun into potential chemical energy.

Although vital activity is in the first instance based upon chemical energy, nevertheless all the natural forms of energy may take part in one or other of the detailed reactions in the plant. Since electrical currents do actually circulate in plants, and since every current radiates magnetic lines of force while the different constituents of the cell have varying magnetic permeabilities, it is impossible to deny that even magnetic forces may take part in certain vital phenomena, more especially where a directive or sorting action is necessary. Thus the direction and maintenance of regular streaming in a constant direction may involve some action dependent upon the paramagnetic properties of the cell-wall and the varying magnetic permeabilities of the remaining cell-contents[1]. In this connexion it is interesting to notice that a constant direction of streaming is only maintained in cells provided with a cell-wall, or in cells containing a single large central vacuole; so that the streaming protoplasm is near to and remains approximately equidistant from the cell-wall at all points. In naked cells, and in cells crossed by strands of streaming protoplasm, the direction of streaming is more or less variable and capable of reversal.

Osmotic energy is of the utmost importance in plants, and is a form of energy dependent upon the number of particles in unit volume and their kinetic energy. It is, therefore, comparable with gaseous pressure, and both osmotic pressure and gaseous pressure are related to diffusion, since all three involve the existence of movement among the molecular or ionic particles[2]. Surface-tension energy is involved in the phenomena of capillarity, imbibition, swelling, and also absorption so far as no chemical reaction takes place, for we may include under this form of energy all energetic manifestations shown between solid and fluid bodies independently of whether these take place between visible or invisible and external or internal component particles.

The energy of crystallization or of precipitation may be used in

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[1] Cf. Ewart, Protoplasmic Streaming in Plants, 1903, pp. 33, 45, 116.

[2] On the different forms of energy cf. Ostwald, Grundriss d. allgem. Chemie, 3. Aufl., 1899, p. 247; Lehrb. d. allgem. Chemie, 2. Aufl., 1893, Bd. II, Th. i, p. 11. In regard to plants cf. Pfeffer, Studien zur Energetik d. Pflanzen, 1892, p. 159, in which work the subject is discussed fully for the first time.

certain cases, although when the freezing of water produces frost-cracks, the liberation of energy is excessive and beyond the plant's power of control. According to the conditions and to the point of view energy produced by the precipitation of a solid or by crystallization may be regarded as a manifestation of volume energy, of chemical energy, or of surface-tension energy[1].

Work is done during all movements in overcoming the resistance of surrounding media and in displacing internal parts. In the latter case the work done may be stored up in the form of potential energy capable of sudden liberation, as in the tissue-tensions, in the pulvinus of *Mimosa*, the leaf of *Dionaea*, and various suddenly-dehiscing fruits. The upright growth of a shoot involves the storage of a certain amount of potential energy, which is manifested as kinetic energy when the trunk is sawn through, and is transformed mainly into heat when the trunk falls upon hard ground. The total amount of energy involved here is, however, trifling as compared with that represented by the raising of water during transpiration, and by the kinetic resistance which the ascending stream has to overcome.

The law of the conservation of energy and of mass holds good during all the transformations of energy in the plant. The energy stored up during life is ultimately set free on death either by decomposition, combustion, or by being drawn into the metabolism of some other organisms. There is no reason for assuming the existence of any special form of vital energy, since the same form of energy may produce the most varied results according to the mechanism on which it acts. The capacity of the organism for continued and automatically regulated growth and the hereditary tendencies of the germ-cells enable the offspring to employ the energy and food-materials in the same manner as the ancestors. Hence the species may remain unaltered although the descendants may contain not a single atom or a single trace of the energy represented in the primitive stock.

These considerations also apply to all stimulatory actions, for although the response may be altogether disproportionate to the stimulus, nevertheless the latter represents a certain amount of energy, independently of whether the exciting agent is a stimulatory substance or is physical in character. It has already been mentioned that by the aid of the regulatory mechanism gradual and continuous as well as sudden and transitory transformations of energy may be produced, and that a local inhibition of a particular energetic manifestation is possible.

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[1] Pfeffer, Studien zur Energetik, 1892, p. 163.

SECTION 88. **The Forms of Physical Energy used by Plants.**

OSMOTIC ENERGY. This special form of volume energy comes into play whenever a soluble substance is unevenly distributed. The diffusion thereby produced takes place in the same way as when different gases are mixed together, and if the particles of the dissolved solid or gas are unable to pass through a separating membrane, they bring to bear a pressure upon it which is dependent upon the number of the molecules in unit volume and upon their average kinetic energy. The latter, again, is constant for any large number of molecules at a given temperature and is equal to half the product of the mass of each molecule multiplied by the square of its average velocity. A rise of temperature which increases the velocity of movement of the molecules causes a slight rise of osmotic pressure, and also of the pressure of a gas kept at constant volume.

A purely physical diffusion movement must take place whenever any difference of concentration is produced in parts separated by permeable partition-walls. If, however, the walls are semipermeable a permanent osmotic pressure can be maintained, such as is commonly used in plants for various mechanical purposes. A naked cell or gymnoplast would be indefinitely stretched or burst by a high internal osmotic pressure, whereas in dermatoplasts covered by a cell-wall a comparatively high pressure is often required to render them fully distended and active. When death or plasmolysis allows the cell-wall to contract, the potential energy latent in it when stretched is manifested. Sudden decreases of turgor produced by a physiological reaction are responsible for the rapid movements of the stamens of Cynareae and of the leaves of *Mimosa*, which can be repeated as soon as the original turgor has been restored. The pulsation of certain vacuoles is, in some cases at least, produced by automatic variations of turgor.

In order to maintain the turgor in a growing and enlarging cell, a regulated production of osmotically active materials is necessary. During plastic growth the mechanical work involved in the stretching of the cell-wall is carried out by the previously accumulated osmotic energy. If, however, the growing organ encounters a resistance, the tension in the apposed cell-wall gradually decreases until nearly the whole of the osmotic pressure is acting against the resistance.

By a similar counteraction of active and passive tissues, tensions and pressures are produced which when released may lead to sudden movements, as during the dehiscence of the fruits of *Impatiens* or of *Momordica*. In these cases the potential energy is stored up by a definite physiological activity, whereas a purely physical action on a given mechanism is involved when the dry valves of the fruits of Leguminosae twist on drying and untwist on moistening, or when leaves droop for want of water and re-expand when supplied with it. The distinction is really one of little value, since in both cases the responding mechanism is a product of vital activity, and physical responses of this character are often capable of frequent repetition and may take place against considerable resistance[1].

The osmotic energy of the cell bears no definite or constant relationship to the energy consumed in the production and accumulation of the osmotic materials[2]. The former is entirely dependent upon the number of molecules, and remains the same whether energy is absorbed or liberated during their production. Furthermore, an osmotic substance may be directly absorbed from without and accumulated in the cell by passive secretion, but it exercises precisely the same osmotic action as if it were a product of anabolic metabolism or of katabolic respiration. The hydrolysis of insoluble starch by an enzyme produces osmotically active sugars, and the osmotic action is doubled when the large molecule of cane-sugar is converted by invertase or by dilute sulphuric acid into two molecules of grape-sugar. Similarly the reverse process, or the conversion of a soluble into an insoluble substance, will lower the osmotic pressure.

