PLANT-GEOGRAPHY

UPON

A PHYSIOLOGICAL BASIS

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PUBLISHER TO THE UNIVERSITY OF OXFORD
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W. Schimper.

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A PHYSIOLOGICAL BASIS

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WITH A PHOTOGRAVURE PORTRAIT, FIVE COLLOTYPES, FOUR MAPS, AND
FOUR HUNDRED AND NINETY-SEVEN OTHER ILLUSTRATIONS

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AUTHOR'S PREFACE

The delimitation of separate floral districts and their grouping into more comprehensive combinations are nearly completed, and the time is not far distant when all species of plants and their geographical distribution will be well known. The objects of geographical botany will not, however, then be attained, as is often assumed, but a foundation merely will have been laid on which science can construct a larger edifice. The essential aim of geographical botany will then be an inquiry into the causes of differences existing among the various floras.

Existing floras exhibit only one moment in the history of the earth's vegetation. A transformation which is sometimes rapid, sometimes slow, but always continuous, is wrought by the reciprocal action of the innate variability of plants and of the variability of the external factors. This change is due partly to the migrations of plants, but chiefly to a transformation of the plants covering the earth. Owing to unknown internal causes, the structure of plants is subject to a process of metamorphosis, which taken as a whole is slow, but apparently uninterrupted, and which gives rise to purely morphological differentiation, i. e. to the acquisition of characters bearing no apparent relation to the environment. Experience shows, however, that this differentiation is profoundly and rapidly modified by changes in the environment, every one of which immediately involves a change in the organization of the plants. If the new characters be useful, they are selected and perfected in the descendants, and constitute the so-called 'adaptations' in which the external factors acting on the plants are reflected. Since these last change with the geographical position, it is by the adaptations that the causes of the differences in the facies of the vegetation at different points on the earth are rendered more comprehensible, so that their investigation is to be numbered among the chief duties of geographical botany.

The connexion between the forms of plants and the external conditions at different points on the earth's surface forms the subject-matter of oecological plant-geography[1], which has only recently become a prominent subject of interest, although it found a place in earlier works, especially in Grisebach's valuable 'Vegetation der Erde,' where, however, it was regarded from obsolete points of view. The greater prominence of physiology in geographical botany dates from the time when physiologists, who formerly worked in European laboratories only, began to study the vegetation of foreign countries in its native land. Europe, with its temperate climate and its vegetation greatly modified by cultivation, is less calculated to stimulate such observations; in moist tropical forests, in the Sahara, and in the tundras, the close connexion between the character of the vegetation and the conditions of extreme climates is revealed by the most evident adaptations.

The physiological branch of geographical botany has made very rapid progress, owing to the foundation of a botanical laboratory at Buitenzorg, and to the unusually favourable opportunity for a residence in the midst of tropical vegetation which is thus offered to botanists in Java, thanks to Treub's praiseworthy exertions. It has thus become possible, as Wiesner's and Haberlandt's pioneering works show, to carry on prolonged and exact physiological research in a tropical climate. It is to be hoped that a counterpart to Buitenzorg may soon be established in the arctic zone; for an arctic laboratory, with a modest equipment corresponding to the poverty of the flora and the relative simplicity of the problems to be solved, would be of great service.

The oecology of plant-distribution will succeed in opening out new paths on condition only that it leans closely on experimental physiology, for it presupposes an accurate knowledge of the conditions of the life of plants which experiment alone can bestow. Thus only will it be possible to sever the study of adaptations from dilettantism which revels in them, and to free it from anthropomorphic trifling, which has threatened to bring it into complete discredit. In this respect, we may congratulate ourselves that scientific botanists are turning more and more to

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[1] Following Häckel's initiative the most recent name for the science of biological adaptations is Oecology.

oecological problems, and are framing their theoretical opinions on the basis of accurately observed facts and critically conducted experiments.

A satisfactory general survey of oecological plant-distribution cannot be attempted with the material at present available. This book is therefore chiefly of a tentative nature, and attempts by a precise statement of pending questions to stimulate further research.

The greatest care has been given to the choice and execution of the illustrations, which, by the delineation partly of single objects and partly of masses of vegetation, portray the connexion between plant-life and its environment much better than the most detailed descriptions. Thanks to the great kindness of a number of fellow botanists and naturalists, I have been able to collect a number of photographic views of characteristic vegetation. I am indebted to the following gentlemen and departments, to whom I now again express my gratitude :—Forest-inspector W. W. Ashe (N. Carolina), Privatdoc. A. Bauer (Marburg), Prof. Bessey (Lincoln, Nebr.), Sir Dietrich Brandis (Bonn), Prof. D. H. Campbell (California), L. Cockayne (Christchurch, New Zealand), Prof. J. M. Coulter (Chicago), Prof. Deichmüller (Bonn), the Geological department of the University of Nebraska, Grigoriew, Secretary of the Imp. Russian Geographical Society (St. Petersburg), P. Groom (Oxford), Prof. G. Karsten (Kiel), Lieutenant Kaznakoff (St. Petersburg), J. Kobus (Pasoeroean, Java), Prof. Krasnov (Kharkov), Dr. P. Kuckuck (Heligoland), G. Küppers-Loosen (Cologne), Prof. Kukenthal (Jena), Prof. Kusnezov (Dorpat), Prof. MacMillan (Minneapolis), Prof. Pohlig (Bonn), Prof. Rothrock (West Chester, Pa.), Prof. Sargent (Brooklyn, Mass.), Privatdoc. A. Schenck (Halle), Prof. H. Schenck (Darmstadt), F. Sonnecken (Bonn), Dr. O. Stapf (Kew), Geheimrath Prof. Strasburger (Bonn), W. Swingle (Florida), Dr. Treub (Buitenzorg, Java), Prof. O. Warburg (Berlin), G. H. Webber (Florida). Lady Brandis of Bonn has also been kind enough to place at my disposal her beautiful Indian water-colour drawings, which are so true to nature.

I have also to thank several of the above-mentioned gentlemen for important assistance in reference to literature, research-material, and the like. In this respect I am indebted also to the following :—The directors of the botanical museums and gardens at Berlin, Buitenzorg, and Kew, Prof. Drude (Dresden), Prof. Dudley (California), Prof. Flahault (Montpellier), Prof. Hieronymus (Berlin), Dr. Körnicke (Bonn), Prof. Noll (Bonn), Geheimrath Prof. Pfitzer (Heidelberg), Obergärtner Purpus (Darmstadt), Geheimrath Prof. Rein (Bonn), Prof. Trabut (Algiers), Prof. Volkens (Berlin).

Most of the illustrations of plants were drawn from nature by Mr. R. Anheisser under my personal supervision and to my complete satisfaction. Relatively few plates are borrowed from other books.

Of the four maps, only the third is original and is intended merely as a preliminary outline. The treatment of the vegetation in Brazil is based on a sketch kindly placed at my disposal by Prof. H. Schenck.

General works on plant-geography are seldom cited in the lists of literature at the end of the chapters. The student of plant-geography must become familiar with the following works of this character :—

Candolle, Alph. de. Géographie botanique raisonnée. Genève, 1855.
Drude, O. Handbuch der Pflanzengeographie. Stuttgart, 1890.
,, Atlas der Pflanzenverbreitung. Gotha, 1877.
Engler, A. Versuch einer Entwicklungsgeschichte der Pflanzenwelt. Leipzig, 1879, 1882.
Grisebach, A. Die Vegetation der Erde nach ihrer klimatischen Anordnung. Leipzig, 1872. French ed. by Tchiatcheff. Paris, 1877.

In conclusion, it is my pleasing duty to offer my sincere thanks to Dr. G. Fischer, the publisher, for the great readiness he has shown in meeting all my wishes.

A. F. W. SCHIMPER.

BONN,
End of July, 1898.

PREFACE TO THE ENGLISH EDITION

The movement which finds expression at the present moment in the study of Oecological Botany amongst English students of plant-life everywhere is the fruition of that earlier movement in the direction of strict observational morphology and experimental physiology which, in the latter half of last century, received its greatest impetus from the lucid work of Sachs, illumined by that of Darwin. Upon that earlier movement the edition of Sachs' 'Textbook of Botany,' published by the Clarendon Press in 1875, had a profound influence. We believe that this edition of Schimper's 'Plant-Geography' will have no less influence upon the movement now in progress, and on that ground the volume is a most important addition to the series of standard botanical books issued from Oxford. There is not, at the present time, any English book dealing comprehensively with the subject of Oecological Botany, and this edition therefore should be welcomed. Its 'precise statement of pending questions' should not only 'stimulate research,' as the author hoped, but should also have a steadying influence in a field of investigation which tempts to trifling.

The untimely death of the author shortly after the translation was begun has robbed the English edition of modifications and improvements which he had intended to make, and the book stands as it is in the German edition.

A portrait of the author and a sympathetic sketch of his life-work have been prefixed to the translation.

The translator has had the active and valuable co-operation of Mrs. Schlich in the preparation of his translation. The Index is also the work of the translator.

Upon critical points the opinion and advice of many colleagues have been sought for and obtained, formally and informally; to all of them grateful thanks are tendered here.

PERCY GROOM.

ISAAC BAYLEY BALFOUR.

A. F. W. SCHIMPER

An Appreciation

The nineteenth century saw the birth of four botanists belonging to the family of Schimper. Of these the first two were the brothers K. F. (1803–1867) and W. (1804–1878), the former famous for his work on phyllotaxis, the latter known as a botanical collector and a traveller; the third was their cousin, W. P. (1808–1880), the professor, distinguished for his work on mosses and palaeophytology; and the fourth was A. F. W. (1856–1901), son of the last-named, and author of the present work.

A. F. W. Schimper was born at Strassburg, where his father held the Chair of Geology. His training as a field-naturalist commenced early, for as a young child he collected and named plants, and as a boy he knew by sight many of the mosses upon which his father was working. A true naturalist and a keen observer he remained to the end of his life.

His four years (1874–1878) of university life Schimper passed at Strassburg, where he studied natural science and devoted especial attention to two subjects—botany and mineralogy. So far did he prosecute his study of mineralogy that he seriously contemplated becoming a mineralogist[1]; indeed his first published papers were two brief mineralogical notes issued in 1877, and his next work, on proteid-crystals, was actually published in two forms, the one for botanists and the other for mineralogists.

Of this paper, Dr. H. Miers, F.R.S., Professor of Mineralogy in the University of Oxford, has recorded his impressions in the following words:—'This research proves him (Schimper) to

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[1] As this has been denied on the authority of Professor P. Groth, I may at once state that I received my information from A. F. W. Schimper himself.

have mastered all the methods of crystallographic investigation, especially the optical methods which are all-important. He was able to extend considerably the investigations of Nägeli and others upon the form and nature of "crystalloids," and particularly to study the change of form which they undergo in swelling. I think that his remains the standard work on these substances. The crystallographic bearing of the work was published by him in a separate paper. I think he was the first to suggest and to give some ground for believing that some of the "crystalloids" may be isomorphous, e. g. *the artificially* prepared Mg-, Ba-, and Ca- compounds, which appear to have a similar composition and nearly the same form.'

Schimper's botanical contributions include work of first-class importance in three branches of the subject—histology, oecology, and geographical distribution of plants, as well as some suggestive papers on a fourth branch—physiology.

Unsurpassed by any histological work of our time was that of Schimper on chromatophores. The first of a series of papers was published in 1880 on 'Starch-producing granules,' in which it was shown that starch arises, not in the general cytoplasm, but in two kinds of homologous protoplasmic bodies, chloroplasts and leucoplasts. Three later papers, issued in 1882, 1883, 1885, upon chromatophores proved the existence of a third form of protoplasm, chromatophore-protoplasm, as distinct from cytoplasm and nucleus as these are from one another. As Schimper's views are still held by the majority of botanists, it may be said that he revolutionized our ideas as to the constitution of vegetable-protoplasm and as to the unit of plant-life.

In the meanwhile Schimper had also fundamentally modified botanists' views as to the nature and growth of starch-grains, by his publication in 1881 of a paper upon the growth of these bodies. The nature of the change may be gleaned by the following quotation from an article written by Schimper in the American Naturalist (1881):—'Nägeli and, after him, most biologists hold that starch-grains agree with protoplasm as to their molecular structure, and are to be considered as living bodies.' This paper, in demonstrating the growth of starch-grains by apposition, dealt Nägeli's theory of the growth of cell-walls and starch-grains exclusively by intussusception a staggering blow from which it never recovered.