As in the case of a compressed gas, the presence of a dissolved substance in a cell only enables a limited amount of external work to be done, for with the increase in volume of the growing cell, the solution is diluted and the number of molecules per unit volume decreased, so that here, as in the case of an expanding gas, the pressure falls[3]. Hence the maintenance of growth involves a continued production of osmotic materials.

When a gas does work in expanding its temperature falls, and in exactly the same way when work is done by osmotic energy, as is the case when a cell grows by plastic stretching, the osmotic pressure falls. In both cases the work done is due to the energy of the moving molecules, and except in so far as the temperature affects the velocity of the molecules, and hence also the osmotic pressure they exert, it is immaterial to the plant whether its temperature is kept higher by respiration than that of the surrounding medium or whether it is kept permanently lower by transpiration. During transpiration itself the heat absorbed from without does work in altering the water from the liquid to the gaseous state, and this work is externally manifested when water is raised up a vertical stem by the suction of the leaves.

Apart from its chemical quality the value of a substance as a source of

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[1] Pfeffer, Studien zur Energetik, 1892, p. 236.

[2] Id., pp. 170, 172, 196, &c.

[3] On the work done during the expansion of gases see the textbooks of Physics. Rodewald (Ber. d. bot. Ges., 1892, p. 83) erroneously assumes that the mechanical equivalent of the heat of combustion of a substance must always be greater than its power of doing work by its osmotic action, and that bodies not produced in the cell can do no osmotic work. The latter statement hardly coincides with the fact that a passive or active absorption from without and an accumulation in the cell of soluble substances is possible.

energy is not measured solely by its heat of combustion, nor is the series of transformations it may undergo in the service of the organism immaterial. The osmotic action depends solely upon the number of the molecules and their kinetic energy, and not upon their potential chemical energy as measured by their heat of combustion. Hence substances may exert a powerful osmotic action when in solution, although completely oxidized compounds. A substance which first exercises an osmotic function and is consumed at a later date in respiration is more important physiologically than one utilized for one function only. If the product of oxidation is to retain an osmotic function and yet yield energy during its production, it is far better when substances like organic acids, having a low heat of combustion, are produced by respiration in place of the volatile carbon dioxide. Thus when a molecule of glucose is oxidized to three molecules of oxalic acid not only is the osmotic action trebled but also the greater part of the available chemical energy is set free in the form of heat[1].

SURFACE-TENSION determines the shape of drops of liquid, but it is not yet certain to what degree amoeboid movements are the results of spontaneous and induced changes of surface-tension coupled with alterations in the cohesion of the outer layers. The same applies to pulsating vacuoles, while protoplasmic streaming has been suggested to be due to the production of differences of surface-tension in the regularly arranged bipolar particles of the protoplasmic emulsion by the action of inwardly- or outwardly-directed electrical currents. It is, however, uncertain how far autogenic changes of surface-tension are responsible for the changes of shape of the nucleus, of plastids, or of the reproductive cells of flowering plants. Surface-tension may also take part in determining the fusion or non-fusion of gametes, and the movements of cilia[2].

When a solid is finely divided the surface-tension of its component particles becomes of increasing importance, since the inwardly-directed pressure exerted by it on a spherical particle is inversely proportional to the radius of the particle. The force with which particles of water or of other fluids are able to penetrate between the molecules or micellae of substances capable of imbibition and of swelling is the result of molecular forces akin to that of surface-tension. Absorption phenomena of this kind form a part of physical chemistry, and indeed the absorption of certain substances involves a loose chemical union, so that the process may be regarded as a physical or as a chemical one according to the point of view. Furthermore, many kinds of imbibition are produced in much the same way as the so-called solid solutions, as when two metals are placed in contact and the particles of one penetrate the other.

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[1] Pfeffer, l. c., pp. 173, 197; Rodewald, l. c.

[2] For theories of streaming cf. Ewart, Protoplasmic Streaming in Plants, 1903, p. 108.

Imbibition and surface-tension energy are probably of as great importance in vital economy as osmotic energy, and all these forms of energy, but especially the first named, may produce pronounced external manifestations, as during the swelling of wood, of seeds, or of starch, or during the imbibition movements of the awns of certain seeds which are repeated with each drying and moistening. The energy manifested in movements of this kind naturally bears no relation to the consumption of energy involved in the production of the reacting mechanism, since the latter merely directs the operation of the heat-energy derived from without. The same applies to movements due to changes of surface-tension resulting from diffusion, evaporation, or the action of electrical currents.

SECTION 89. **Chemical Energy.**

The production and accumulation of various substances enables the plant to utilize osmotic and surface-tension forces, and metabolism may also produce electrical currents, though it is uncertain whether these are of much value in the vital economy. By means of the former forces, however, the plant is able to convert heat into work, whereas the direct production of heat by respiration serves no such useful purpose as does the fire in a steam-engine, and it is almost entirely dissipated by radiation, conduction, and evaporation. In other words, the protoplast is neither a thermodynamic nor an electro-dynamic machine.

It is by no means certain to what extent chemical energy may be directly utilized for chemical purposes, either within the plant or outside of it. In any case, mechanical work is done when a chemical action involves the dissociation and recombination or rearrangement of molecules. The same applies whenever a chemical action involves an increase in volume which takes place against the atmospheric pressure, or when a substance is crystallized or precipitated in a colloid medium whose resistance has to be overcome. In the latter case, however, if the production and separation of the substance are distinct phenomena, the separation may be regarded as a physical manifestation of volume energy independently of whether it is produced by crystallization, by absorption, or by the removal of a solvent.

Phenomena of this kind play a prominent part in all vital actions, for the growth of the protoplasm by intussusception involves the intercalation of new particles between pre-existent ones. Chemical changes, surface-tension energy, the chemical affinities of the various materials, and imbibition may all take part in this process and determine whether the new material shall be tacked on to particular micellae or placed between them. During the growth by intussusception of the cell-wall, the influences radiating from the pre-existent particles take an important part in determining the character of growth, and the penetration of the new particles, whether produced by chemical or physical attraction, may take place against considerable external resistance, and hence may render the plant capable of performing pronounced external work.

The production of heat by an ordinary plant has no direct importance in metabolism, for this is not appreciably affected by a rise of a fraction of a degree, and plants develop normally when kept slightly cooler by transpiration than the surrounding medium. Although aerobic respiration is always connected with a production of heat, this need not always be essential, and it is not impossible that anaerobic organisms may exist whose metabolism involves a lowering of temperature. It is in fact, as far as our present knowledge goes, impossible to affirm that no existence is possible without the production of heat by metabolism. In the case of all physiological actions due to a chemical product, it is immaterial whether the product is the result of an endothermic or exothermic reaction. Chemical actions involving a liberation of heat are more readily induced than exothermic ones, and hence may be preferably employed by the organism[1].

Vital activity is inseparable from metabolism, and even adult organs which have ceased to grow must respire as long as they live. The plant may be compared to a factory in which all work ceases when the fire is drawn, although the capacity for work may be retained during short periods when the energy of the steam-engine is put to other purposes than driving the different bench-machines. If the energy of the steam is mainly employed in overcoming frictional resistance in the different mechanisms, practically the whole of the chemical energy of the coal may be manifested as heat.