Schimper issued only three purely physiological papers, all devoted in the main to metabolic processes in green leaves, and in particular to the manufacture and conduction of carbohydrates and the assimilation of salts in leaves. Though they contained a number of new facts and ideas, and were admirable models of method, they belonged not to the same rank as the histological work on chromatophores, or as the oecological work.

It was in his oecological work that Schimper revealed himself a true genius. Before he commenced this, oecology, so far as the vegetative organs were concerned, could scarcely be said to exist as a science. True it is that Darwin had shed light upon the oecology of climbing and carnivorous plants; that plants living in deserts or dry spots were recognized as adapted to resist desiccation; that anatomical and morphological investigation had been made upon selected parasites, saprophytes, aquatic plants, and the like. But the subject did not exist because the methods pursued in the solution of oecological problems were singularly inadequate and often utterly unscientific. To observe a plant with a spotted snake-like stem, or a seed that somewhat resembled an insect, was enough to call into existence theories of mimicry as applied to plants; to note the air-spaces in aquatic plants was to assume that they were flotation-devices. The subject therefore attracted but few botanists; for the serious botanists were mainly working in their laboratories or in their herbaria.

Far-reaching and highly original as Schimper's direct discoveries on oecological questions have been, botanical science owes to him a deeper debt for his foundation of a truly scientific and comprehensive method of oecological investigation resulting in the attraction of able botanists to work at this branch of the subject. Schimper from the first insisted on the employment of methods as strict as those used in solving morphological and physiological problems. And he showed himself the master of oecological method by his critical and concurrent use of three distinct modes of investigation, namely, of observations on the comparative morphology including histology, on the physiology, and on the geographical distribution of plants.

An analysis of Schimper's oecological methods may therefore be of interest.

To explain how plants are fitted to subsist in the precise environment that they occupy demands an elaborate inquiry into the form, structure, physiology, and life-history of the plants, and an equally exhaustive analysis of their animate and inanimate surroundings. But to solve the still further problem as to the original source and evolution of the plants and of the whole community, necessitates a corresponding investigation relating to the immediate allies of these plants living under other conditions.

Such an exhaustive oecological research is at present only theoretically possible, and it is practicable only to get definite answers to our questions by an investigation of one or more dominant factors which impress themselves strongly on the forms and behaviour of the plants under their influence. Such dominant factors we may consider insects in relation to flowers, and drought in relation to desert plants. Schimper always worked with plants under the influence of some such dominant factor. In all his oecological papers, save one on myrmecophilous plants and two short early papers, the dominant factor under which the investigated plants (epiphytes, alpine and littoral plants, halophytes) lived was scarcity of available water.

Such a dominant factor, in impressing itself on the form of the plants, will lead to the occurrence of some structural feature or features common to all or to many of the plants. In fact, in ordinary work it may be that these features, in largely determining the facies of the vegetation, first suggest the existence of a dominant factor. The first obligation is to prove that these features are absolutely necessary, or at least highly advantageous, to the plants possessing them. Physiological experiments or observations on the life-history of the plants alone can give this proof. It was thus that Schimper showed the xerophilous nature of the leaves of epiphytes, halophytes, and alpine plants, which dwell in physiologically dry places, whether the physiological drought be due to scanty supply of water, or to unavailability of the water by reason of its salinity, or to external influences promoting transpiration.

But observation further shows that in the same environment many of the plants not possessing the common features above mentioned yet have characters subserving the same end, so that they as well as the first group are machines having one common object, that of working in harmony with the dominant factor. Consequently, comparative observations upon the various members of one community or guild of plants afford another method of investigation. This is brought out vividly in Schimper's papers on epiphytes and littoral plants, where the various mechanisms are described by which water is stored or economized by leaves, stems, or roots. One admirable example is specially given in the form of a comparison between the structure of the two epiphytes, *Tillandsia usneoides*, composed solely of shoots, and an *Aeranthus*, whose vegetative organs consist entirely of green roots.

But further morphological and histological examination of members of the same community or guild may reveal the existence of some apparently devoid of any peculiar structural features fitting them for their special mode of life. An investigation into their physiology and mode of life may at once show that they are really not under the control of the dominant factor, or like ephemerals in the desert evade it by the periodicity of their life, though their environment may appear at first sight to be all but identical with that of their elaborately adapted neighbours. This lack of need for working in harmony with the dominant factor affords a third means of testing the conclusions previously arrived at in reference to the other plants. Thus Schimper pointed out the existence of many epiphytes which are not xerophytic, but may even be hygrophytic in structure, and he further correlated this with the fact that these particular plants exist as epiphytes only on very moist and shady parts of tree-trunks, and consequently require no careful provision against excessive transpiration.

Having thus demonstrated the intimate and necessary relation between the structure of the plants and the dominant factor, the next work might be an investigation into the extent to which the peculiar structure of the plant is the direct result of the environment. This matter Schimper scarcely touched, except in the case of halophytes, where he cited the observations of others and recorded his own.

Much more attention he devoted to the adaptive nature of structural peculiarities fitting the plants for their mode of life. He asked whether particular peculiarities of a plant were truly adaptive, that is, whether they had been evolved for the specific purpose of enabling the plant to exist in its present surroundings, or to what extent they were previously possessed by the plant, thus enabling it to enter its present home. This entailed an investigation into the structure of allied plants living under other surroundings. As examples of such comparative investigations may be cited Schimper's discussions on the velamen of orchids and aroids, on vivipary in mangrove-plants, on mechanisms of seed-dispersal of littoral plants, and in particular on the evolution of floating tissue, which he investigated by comparisons between the fruits of inland and littoral species of one genus. His investigation of the myrmecophilous *Cecropia* is an excellent example of this method. Having demonstrated the necessity of the protection against leaf-cutting ants, and having recalled known facts, that the *Cecropia* supplies food and home to the protecting army of ants, Schimper rendered probable the adaptive nature of the food-bodies by showing their composition and behaviour, and their absence in a non-myrmecophilous species of *Cecropia* likewise growing in Brazil; and by a further comparison of the two species he also showed that there was a definite structural adaptation for facilitating the entrance of the protective ants into the hollow internodes of the myrmecophilous plant.

Change in the environment occasions change in the composition and oecology of the vegetation. There is thus between the oecology and the geographical distribution of plants a reciprocal relation which renders observations on either of these subjects helpful in the explanation of the other.