It has already been mentioned that the accumulation of waste products has to be avoided as far as possible, and it is of interest to notice that for the most part carbo-hydrates capable of oxidation into carbon dioxide and water are used in metabolism. The nitrate and nitrite bacteria, which oxidize ammonia and nitrous acid, as well as the sulphur bacteria which oxidize sulphuretted hydrogen, derive in this way energy for the synthesis of organic food and probably for the whole of their vital activity as well. If this is so, and these organisms use carbon compounds solely as building-materials and directly utilize the energy obtained by the oxidation of inorganic compounds in place of ordinary respiration, then a close study of these organisms should throw much light upon the nature of life[2].

It might also be possible to determine whether proteid molecules are continually decomposed and regenerated during respiration, or whether

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[1] Cf. Pfeffer, Studien zur Energetik, 1892, p. 174.

[2] Nathansohn, Mittheil. a. d. zool. Station zu Neapel, 1902, Bd. XV, p. 655, finds that no carbon dioxide is produced during the respiration of certain aerobic Bacteria, which carry out chemosynthetic assimilation by the aid of the energy derived from the oxidation of thiosulphates.

the respiratory materials, such as sugar or oil, are able to be directly oxidized owing to their fine subdivision and intimate association with protoplasmic molecules[1]. The fact that during the anaerobiosis of yeast and of butyric bacteria sufficient energy is obtained by the intracellular fermentation of sugar produced by an enzyme capable of isolation[2] points to the fact that sugar present in the cell can be decomposed without its being chemically united with the protoplasm.

The exact extent to which chemical, surface-tension, or osmotic energy is used for the different forms of work carried out by the organism is uncertain, but even if the chemical energy is not directly utilized, its transformation still forms the essential accompaniment of all vital activity. Similarly, the work done by all the machines in a factory is derived from the chemical energy of the coal consumed, even when the energy of expansion of the heated steam is used to drive an electric motor and the electric energy transmitted to the different machines[3]. The special advantage attached to the use of chemical energy in both manufactories and in organisms is due to its forming a specially concentrated form of potential energy which is readily rendered kinetic.

The difference between the heat of partial or complete combustion of the substance used in respiration and the actual production of heat indicates how much of the realized chemical energy is converted into work, but says nothing as to the details of the processes involved. Calorimetric investigations are nevertheless of great importance in the study of special questions, although the utmost care is required even to obtain approximately accurate results. In many cases, for instance, the quality and quantity of the substances consumed and the degree of oxidation they undergo cannot be exactly determined, so the amount of oxygen absorbed and of carbon dioxide exhaled form unsafe guides as to the total heat of combustion[4].

Nor are we able to determine the heat equivalent of the mechanical and other activities of the plant with sufficient accuracy. Owing to the high mechanical equivalent of heat a considerable amount of work might be done without the amount of heat liberated being appreciably lowered. Furthermore, all energy used in overcoming friction or viscosity, or in producing swelling, ultimately appears in the form of heat. Hence it is not surprising to find that Rodewald observed that in the case of apples and kohlrabi all the chemical energy of respiration appeared in the form of heat, the estimated and observed values practically balancing. The differences observed by Bonnier between the calculated and actual amounts of

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[1] Cf. Nathansohn, Mittheil. a. d. zool. Station zu Neapel, 1902, Bd. XV, p. 655.

[2] See Buchner, Die Zymasegährung, 1903, where all the latest literature is collected.

[3] The production of differences of potential enables particular partial functions to continue for a time in the absence of oxygen.

[4] Cf. Pfeffer, l. c., 1892, p. 201.

heat in the case of seedlings are probably due to the fact that the respiratory oxidation is not in all cases complete, and that endothermic changes preponderate in growth and constructive metabolism.

The whole of the energy transformed into heat is gradually lost by the plant, although it may aid in maintaining transpiration when the temperature of the plant is lower than that of its surroundings. In aquatic plants, however, and in general in the absence of transpiration, the production of heat serves no useful purpose apart from its biological significance in Aroids. Poikilothermic organisms like plants lose much less energy in the form of heat than megatherms like mammals and birds whose body-temperature must be kept approximately constant, but in general the modes of utilization of the liberated chemical energy for mechanical purposes are approximately the same in plants and animals[1].

In plants, however, the chemical energy liberated by metabolism seems to appear almost entirely in the form of heat, and hence very little can be used for mechanical purposes. In some cases, however, a reaction may be performed very economically as, for instance, during the contraction of a muscle or of the stamens of Cynareae, in which less heat is produced relatively to the work done than in a steam-engine or gas-motor[2]. In a muscle performing maximal work one-half of the liberated chemical energy may appear in the form of work, and one-half as heat, whereas it requires a good engine to utilize more than ten per cent. of the energy of the coal consumed; and during the protoplasmic streaming of an ordinary plant-cell not more than $\frac{1}{10000}$ of the energy of respiration is consumed in this form of work[3]. The plant may work more economically under certain conditions than under others. Thus respiration increases continuously up to the lethal temperature, whereas growth and other manifestations of energy are retarded beyond the optimum. Hence in general the plant works more economically at moderate temperatures than at high ones. It must further be remembered that chemical composition is a more important factor in a living organism than in a machine, and that the economic coefficient, that is the ratio between the food absorbed and the increase of body-weight, may vary according to the prevailing conditions. Since the nutritive value of a substance depends upon its chemical constitution, its heat of combustion forms no sure guide as to its nutritive value[4], although when different materials are consumed

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[1] Plants consume their food more completely than animals, which excrete combustible end-products of metabolism.

[2] Cf. textbooks of Physics and Animal Physiology, as well as the Traité de physique biologique published by d'Arsonval, 1901, T. I, p. 982.

[3] Ewart, Protoplasmic Streaming in Plants, 1903, p. 29.

[4] Cf. Pfeffer, Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 258.

in respiration each liberates exactly the same amount of energy as when similarly decomposed or oxidized outside the plant[1].

SECTION 90. **Special Cases.**

A few special instances may be discussed to illustrate the application of the foregoing principles to concrete cases in which energy is consumed in overcoming resistance, independently of whether the energy used is at once dissipated or is in part stored up again for future use.

ABSORPTION AND TRANSLOCATION[2]. Any unequal distribution, however produced, tends to set up purely physical diffusion-currents which ultimately restore equilibrium. It is immaterial whether the unequal distribution is produced by the organism with or without a consumption of energy by solvent enzyme action, or by the absorption or separation of soluble constituents of the cell-sap. Since diffusion movements are extremely slow, mechanical mixing and streaming movements become of great importance in ensuring the rapid transference of substances from one place to another[3]. Plants fixed to the soil are in part dependent upon the movements of the surrounding air or water for a rapid supply of food-materials.

Diffusion and currents of wind carry carbon dioxide to the summit of a tree, and the carbon accumulated there represents stored potential energy without the tree having raised any portion of it to this height. The same is the case when a dissolved substance diffuses upwards from the roots, and even although the upward passage may be aided by mixing or bending movements, by thermo-diffusion, or by convection currents, and by upward streams of water produced by transpiration, none of these necessarily involves any consumption of energy on the part of the plant. In other cases, again, streaming and mixing movements resulting from protoplasmic activity may aid in translocation without being essential, although the translocation of dead or living materials through the pores of sieve-tubes and through the inter-protoplasmic connexions of ordinary cells could hardly take place without the aid of the protoplasm[4]. In

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[1] See Rubner, Die Gesetze des Energieverbrauchs bei der Ernährung, 1902. Cf. also F. Mares, Biol. Centralbl., 1902, Bd. XXII, p. 282.

[2] Cf. Pfeffer, Studien zur Energetik, 1892, p. 268.