Observations on the local distribution of types of vegetation, in that they deal with variations of environment associated with little or no change in climate, frequently render possible the recognition of the factors determining the original formation of definite communities of plants, and the analysis of the primary and some of the secondary factors influencing the structure of the constituent plants. It was by observations on the local distribution of epiphytes in the American tropics that Schimper was able to explain the significance of the epiphytic habit and structure. In the forests he noted that the least modified types were those living in moist and shady crevices of the bark low down the tree-trunks, and that the more elaborate ones lived in the drier but better lighted situations higher up the trees. In the open country, especially in savannahs, he observed that the few epiphytes growing on trees, and the lithophytes, were identical with the elaborate xerophytes perched on the tree-tops in the forest. Thus he concluded that epiphytes were derived from terrestrial forest-plants, the key to whose evolution lay in the struggle to reach the light without the expenditure of the material necessary to raise the leaves of a terrestrial plant to an equivalently illuminated spot, and the key to whose success lay in the successful adoption of a xerophilous habit. Other observations showing the interchange of positions among epiphytes, plants occupying shores, rocks, alpine heights, the vicinity of salt-springs, and their absence from other intervening spots confirmed the view that they are all true xerophytes. Again appealing to the fact established by cultivation that shore-plants grow equally well inland away from saline soils, Schimper was able to draw the conclusion that they were salt-enduring xerophytes driven to the shore by competition.

Observations on the general distribution of types of vegetation over the surface of the earth provide additional means of arriving at important oecological conclusions; for they deal on the one hand with great climatic and other changes of the environment, and on the other hand with more or less similar conditions prevailing at widely distant spots. Schimper was thus able to point out that it is a moist climate that determines the existence of phanerogamous and vascular epiphytes, excepting where a cold winter steps in to prevent the roots from absorbing water. Again, by comparing tropical and temperate alpine plants he was able to show that cold is not the controlling factor in the case of these xerophytes.

The present work, his masterpiece, shows the manner in which Schimper regarded plant-life. It reveals him, not as merely the keen observer and subtle critic of Nature, but rather as her intimate friend from whose watchful eyes and sympathetic mind she cannot hide her mysteries. It reveals him, not as the idle creator of airy hypothesis, which the first breath of fact can dissipate, but as the genius of industry and thought, patiently watching Nature's experiments and supplementing them with his own, searching deep into the discoveries of fellow workers to find the meaning of facts they had disclosed, and travelling far and wide to win from the plants he loved their inmost secrets.

PERCY GROOM.

CORRECTIONS

PAGE
5. Description of Fig. 1, line 3. For *a.s.* read *u.s.*
31. Line 19 from top. *After* VII *insert* 1888
32. Line 15 from top. *For* Bd. *read* Vol.
55. Footnote 2. *For* Wiener's *read* Wiesner's
62. Line 14 from bottom. *For* droughts *read* drought
118. Line 21 from top. *For* Tome *read* Vol.
155. Line 10 from top. *For* Kjöbenhavn *read* Kjobenhavn
Line 21 from bottom. *After* Forbes. H. *insert* O.
,, ,, *After* Archipelago *insert* , London
160. Line 10 from bottom. For *vegetation* read *plant-covering*
190. Line 3 from top. *After* Fliche *insert* , P.
Line 9 from top. *For* Bd. *read* Vol.
Line 20 from top. *Before* Gesellsch. *insert* Österr.
191. Line 11 from top. *For* Kjöbenhavn *read* Kjobenhavn
Line 12 from top. *For* Band *read* Bind
205. Line 16 from bottom. *For* 1897 *read* 1892
206. Line 4 from bottom. *For* Anzeigen *read* Anzeiger
211. Line 16 from top. *For* Zone *read* Zones
236. Line 21 from top. *For* exclusively *read* essentially
Line 7 from bottom. *For* purely *read* really
237. Line 10 from top. *For* purely *read* pre-eminently
238. Line 18 from bottom. *Before* exclusively *insert* almost
240. Last line. *For* Moller *read* Moller
,, *For* 1898 *read* Botanisches Centralblatt. Bd. LXXII. 1897.
332. Description of Fig. 173. *For* Tabernaemontana dichotoma *read* Clusia grandiflora (?)

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No factor affecting plant-life is so thoroughly clear as the influence of water. From its entrance to its exit, the transpiration-current may be followed, step by step; the physiological processes of the intake, conduction, and exit of water have in many respects been explained; the structure of the organs concerned in these processes and in storing water have been accurately investigated; and the theory of the co-operation of all these factors is practically completed. In demonstrating, therefore, the share taken by climate and soil in causing the characteristics of the vegetation of any region, water claims a foremost place in our consideration.

1. THE VEGETATIVE ORGANS OF TERRESTRIAL PLANTS.

i. *GENERAL CONSIDERATIONS.*

The absorption and emission of water by plants depends on external conditions. In nature, however, these are very varied, and, in harmony with the adaptability of the organisms, call forth very varied contrivances for regulating the passage of water through a plant. *The structure of* *many plants favours the exit of the water which has been absorbed, that of some impedes it.*

Contrivances for expediting the exit of water are characteristic of *hygrophytes*, or plants whose conditions of life exclude all danger of desiccation, and in which a stagnation of the water, which brings nutritive salts to the parts requiring them, may be feared. On the other hand, difficulties in obtaining a supply of water lead to the formation of devices for assisting absorption and limiting transpiration ; *xerophytes* are provided with contrivances of this kind.