[3] [The rate of diffusion is more rapid than is usually supposed, especially when chemical fixation aids in maintaining a high gradient of concentration along the path of the diffusion currents. Even without this, less time is required for the complete diffusion of a dissolved salt through an ordinary plant-cell than the protoplasm takes to stream around it when streaming is active. The transference of a substance across a broad band of tissue by diffusion alone would, however, still be an extremely slow process. Cf. Ewart, On the Ascent of Water in Trees, Phil. Trans., 1905, p. 40 of reprint.]

[4] [The inter-protoplasmic connexions of ordinary cells are of no importance in translocation. Thus under normal conditions it would take 100 years for the transference of 1 cub. mm. of the cell-

discussions of this kind the activity of the living organism and the existence of the potential differences it produces are taken for granted, and even during absorption, especially when preceded by digestion, activities may be involved which are directly due to the living plant.

THE MOVEMENTS OF WATER. The loss of water by transpiration, or any production of osmotic substances in a cell capable of further distension, will tend to draw water to the region affected from surrounding parts richer in water. This action is capable of exerting suction over a greater or less distance, according to whether the suction is exerted upon vessels filled with water or containing chains of water-columns and air-bubbles. In the former case the resistance to flow is directly proportional to the viscosity of the liquid, to the internal surface of the tube through which flow occurs, and to the velocity of flow. In the case of circular tubes with smooth walls the volume passing is greater than with any other shape of bore, and the rate of flow under equal pressures in such tubes is inversely proportional to the square of the radius and the length of the tube. The total resistance due to the viscosity of the water flowing through the vessels is less than the height of the tree when the vessels are filled with water, but when they contain alternating columns of water and air another resistance is introduced which is due to the adhesion of the surface-tension films at the ends of the air-bubbles to the inward projections or perforate partitions where the segments of the vessel join. This resistance is inversely proportional to the diameters of the vessels or pores, and to the difference in convexity between the ends of the bubbles, and it is usually sufficient to produce a total resistance equivalent to a head of water many times the height of the tree.

Ewart[1] has, in fact, calculated that the total resistance to an average rate of flow in the trunks of the tallest trees may be equivalent to pressures of as much as 100 atmospheres, suction-pressures which are not only incapable of being generated by transpiration and osmotic action in the leaves, but which also cannot be transmitted through the wood-vessels to the roots. The maximal strain which a water-column free from air-bubbles is able to withstand appears to be about five atmospheres, and in the presence of air the greatest negative pressure produced in the wood-vessels is usually not more than half an atmosphere.

Hence it appears that a continuous adjustment equivalent to a stair-case pumping action must go on in the trunks of tall transpiring trees, and Ewart[1]

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contents from one cell to another through 3,000 threads of $\frac{1}{10}\,\mu$ diameter, and the surface-tension pressure exerted at the end of the thread, if in air, is as much as 34 atmospheres. In 50 cm. length of the cribral system of *Cucurbita*, however, a pressure of only $\frac{1}{2}$ an atmosphere would suffice to produce an approximate rate of flow of 5 mm. per minute. See Ewart, On Protoplasmic Streaming in Plants, 1903, pp. 29-30.]

[1] Ewart, On the Ascent of Water in Trees, Phil. Trans., 1905, p. 15 of reprint.

has suggested that surface-tension actions of this character may be exercised by the wood-parenchyma cells along the path of the current. This has still to be proved, however, and also whether the breaking strain for continuous water-columns is the same in such tubes as the tracheae and tracheides as in glass tubes of larger bore.

The exact causation of bleeding is by no means clear, and in fact it is quite possible that in some cases it may be produced in the same way as the plasmolytic excretion of water from nectaries, with the exception that the osmotic substances which have drawn water into the vessels may be reabsorbed in their upward passage [1].

During the plasmolytic excretion of water from nectaries the plant provides for the external deposition of the sugar, which draws out water from the turgid cells beneath and so produces nectar. This physical action takes place whatever the source of the sugar, and in this respect it is immaterial whether the sugar is produced by a metamorphosis of the cell-wall, or is formed in the cell, and excreted externally.

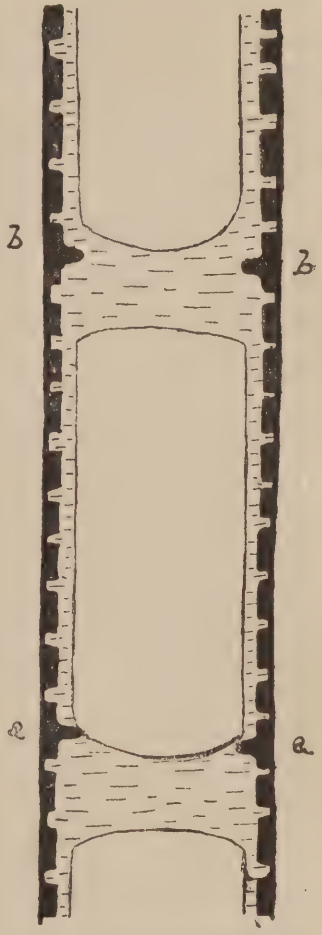

FIG. 69. Diagrammatic longitudinal section of a segment of a vessel. The ends of the segments at *a a*, *b b*, form the adhesion points of the surface-tension films. (After Ewart.)

GROWTH. During plastic growth the stretching of the cell-wall is due to the osmotic pressure in the cell, whereas when the cell-wall grows by intussusception, growth may take place against the osmotic pressure, as during the internal thickening of cell-walls. When a growing cell encounters a resistance, the tension of the cell-wall is gradually counteracted until the full osmotic pressure is acting against the resistance. In some cases the mechanical retardation of growth produces a rise of osmotic pressure, but the latter determines in all cases the maximal pressure which a thin-walled growing organ can exert. Thick-walled organs, however, so long as the cells grow by intussusception, can exert greater pressures than those corresponding to the osmotic pressures of the component cells [2].

If the resistance is not too great growth is resumed as soon as the organ exercises a pressure greater than the resistance, and if the latter is pushed in front of the growing organ the work done is equal to the product of the force applied and the distance its point of application is moved. With moderate resistances or loads the original activity of growth is soon

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[1] Ewart, Phil. Trans., 1905, p. 42.

[2] Cf. Pfeffer, Druck- und Arbeitsleistungen, 1893.

nearly or entirely resumed, but when the resistance increases progressively growth is naturally more and more retarded. In the former case, however, more work is done than when growth is entirely unrestricted, just as in the case of a man walking at the same rate in still air and against a strong wind.

The external work done must reach a maximal value with a definite resistance, since no work at all is done at either extreme, that is, when no growth is possible or when no resistance is applied. The actual amount of external work done affords, however, no criterion as to the internal work involved in growth, and the latter may remain unaltered when the plant is caused to do considerable external work against a resistance [1].

Similar considerations apply to tissues [2], for in them the slowly growing or inactive cells constitute the resistance which is subjected to tension by the elongation of the more rapidly growing cells. The conditions are, however, somewhat more complicated, since, in part at least, we are dealing with cells capable of growth-responses, and if the stretched tissues continue to grow when the organ is enclosed in a rigid plaster cast, their tension disappears and the compressed tissues act against the cast. This occurs in the nodes of grass-haulms, whereas in many cases the tissue-tensions do not entirely disappear even after prolonged enclosure in a plaster cast. On setting free the organ the original tissue-strains are gradually restored, and the same applies to the individual cells whose walls are again stretched by the internal osmotic pressure. Since, however, the cohesion of the cell-wall is unaltered, no ruptures occur however suddenly the external resistance is removed.

Curving organs are often able to perform considerable external work. Thus a horizontally-placed shoot may still be capable of a geotropic curvature although it is forced to counteract from four to thirty times the normal mechanical moment, and the curvature is only slightly retarded with a moderate load, although much retarded by a considerable one. Even a slender root may exert a considerable thrust if lateral displacement is prevented, and in the same way shoots are able to break through stiff soil.

The bursting of the hard coats of seeds, the splitting of the bark by the growth of the wood, and the strangulation of trees by lianes, are all instances in which a considerable external force is exercised as the result of physiological activity.

The rapid movements of the stamens of *Parietaria*, the sudden dehiscence of the fruits of *Impatiens* and *Momordica*, are produced by the sudden release of tensions gradually built up during growth. The twisting and untwisting of the fruit-valves of Leguminosae produced by imbibition and drying, as well as the similar movements of the awns of certain

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[1] Pfeffer, Druck- und Arbeitsleistungen, 1893, pp. 330, 419.

[2] Id., 1893, pp. 379, 400, 426.

grasses, are purely physical in origin. Whereas in the first-named cases not only does the plant see to the storage of the required potential energy, but also so regulates matters that the tensions are released spontaneously or by an external agency at a definite time. Since the contracting tissues are never perfectly elastic, the full amount of the stored energy can never be used in propelling the seeds[1].

Mechanisms of this kind are only capable of a single response, whereas the regeneration of the tissue-tensions in the stamens of Cynareae, and in the pulvini of *Mimosa*, renders frequent repetition possible. A sudden fall of turgor allows the elastic walls to contract, the restoration of turgor redistends them, but whether changes in the elasticity of the cell-wall may also occur is uncertain. From a mechanical point of view the mode in which turgidity is restored is immaterial, and the escape of water is the result of the fall of turgor, so that sudden contraction can only take place when a rapid filtration of water under pressure through the cell-wall is possible.

The energy of contraction is as great in these motile tissues as in animal muscle, in which it may be from 1 to 10 kilograms per sq. cm., while a load of 5 kilograms per sq. cm. is required to prevent a staminal filament of one of the Cynareae from contracting. In both cases most work is done when the load is such that contraction is just possible, and to get the full contraction the load must be steadily decreased as contraction continues[2]. Otherwise an excessive load at any phase of contraction prevents the shortening and hence also prevents work from being done. In precisely the same way the maximal work is done during the subsequent elongation of the filament, if a resistance is interposed of sufficient intensity to prevent movement until turgor is fully restored, and if the filament is then allowed to elongate to its full extent by gradually removing the resistance. A growing organ, on the other hand, which exerts a constant pressure upon a resistance pushed in front of it, performs the same amount of work in unit time so long as the rate of growth remains the same.

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[1] Pfeffer, Studien zur Energetik, 1892, p. 239.

[2] Pfeffer, l. c., pp. 236, 238. The same applies to the work done during the expansion of a compressed gas, or the contraction of a rarefied one. It is uncertain whether the slight increase in the production of heat in the pulvinus of *Mimosa pudica* during a movement produced by stimulation is due to a chemical reaction, or to the internal friction produced as the water escapes through the cell-sap. [The latter is hardly probable. Suppose a total of 5 gram. centimetres of work were done, a high estimate, this would represent $\frac{1}{10^4}$ of a calorie. If the region warmed corresponded to 5 mg. of water, it would be raised only $\frac{1}{50}$° C. in temperature, even if all the heat was retained during the whole time of contraction. It must further be remembered that in cells bounding intercellular spaces the surfaces of the cell are, owing to evaporation, colder than the cell-sap, which is entirely enclosed by the heat-producing layer of protoplasm. Hence a thermo-electric needle lying in an intercellular space or in a pierced and collapsed cell will show a rise of temperature as the warmer cell-sap exudes from the surrounding cells.]

The high energy of expansion and contraction in the stamens of Cynareae and in the leaves of *Mimosa* enables these organs to raise a considerable weight in addition to their own. According to Schilling[1], a stimulated leaf of *Mimosa pudica* returns to its original position after the statical moment exercised upon the primary pulvinus has been increased from two to four times by the attachment of weights. This is probably due to the fact that the change of position produced by stimulation awakens reactions directed towards the restoration of the original position ; and hence a leaf slowly rises up again after it has been merely bent somewhat downwards by the addition of a weight without being stimulated. The exact causal relationship of these phenomena is, however, not satisfactorily determined by Schilling's experiments, which also leave it uncertain to what degree a similar power of reaction is possessed by other pulvini. In any case, however, the mechanical factors concerned in the movements of irritable pulvini and of the stamens of Cynareae have been more fully explained than those involved in muscular movement.

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[1] A. J. Schilling, Der Einfluss von Bewegungshemmungen auf die Arbeitsleistungen d. Blattgelenke von *Mimosa pudica*, 1895, p. 11.

APPENDIX

In the following pages some important facts not mentioned in the first two volumes are given, and also a summary of the more recent literature, especially that connected with the present volume.

Action of Röntgen and Radium Rays. Koernicke (Ber. d. D. bot. Ges., Bd. XXII, 1904, pp. 148–55) finds that the Röntgen and radium rays slightly accelerate the germination of dry seeds, and retard growth if the exposure is sufficiently intense and prolonged. The retarding effect may remain latent for a time, and may be preceded by a temporary acceleration.

Correlation and Growth. Lindemuth (Ber. d. D. bot. Ges., Bd. XXII, 1904, p. 171) states that the leaves of *Begonia rex*, of *Iresine Lindeni*, and of other plants on rooting increase in size, and concludes that this is due to the enlargement of the individual cells. The latter can hardly apply to the non-living cells of the leaf so that internal distorsions or ruptures should ensue in such leaves.

Ewart (Annals of Botany, Jan., 1906) has shown that by an early removal of all the buds but one, the leaves of the Lime (*Tilia europaea*) may be caused to develop to twice or thrice their normal size, and that this increase in size is due to an increase in the number of cells in each leaf, their sizes being approximately constant. No growth could be awakened in leaves which had ceased to grow.

The Phloroglucin Reaction is due to the presence of *Hadromal*, an aromatic aldehyde which is destroyed by potassium permanganate or hydroxylamine.

Wood sections treated with hydroxylamine no longer give the phloroglucin reaction, but if treated for five minutes with 1 per cent. $KMnO_4$, washed with HCl, and then exposed to NH_3 vapour they turn red, giving a true 'lignin' reaction. Hadromal occurs in many non-lignified cells (hard bast of certain plants, endodermal cells and cork cells). These give no reaction with $KMnO_4$, except in the case of the endodermal cell-walls of *Iris*, which appear to be truly lignified.

Cleistogamy. On the causes and occurrence of cleistogamy, see K. Goebel, Biol. Centralbl., 1904, Bd. XXIV, p. 673 seq. See also Klebs, ibid., p. 545 (Ueber Probleme der Entwickelung).