Wiesner[1] has pointed out another difference between hygrophytes and xerophytes, but it does not appear to be fundamental, and in any case requires further investigation. Xerophytes perish after two or three days of continuous rain ; they are rain-avoiding, *ombrophobous*, whereas hygrophytes are, as a rule, *ombrophilous*. This latter characteristic is especially observable in the plants of very rainy climates : for instance, according to Wiesner, the vegetation of West Java (Buitenzorg) is ombrophilous. On the other hand, there are in the moderately moist climate of Central Europe ombrophobous hygrophytes, such as Impatiens Noli-me-tangere. The feature to which Wiesner has drawn attention is externally distinguishable thus : *ombrophilous foliage is capable of being wetted, ombrophobous foliage is unwettable.*

It is usual to designate the plants of moist localities as hygrophytes and those of dry localities as xerophytes, but in this due attention is not paid to the fact that the characteristics of organisms are physiological, those of habitats are physical, and that there is no necessary connexion between these two groups of characteristics. In reality, a very wet substratum is quite dry to a plant if the latter cannot absorb water from it, whilst a soil, that appears to us to be quite dry, may supply sufficient water to many accommodating plants. *A distinction should therefore be made between physical and physiological dryness and between physical and physiological moistness* ; only the physiological characteristics need be considered in plant-life and in geographical botany. *A hygrophilous vegetation corresponds to physiological moistness and a xerophilous vegetation to physiological dryness.*

Xerophytes and hygrophytes are connected by transitional forms which obscure the boundaries between them as two great oecological categories ; it would therefore be useless to attempt to give the matter a statistical basis. The unavoidable arbitrary convention adopted here does not, however, actually involve so much confusion as might have been anticipated. On the other hand, the constitution of a special category to include all plants which are neither pronounced xerophytes nor pronounced hygrophytes would certainly add to the confusion. It appears, therefore,

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[1] Wiesner, IV.

necessary to place in a third category *all plants whose conditions of life are, according to the season of the year, alternately those of hygrophytes or of xerophytes.* All such plants, including, for instance, the great majority of the plants composing the Central European flora, should be termed *tropophytes. The structure of their perennial parts is xerophilous, and that of their parts that are present only in the wet season is hygrophilous.*

The classification of plants as hygrophytes, tropophytes, and xerophytes is the first step towards the physiological comprehension of the earth's vegetation and its components, the formations. Extensive districts, for instance a large portion of the tropical coasts and mountain ranges, are marked by the prevalence of hygrophytes; others, such as steppes, deserts, and polar zones, of xerophytes; and others, again, for instance the greater part of the north temperate zone, of tropophytes. There are *hygrophytic, xerophytic, and tropophytic climates.* Every climatic district exhibits, besides the corresponding oecological type of vegetation, one of the two other types in certain localities, because the properties of certain kinds of soil weaken, or strengthen, the influence of the climate. The influence of the soil may be termed *edaphic*[1]. *There are climatic and edaphic hygrophytes, xerophytes, and tropophytes.*

Characteristics occasioned by physiological humidity or drought determine the physiognomic, or rather, oecological aspect of the vegetation of the districts[2] and of the separate stations within them. Systematic phytogeography must therefore reckon these differences amongst the most important, for there are also hygrophilous, tropophilous, and xerophilous species. There are, further, some species—and this fact is as important to the systematist as to the physiologist—which adapt themselves to the varying conditions of humidity so completely that their extreme forms appear to belong to different species, but these by a change in the supply of moisture may pass over into one another.

ii. *XEROPHYTES.*

Physiological drought is caused by external factors which either reduce absorption or which favour transpiration, or, and this the most frequently, there is a combination of these influences[3].

Factors reducing Absorption.

1. *Scarcity of free water in the soil,* that is to say, of water that is less attracted by the particles of soil than it is by roots. According to their physical nature different soils exhibit very unequal degrees of physiological dryness[4].

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[1] *τὸ ἔδαφος*, 'the soil.'

[2] The *Zones* depending on heat are subdivided into *Districts* depending on the quantity of atmospheric precipitation. See Part III, Introduction.

[3] Schimper, I.

[4] See Part I, Chap. V, The Soil.

2. *Abundance of soluble salts in the soil.* A small quantity of salt favours absorption, whilst a large quantity impedes it. The degree of concentration at which the retardation commences varies with the species of plant, but rarely exceeds 0·5 %. Mixtures of salts impede absorption more than pure salts, and certain kinds, for example sodium chloride, act more energetically than others, for example saltpetre [1].

3. *Richness of the soil in humous acids.*

4. *Low temperature of the soil.* A frozen soil is quite dry to all plants; one at a temperature slightly above freezing-point is nearly dry to most plants. The minimum temperature for a normal absorption of water, that is to say for an absorption of water sufficient to compensate for the loss by transpiration through open stomata, varies with the species of plant, being generally much higher for those of warm zones than for plants whose lives are spent in colder zones.

Factors favouring Transpiration.

1. *A dry atmosphere.* Although transpiration is a physiological and not a physical process, yet it behaves in respect of this factor essentially like evaporation: it constantly increases in proportion to the dryness of the air.

2. *High temperature of the atmosphere.* Transpiration increases with the temperature up to a maximum which varies with the species, and beyond which pathological changes cause a diminution.

3. *Rarefaction of the air.* A reduction in the atmospheric pressure accelerates transpiration, not directly, as in the case of evaporation, but indirectly by accelerating the diffusion of the water-vapour.

4. *Light.* Transpiration is greater in the presence of light than in darkness, and it increases with the intensity of the illumination. The more effective rays of light, according to Wiesner, are, first, the blue; secondly, the red; while the green rays exercise only a feeble influence.

Of the factors that accelerate transpiration, temperature and light are the weakest, and do not in themselves suffice to produce decided xerophilous characteristics.

All plants with an environment involving either one or other or a combination of any of the above factors, excepting light and temperature, possess the structure and characteristics of xerophytes.

Xerophilous Structure.

As has been already stated, many plants are able to thrive under very diverse conditions of water-supply by altering their structure in relation to their environment. The necessary investigations have been made as regards four of the above factors—dryness of the substratum, atmospheric

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[1] See Part I, Chap V, The Soil.

dryness, salinity of the substratum, illumination. Attention has been chiefly directed to the leaves, as being the chief organs of transpiration.

All experiments have led to essentially similar results. External conditions which, either by diminishing the absorption of water or by accelerating its exit from the plant, disturb the equilibrium in a sense hostile to the plant, occasion, as a rule, the following deviations from normal structure: (1) Reduction of surface, the volume being assumed

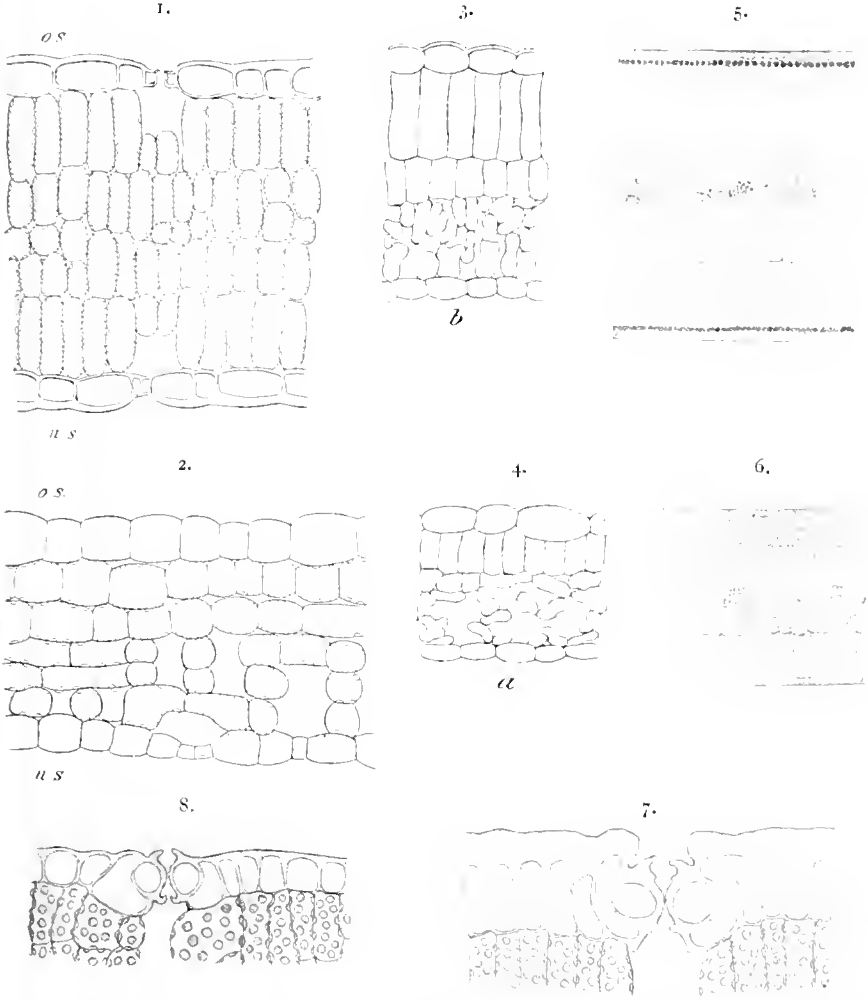


FIG. 1. Influence of transpiration on the differentiation of the leaf-tissue. Transverse sections of leaves and stomata. 1 and 2. Lactuca Scariola: 1 exposed to sunlight, 2 grown in shade. o.s. upper surface, *a.s.* under surface. 3 and 4. Robinia Pseud-acacia: 3 in ordinary air, 4 in air saturated with vapour. 5–8. Sonneratia acida: 5 on wet saline soil, 6 on ordinary soil in the Buitenzorg garden, 7 on saline soil, 8 on ordinary soil. 1–2 after Stahl, 3–4 after Lothelier, 5–8 from nature.

constant. (2) Diminution of intercellular spaces containing air. (3) Augmentation of the vessels and sclerenchyma. (4) Lengthening of the palisade-cells. Frequent but not universal. (5) Increase in the thickness and amount of cutin of the outer wall of the epidermis. (6) Sinking of the stomata. (7) Increased number of air-containing hairs. (8) Supply of

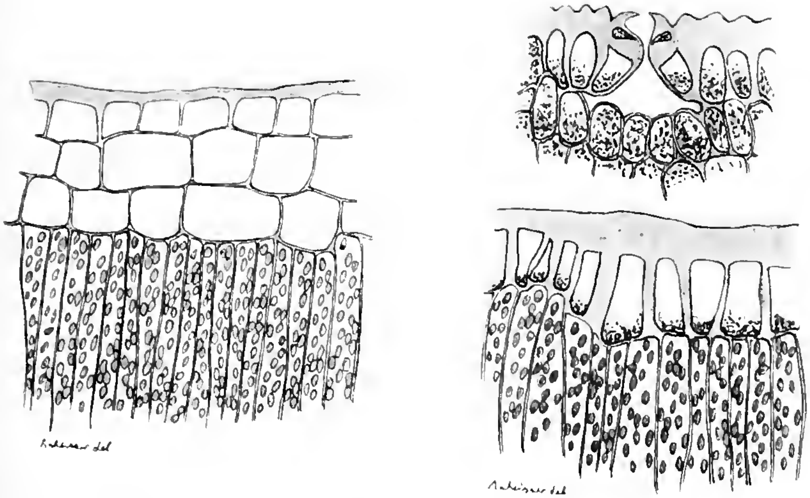
Fig. 2. Xerophilous structure. *Dry climate in Temperate Australia.* Stomata. *a* Franklandia fucifolia. *b* Eucalyptus giganteus. After Tschirch.

Figs. 3 and 4. Xerophilous structure. *Wet saline soil of Javanese mangrove-swamp.* Left hand: Aegiceras majus. The upper surface of a leaf. Magnified 260. Right hand: Rhizophora mucronata. Stoma and epidermis of the lower surface of leaf. Magnified 550.

Figs. 5 and 6. Xerophilous structure. *Cold soil of Greenland.* Left hand: Dryas integrifolia. Transverse section of leaf. Right hand: Loiseleuria procumbens. Part of transverse section of leaf; *B* palisade-cells, *V* outer wall of epidermis, *c* cuticle, *R* lumen of epidermis-cell, *g* inner wall of epidermis. After Warming.

water-storing cells (double epidermis, aqueous tissue, mucilage-cells, &c.) (Figs. 1–8).

With the exception of the increase in the sclerenchyma and the lengthening of the palisade-cells, the above-mentioned modifications appear to be well adapted for resisting the danger of excessive loss of water, whether the danger arises from too little absorption or from excessive transpiration. By a reduction in the size of the leaf and of the intercellular spaces the transpiring surface becomes smaller for a given mass of plant-substance; the conduction of water is facilitated by the increase in the vessels; transpiration is reduced by a thicker cuticle, by the presence of air-containing felted or silky hairs, and by the sinking of the stomata; water-cells have a similar action, and besides this they rapidly fill whenever the water-supply is increased, and yield their contents to the assimilating cells as the supply of water is reduced.



FIGS. 7 and 8. Xerophilous structure. *Alpine climate.* Left hand: Myrica javanica. Part of the transverse section of a leaf. Gedeh, Java, 2,900 m. Right hand: Photinia integrifolia. Transverse section (above) of lower, and (below) of upper surface of leaf. Ardjuno, Java, 3,300 m. Magnified 200.