The Mechanical Properties of the Red and White Wood of Conifers have been investigated by Sonntag (Jahrb. f. wiss. Bot., Bd. XXXIX, p. 71), with the following results:

	Red wood tracheides.	White wood tracheides.
Length	2	1
Incrusting materials	$80x$ %	$60x$ %
Tensile strength of walls	1	3
Resistance to pressure per unit area of wood	(walls thicker) higher	lower
Comparing walls alone	slightly higher	slightly lower
Capacity for stretching	1·5 to 2·5 % of length	the same
But Modulus of elasticity	1	2 (Hartig).

Branches are as strong in the inverted as in the normal positions, until the limit of elasticity is reached with increasing loads, when the normal position is best. The red wood is more strongly lignified and swells less. It appears on the pressure side, in all cases, even when this is the side in the erect position compressed by the wind. The response, hence, does not appear to be due to the stimulatory action of gravity, but Sonntag concludes that heliotropic influences take part in inducing the differentiation.

Observations by Ewart and Mason-Jones (Annals of Botany, 1906) upon the formation of red wood in lateral and main axes of *Cupressus* and *Pinus* bent forcibly into a circular form, show that the red wood mainly appears upon the under-surfaces whether these are stretched or compressed, and thence spreads into the neighbouring vertical or nearly vertical regions of the curved axis. It appears therefore to be the result of a gravitational stimulus, which spreads along the same side from the point directly stimulated. It is difficult to see how differences in the intensities of illumination on the upper- and under-surfaces could act in the way Sonntag supposes upon the living cambium of old stems covered by thick opaque layers of bark. Nor can differences of temperature come into play since otherwise red wood would appear on the sunny side of an erect stem.

Formative and Inductive Action of Light. According to observations made by Dr. Buller at Birmingham, one half to one hour's exposure to light is sufficient to induce the formation of a pileus upon the branching strands of *Polyporus squamosus* developed in darkness. After several weeks' continuous darkness, however, small patches of spore-bearing tubes are formed at intervals on the under-surfaces of the strands, but some were even formed upon the upper-surface of an imperfectly developed pileus. In normal healthy pilei, the hymenial tubes are positively geotropic in both light and darkness.

Autonomic Movements. Molisch (Ber. d. D. bot. Ges., Bd. XXII, 1904, p. 372) observed very rapid autonomic movements in *Oxalis hedysaroides*, H. B. K., the leaflets falling suddenly or in jerks through 1 to 1½ cm. in 1–12 seconds.

Photonastic and Thermonastic Movements. W. Wiedersheim (Jahrb. f. wiss. Bot., 1904, Bd. XL, p. 230) finds that the photonastic and thermonastic movements of flowers and leaves involve a general acceleration of the average rate of growth, which is shown even when movement is prevented. This is produced first on the concave side, and later on the convex, which latter results in a more or less pronounced return curvature. Since a forced mechanical curvature does not cause any such return curvature when the leaf is released, it can hardly be due to an autonomic orthotropic response, as Schwendener and Jost suppose it to be. In other words, both sides of the leaf or halves of the pulvinus react in the same way, but one responds more rapidly than the other. The fact that *Impatiens parviflora* performs its sleep-movements on a klinostat, and hence is 'autonyctitropic,' was first observed by Fischer (Bot. Ztg., Bd. XLVIII, 1890, No. 42).

Dispersal Movements. The spores of *Agaricus*, *Polyporus*, *Boletus*, *Coprinus*, and other Hymenomycetes, do not merely fall off, but owing to the sudden rupture of the stretched cuticle are jerked off with sufficient energy to clear the hymenium, without striking the opposite gill-lamella or pore-wall. The vertical arrangement allows them to fall clear, but, owing to their small size, they descend in still air, in accordance with Stokes' formula with a constant velocity of from a few mm. to cms. per second. (Observations by Buller at Birmingham.)

Geotropism. Figdor (Ber. d. D. bot. Ges., 1905, Bd. XXIII, p. 182) finds that the leaf-sheaths of various grasses perceive and respond to geotropic and heliotropic stimuli, whereas the laminas (Rothert) are irresponsive.

H. Fitting (Jahrb. f. wiss. Bot., 1905, p. 221) finds that in all cases the maximal excitation is produced in the horizontal position, and not at an angular deviation of 135° from the equilibrium position, as is usually supposed. With angles less than 30° the excitation decreases somewhat more rapidly than the size of the angle of divergence, but otherwise they are approximately proportional. Plants rotated obliquely once every second show a geotropic curvature as the result of the summation of successive geotropic stimuli.

Large angles of divergence must differ more to produce unequal results than when the angles are small (Weber-Fechner's law).

The presentation periods for epicotyls of *Vicia Faba* and *Phaseolus* are from 6 to 7 minutes, and for hypocotyls of *Helianthus* from 5 to 6 minutes.

Rapid intermittent stimulation is not more active than constant stimulation, and the duration of the individual periods of stimulation is almost immaterial. If they bear a ratio of 1 : 5 to the periods of rest, the response is nearly as rapid as with continuous stimulation.

The length of the induction-period and the time of response afford no criterion as to the geotropic irritability, which, in sensitive organs, involves a discriminatory power equal to that possessed by heliotropic organs.

Newcombe (Annals of Botany, 1905, Vol. XIX, p. 313) now considers that orthotropic stems and roots are equally stimulated geotropically by similar angular divergences above and below the horizontal, whereas lateral roots when displaced curve more readily downwards than upwards.

Luxburg (Jahrb. f. wiss. Bot., 1905, p. 399) states that in shoots with apical growth (excepting *Hippuris*) the average rate of growth is slightly retarded on a klinostat, whereas in plants with nodes it is accelerated, and in *Tradescantia fluminensis* more than when the nodes are placed horizontally so that they are under the continuous unilateral action of gravity. In *T. virginica*, however, growth is unaltered on the klinostat, but accelerated in the horizontal position.

The action of unilateral geotropic stimuli is, therefore, twofold, involving:

1. A change in the general rate of growth,
2. A change in the distribution of the rate of growth;

but the exact relationship between them is uncertain.

Hering (Jahrb. f. wiss. Bot., Bd. XL, Heft 4) found that the growth of parallelo-geotropic organs was directly retarded in the inverse position.

Portheim (Sitzungsb. d. k. Akad. der Wiss. Wien, October, 1904) discusses the influence of gravity upon the orientation of flowers.

The Statolith Theory of Geotropism. Tondera (Anz. d. Akad. d. Wiss. in Krakau, 1903, p. 512) states that the youngest geotropic internodes of Cucurbitaceae possess no movable starch-grains; but Jost (Bot. Ztg., 1904, p. 277) was unable to confirm this observation.

F. Darwin (Proc. Royal Soc., 1903, Vol. LXXI, p. 362) confirms Haberlandt's observation that in plants kept at high temperatures, as the starch disappears, the geotropic irritability diminishes, but finds that the same applies to the heliotropic irritability, and concludes that the general decrease of irritability is due to the direct action of the high temperature.

He also finds that shaking favours geotropic responses as found by Haberlandt, but does not appreciably affect heliotropic reactions. This affords no proof of the starch statolith theory, since not only will all other dense particles be affected, but also intermittent variations of hydrostatic pressure in the cell will be produced by every up and down movement. Jost found that roots subjected to centrifugal forces of 0·02 to 0·05 g. showed geotropic curvatures before any appreciable unilateral accumulation of starch had taken place, and found movable starch in tertiary non-geotropic roots. Darwin and Pertz (Proc. Royal Soc., 1904, Vol. LXXIII, p. 477) have shown, however, that these roots become geotropic when the others are removed, and they were unable to find any geotropic response without a movement of the starch-grains, probably because less sensitive plants and longer exposures were used.