The possession of protective means, such as those just mentioned, is usually, but incorrectly, described as the result of strong transpiration. In reality they accompany weak transpiration, as for instance on dry or saline soil, as well as strong transpiration in dry air. On the other hand, plants on a damp soil transpire energetically (Gain), and yet, as a rule, dispense with a xerophilous structure. It is not the absolute strength of transpiration but its amount relatively to the water-supply that leads to protective mechanisms. The causal-mechanical explanation attempted by Kohl, according to which strong transpiration is the cause and modified structure the effect, as in a purely physical process, is refuted by such facts as those just mentioned. With greater probability we might regard the varying degree of concentration of the cell-sap as the first cause, that is to say the stimulus acting on the protoplasm, for this is increased by an insufficient supply of water, as well as by excessive transpiration. But even this assumption in no way explains the suitability of the above-mentioned structures. This depends on an adaptability gained in the struggle for existence, and, like all true vital phenomena, it does not yet admit of any physical explanation.

The most important natural regions and habitats where physiological dryness prevails and only xerophytes therefore thrive, are grouped as follows, according to their physical characters:—

1. *Deserts, Steppes*, and other districts with a dry substratum and dry air, occasional or persistent great heat, and intense illumination.

2. *The Bark of Trees, Rocks* where there is rapid drying up of the substratum, owing to deficient depth.

3. *Sandy soil, Gravel*, and the like, on account of the rapid drying up of the substratum owing to its great permeability.

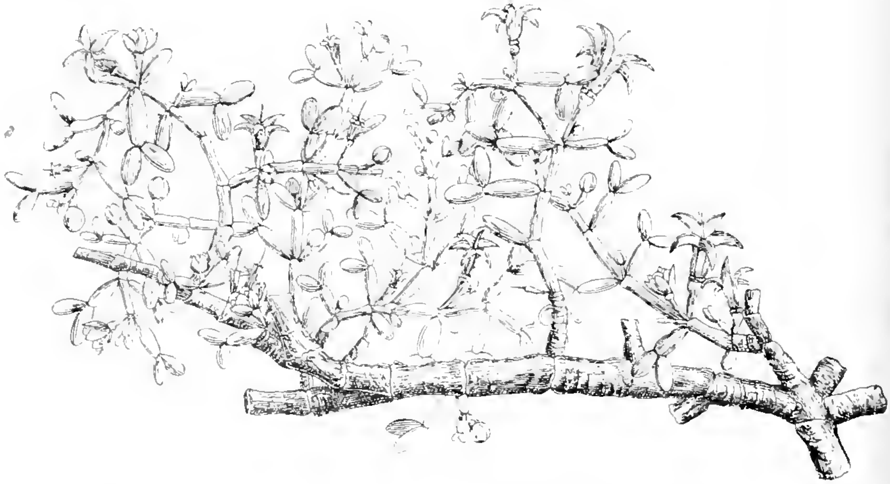


FIG. 9. Xerophilous structure. *Dry hot climate of Algerian and Moorish deserts.* Zygophyllum cornutum. Plant with succulent leaves. Natural size. After Engler.

4. *Sea-shores. Solfataras,* which have abundance of soluble salts in the soil.

5. *Peat-bogs*, because of the humous acids in the soil.

6. *Polar zones. Vicinity of Glaciers in high mountains*, where the temperature of the soil is low.

7. *Alpine Highlands*, which are under rarefied air and strong insolation characteristic of the alpine climate.

The plants of all these stations are provided with devices for the safeguarding of their transpiration; they are xerophytes. Reduced surface is very general in their case. With increasing physiological dryness, the leaves become smaller in surface but proportionally thicker, more leathery (*sclerophylly*) (Figs. 11, 12), fleshy (*chylophylly* or *leaf-succulence*) (Figs. 9, 10), or rudimentary and caducous (*aphylly*). In the last cases, the axes are rich in chlorophyll and carry on the process of assimilation. The axes are sometimes slender like rods, dry and hard, as in Ephedra, Spartium, and other plants (*sclerocauly*), or they become short and thick, often even spheroidal, and filled with mucilaginous sap, as in the Cactaceae (*chylocauly* or *stem-succulence*).

Reduction in surface is often associated with the production of thorns, because shoots or leaves become pointed structures rich in sclerenchyma and transpiring but slightly, if at all; their utility in this form, as protective organs against animals, if a reality, is only of a secondary nature.

Xerophytes with pinnate leaves have the power of automatically adjusting the transpiring leaf-surface. The mobile leaflets open out under the moderate illumination of the early morning, or of a dull day, but close up under intense insolation and the profuse transpiration which accompanies it. The fact that plants possessing pinnate leaves with a relatively large and thin leaf-surface thrive alongside of aphyllous plants in the driest regions proves how perfectly this arrangement works.

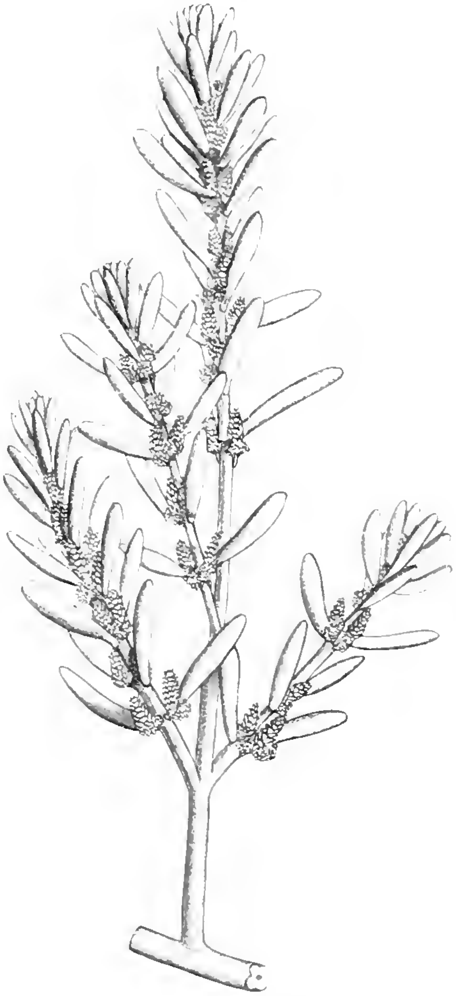


FIG. 10. Xerophilous structure. *Wet saline soil of tropical shores.* Batis maritima. Plant with succulent leaves. Natural size. After Dammer.