Němec (Beih. z. bot. Centralbl., 1904, Bd. XVII, p. 45) states that after the removal of the starch-bearing columella of *Lupinus* roots, a geotropic curvature takes twenty hours, and by this time movable starch-grains have reappeared.

The geotropic flowers of *Clivia nobilis* have motile starch-grains, which are absent from the non-geotropic flowers of *Clivia miniata*. Many non-geotropic organs have motile starch-grains, however.

Fitting (Jahrb. f. wiss. Bot., 1905, p. 331) has shown that the collection and movement of the starch-grains are of no importance in geotropic perception, for the response may be as rapid when the starch-grains do not move as when they do, independently of whether they are regularly or irregularly distributed.

In a strong magnetic field the diamagnetic starch-grains would tend to be repelled from the neighbourhood of either pole-piece, and the paramagnetic constituents of the protoplasm to be attracted. Hence if the starch statolith theory were correct, roots of *Pisum* placed horizontally above and below one pole of an extremely powerful electromagnet should show stronger and more rapid curvatures in the lower than in the upper series. The reverse is, however, the case, according to the observations of Bayliss and Ewart, so that the gravitational and magnetic forces appear to directly stimulate the protoplasm. The exposures were for periods of four to six hours in a room heated to 23° C. The possibility of a thermotropic action of the heated magnet upon the radicles was avoided by enclosing them in moist cotton wool, or by interposing layers of wet blotting-paper. Short exposures appear merely to exercise a disturbing action on the roots, and even with prolonged exposures in so intense a field as that used for these experiments, the magnetic action is feeble as compared with that of gravity. Vertically placed roots showed no perceptible tendency to curve towards or away from either pole of the magnet, either during the exposure or when subsequently rotated on a klinostat.

The Localization of the Geotropic Irritability of the Root-tip. Piccard (Jahrb. f. wiss. Bot., 1904, Bd. XL, p. 94) rotated kidney-bean roots 30 to 40 times per second, arranged obliquely to the axis of rotation which passed just behind the sensitive apex (Fig. 70). Hence the apical and growing zones were subjected to opposed centrifugal components, with the result that an S-shaped curvature was formed. Piccard concludes that each part of the root is able to perceive and respond to geotropic stimuli. In this case Czapek's results would be due to the root-apex suppressing or overcoming the stimuli generated in the regions behind. Piccard's curvatures might, however, possibly be plastic in origin; and ten experiments failed out of twenty-four tried.

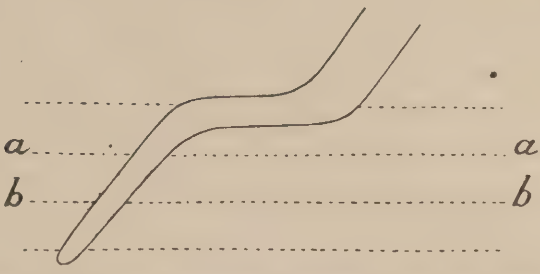

FIG. 70. Diagram showing position of axis of rotation between *a a* and *b b* in regard to the obliquely-inclined apex of the root.

Piccard also found that a root curved towards a wire kept at high potential, and that when root and wire were at still higher but like potentials the root curved away. The first effect is undoubtedly a more or less 'galvanotropic' one due to the silent discharge from the electrified wire. The other may be of the nature of a 'geotropic' repulsion or rather of a 'magneto-tropic' response, produced owing to the varying magnetic permeabilities of the cell-constituents. Piccard supposes that it is due to the direct repulsion acting on the surface-layers, and hence concludes that the 'geotropic' irritability is localized in the superficial layers. This assumption is, however, not justified; and judgement must be suspended until details of the experiments are given, or confirmation obtained. The roots were, however, often injured by sparking and ozone. In fact, since leaking is always occurring, and since the root has a high resistance and may undergo polarization, it will always be at a lower potential than the wire when both are attached to the same terminal of the electrical machine. It is also worthy of note that the root and wire were only 3 mm. apart.

Richter (Zur Frage nach der Function der Wurzelspitze, Wien, 1902; Inaug.-Diss. Freiburg) failed to obtain Czapek's results, but F. Darwin (Linn. Soc. Journal Bot., 1904, Vol. xxxiv, pp. 266–74) and Massart (Mém. par l'Acad. de Belgique, 1902) confirm Czapek's work by other methods. See also Czapek, Jahrb. f. wiss. Bot., Bd. xxxv.

Newcombe (Bot. Gazette, 1902, Vol. xxxii, p. 177) finds that the non-growing zones of roots as well as the apex are sensitive to rheotropic stimuli.

The Light Position of Leaves. G. Haberlandt (Ber. d. D. bot. Ges., Bd. xxii, 1904, p. 105) finds that in various species of *Tropaeolum* the lamina is able to perceive light stimuli and transmit them to the upper part of the darkened pulvinus; but the response is slower than normal, and the full position is not always assumed. He concludes that the petiole is responsible for the coarse, and the lamina for the fine adjustment of the leaf. In *Begonia discolor* the influence of the lamina predominates, and the same applies to *Monstera deliciosa*, which possesses large pulvini.

Vöchting (Bot. Ztg., 1888) found that on the removal of the laminas of *Malva verticillata*, the petioles performed no orienting curvatures.

Krabbe (Jahrb. f. wiss. Bot., Bd. xx, 1889) stated that the leaves of *Phaseolus* and *Fuchsia* assumed fixed proper light positions when the lamina was covered with dark paper, but not when the pulvinus was darkened.

Rothert and Darwin also found that the petiole of *Tropaeolum minus* was heliotropic, even when the lamina was darkened.

Haberlandt confirms all the above results—leaves differing from one another, and falling into three types.

1. The lamina predominates. *Begonia discolor.*
2. The lamina and petiole co-operate, the fine adjustment being regulated by the lamina. *Tropaeolum* and *Malva verticillata.*
3. The pulvinus alone is the responsive and percipient organ. *Phaseolus.*

Haberlandt suggests that since the pressure of sunlight amounts to 0·5 mg. per sq. metre, according to Maxwell, it is possible that the heliotropic perception may involve a power of discrimination to light pressure on the part of the plasmatic membrane. It must, however, be remembered that the pressure exercised by the incident light upon the peripheral surface of the transparent plasmatic membrane is only a very minute fraction of the total pressure exercised upon an opaque surface.

Phototaxis. Th. Frank (Bot. Ztg., 1904, orig., p. 162) finds that the zoospores of *Chlamydomonas tingens,* which are negatively phototactic in strong light, and positively so in feeble light, come slowly to rest in darkness without losing their vitality. Light stimuli easily overcome their feeble chemotactic irritability.

Thermotropism. Ganong (Annals of Botany, 1904, Vol. XVIII, p. 631) finds that leafless shoots in winter move upwards and inwards until March, and then outwards. The latter movement is shown to a less degree whenever the temperature rises during winter. Young shoots show the movement best, and he concludes that it results from a rise of turgidity in the cells due to the direct or stimulating action of temperature. It is, however, possible that the wood on the upper and lower surfaces may differ anatomically and in power of swelling, as was shown by Hartig to be the case in the pine.

Lidforss, however (Jahrb. f. wiss. Bot., 1902, Bd. XXXVIII, pp. 343–76) concludes that the raising of the shoots of certain herbs in warm weather is due to negative geotropism, and their horizontal position to diageotropism, their rapid fall at low temperatures being due to epinasty.

Chemotropism. Lilienfeld (Ber. d. D. bot. Ges., Bd. XXXIII, 1905, p. 91) found that the radicles of *Lupinus albus* curved in gelatine towards phosphates and carbonates, but away from salt and poisons, and were indifferent to KNO_3. It may be noted that alkaline (Na_2HPO_4) or acid (KH_2PO_4) phosphates and alkaline carbonates were used, so that the curvatures may be due to the action of the acidity and alkalinity. The poisons might accelerate growth on the exposed side; and, experimenting in a somewhat different manner, this author, and also Newcombe and Rhodes (Bot. Gaz., Bd. XXXVII, 1904, p. 23) found that the roots of the same plant grew into slabs of gelatine containing strong solutions of the feebly alkaline phosphate of sodium (Na_2HPO_4) and were killed.

The local application of dilute acid or alkali does induce curvatures in roots, and since these curvatures do not necessarily involve any injury, they cannot be traumatropic in origin (Ewart and Bayliss, Proc. of Royal Soc., 1905, Vol. LXXVII, p. 64).

Chemotaxis. According to Senn (Schweiz. naturf. Ges., July, 1904), the chloroplastids of *Funaria* are positively chemotactic to CO_2 and sulphates, organic acids, and certain assimilatory products, but not to cane-sugar. They are negatively chemotropic to nitrates and phosphates, and this feeble chemotropism is responsible for the normal position on the contact-walls assumed in darkness, but is readily overcome by their more powerful phototropism on exposure to diffuse or strong light.

Frank (Bot. Ztg., 1904, orig., p. 162) finds that the zoospores of *Chlamydomonas tingens* are attracted by nitrates, phosphates, nitric and carbonic acids, whereas sulphuric and hydrochloric acids, salts of ammonium and metals, cane-sugar, glycerine, asparagin, and peptone are indifferent. Strong acids and alkali repel, and strong meat-extract (0·3 to 2·0 per cent.) attracts.

Shibata has investigated the chemotaxis of *Isoetes* spermatozoids (Jahrb. f. wiss. Bot., Bd. XLI, 1905, p. 561; Ber. d. D. Bot. Ges., Bd. XXII, 1905, p. 478). Malic acid and its salts attract in a concentration of 0·00067 per cent., but free acid repels in one of 0·026 per cent. A few organic acids of similar constitution, such as fumaric acid, act similarly, but more feebly, whereas its stereoisomer, maleic acid, has no attractive action. H, HO, and acid ions repel, as is shown by the dependence of the repellent action on dissociation and concentration.

Dissociating salts of Ag, and to a less degree of Hg, Cu, Zn, Ni, and Co, exercise a very strong repellent action, but not poisonous alkaloids. Anaesthetics suspend the irritability while locomotion continues. The repulsion is phobic, the attraction tactic. On the chemotaxis of the sperms of *Equisetum* and of *Salvinia* see Shibata, Bot. Magazine, Tokyo, Vol. XIX, 1905, pp. 39, 51, 79.

Lidforss (Jahrb. f. wiss. Bot., 1905, Bd. XLI, pp. 65–87) finds that the antherozoids of *Marchantia* are positively chemotactic to albumins, globulins, nucleo-albumins, and other proteids, the minimum dilution being 0·0005 per cent., while 5 per cent. solutions repel by negative chemotaxis, since the organisms have no osmotactic irritability. They are, however, feebly aerotactic, and are attracted by an extract of the archegoniate heads made in the same way as diastase is extracted from leaves. The proteids mentioned above also attract pollen-tubes (Lidforss, Ber. d. D. bot. Ges., 1899, Bd. XVII, p. 236).

Chemotaxis (infl. of anaesthetics). According to Rothert (Jahrb. f. wiss. Bot., 1904, Bd. XXXIX, p. 1), chloroform and ether immediately suppress the chemotaxis, aerotaxis, and osmotaxis of *Bacterium termo* forms, the chemotaxis of *Spirillum tenue* and *Bacillus Solmsii*, the aerotaxis of *Beggiatoa alba*, the chemotaxis of *Trepomonas agilis*, the chemo- and osmotaxis of *Saprolegnia* zoospores, and the phototaxis of *Euglena viridis*, *Chlamydomonas*, *Gonium pectorale*, *Pandorina morum*. In some cases the locomotion is as active as before, in others more or less retarded.

Weak chloroforming changes the negative phototaxis of *Chlamydomonas* and *Gonium* to positive, i.e. renders them less responsive to the higher intensity of light, whereas ether exercises no such effect even in fatal concentrations.

Elfving, Ueber die Einwirkung von Aether und Chloroform auf die Pflanzen, Öfversigt af Finska Vetenskaps Soc. Förhandlingar XXVIII, 1886, found that ether produced this effect, but not chloroform.

All these reactions are instantaneous, and are independent of the duration of the anaesthetization; whereas slight doses, which at first affect neither locomotion nor irritability, gradually retard the movement and may exert an ultimately fatal effect before locomotion has ceased. In all cases individual differences are shown, some forms being more sensitive than others. In the case of *Gonium*, after anaesthetization the organisms appear temporarily to be more sensitive to light, and show a stronger tendency to negative phototaxis.

Galvanotropism. Ewart and Bayliss (Proc. Royal Soc., 1905, Vol. LXXVII, B., p. 63) have shown that the supposed positive parallelo-galvanotropism of roots does not exist, and that this galvanogenic curvature is due to the stimulatory chemotropic action of the products of electrolysis. When one electrode only is on the irritable zone the curvature always takes place towards the stimulated side whether it becomes acid or alkaline, but when a current of about 0·000001 of an ampère is led transversely through the irritable zone the curvature takes place towards the acid side. A similar curvature without injury is produced by the direct application of decinormal acid and alkali on opposite sides of the root, and the application of an excised electrolysed region of a root to another one produces in it a curvature towards the acid side. Neither this 'positive' curvature nor the 'negative' one is traumatropic in origin, since they are not necessarily accompanied by injury even to the superficial tissues of the root.

The negative curvatures are only shown when the direct action of the travelling ions is not overpowered by the action of the accumulated products of electrolytic decomposition in or around the root. If roots are imbedded in 3 per cent. gelatine, in which the deficiency of oxygen almost entirely suppresses the geotropic irritability, negative curvatures appear in the median region of the gelatine two or more hours after passing through a four-volt current at right angles to the roots. This is owing to the acid ions coming from the negative electrode exercising a greater stimulating action than the alkaline ones repelled from the positive electrode. Roots near to either electrode curve strongly towards them as the direct result of the action of the accumulated acid and alkali at these points. Hence three types of response are possible to the same current according to the position of the roots, and all may be shown without injury.

Transference of Stimuli. Kretschmar (Jahrb. f. wiss. Bot., 1904, Bd. XXXIX, p. 273) finds that an injury-stimulus causing streaming travels in the vascular bundles of *Vallisneria* through distances of from 0·6 to 1·5 centimetres per minute, and more rapidly towards older parts than acropetally.

Phosphorescence. According to Molisch (Bot. Ztg., 1903, p. 1), the best luminous Bacterium is *Micrococcus phosphoreus*, which is readily obtained by laying meat in 3 per cent. salt solution and keeping it moist at from 9° to 12° C.

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