Other leaf-bearing xerophytes have their leaves, or leaf-like cladodes, arranged parallel to the incident rays of sunlight, and are consequently less intensely heated and illuminated. This peculiarity disappears in many species when there is no longer any danger of excessive loss of water, for instance in the mangrove-tree, Sonneratia acida, when it is grown on a soil poor in salts, whilst in other plants, such as Eucalyptus, the position has become hereditary.

It has been already pointed out that many plants growing in dry places develop water-storing cells. Such water-reservoirs are constantly met with in the vegetation of dry stations—if they be not universally present. They are sometimes thin-walled living cells, sometimes dead cells like tracheids,

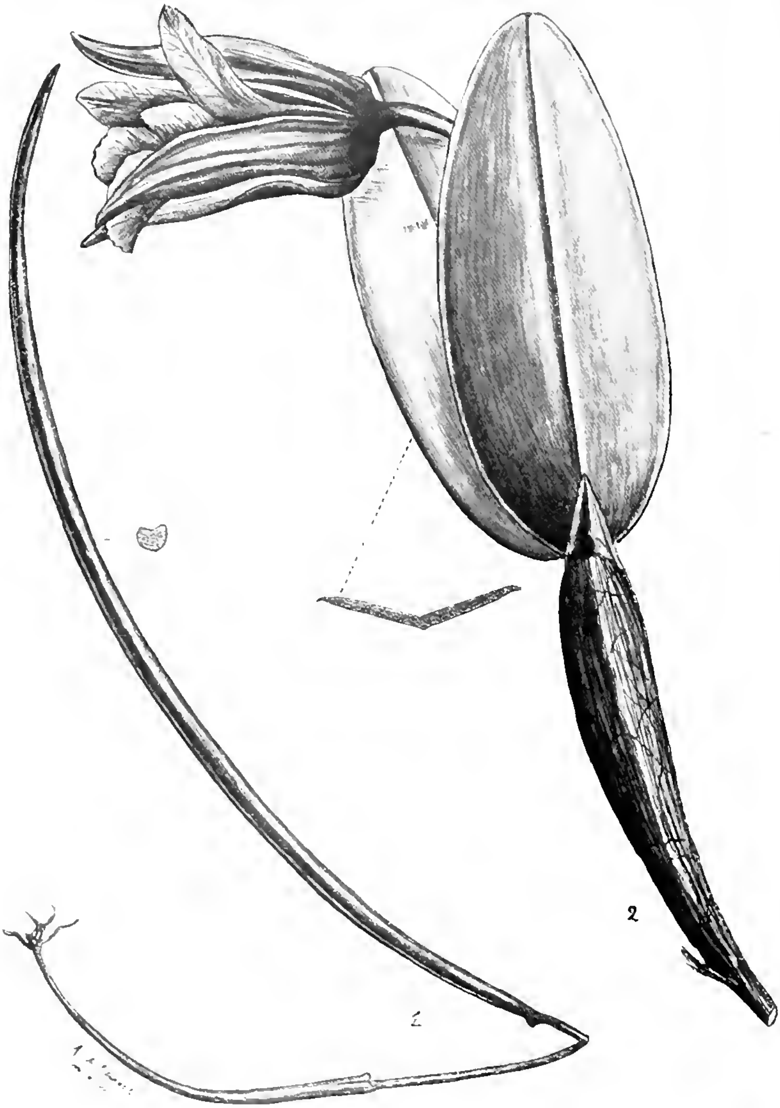


FIG. 11. Xerophilous structure. *Dry substratum of tree-bark and rocks.* 1. Octomeria sp. 2. Cattleya bicolor. Desterro, Brazil. Natural size.

occurring singly or united into tissues; sometimes, as in Philodendron cannaefolium, intercellular spaces assume the same function. A rich development of parenchymatous living aqueous tissue occasions the succulence of leaves and axes which has been already described. This aqueous tissue is either external, between the epidermis and the chlorenchyma (*perichylous*), as in many Bromeliaceae, Rhizophora (Fig. 17), and other plants; or internal, and then within the chlorenchyma (*endochylous*), as in Cactaceae, succulent Euphorbiaceae, and most other stem-succulents (Figs. 13, 14). In perichylous construction the aqueous cells have a watery sap, in endochylous construction they are usually filled with mucilaginous contents.

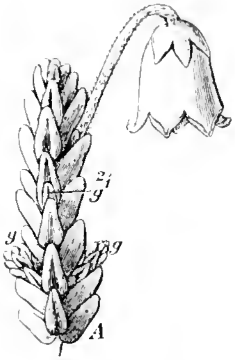


FIG. 12. Xerophilous structure. *Cold soil of Greenland.* Cassiope tetragona with small leathery leaves folded inwards. *g* Young shoots. Magnified 2. After Warming.

Solitary living aqueous cells are less frequent than aqueous tissue. They are very conspicuous, for instance, in Mesembryanthemum crystallinum, where certain epidermal cells expand into large water-bladders; in Tillandsia usneoides and others they are scattered in the chlorenchyma.

Living aqueous cells always remain filled with protoplasm and cell-sap; they never contain air. The volume of water that they contain, however, varies between wide limits. When transpiration is slack, they may be gorged with water, for instance at night or in dull weather, but during strong transpiration they supply the assimilating cells with water, and then they collapse strongly.

Water-storing tracheids, as opposed to living water-cells, contain air or water according to the amount—greater or less—of transpiration of the green tissues. They are most frequently present at the ends of vascular bundles in leaves; and only in the leaves of certain xerophilous orchids are they found distributed through chlorenchyma (Figs. 15, 16).

The water-reservoirs in many xerophytes are not uniformly distributed in the leaves or axes, but are confined to certain members, whose chief function is the storage of water. Leaves that are ageing and have become abnormally thick owing to the subsequent great enlargement of their aqueous tissues in many cases serve as water-reservoirs of this kind, as we see in epiphytic Gesneraceae and species of Peperomia, Rhizophora, Sonneratia and other mangrove-trees; and these older leaves supply the younger ones—which are at the height of their assimilating activity—with water until their store is completely exhausted[1] (Figs. 16a and 17). Amongst such water-reservoirs are numbered the well-known pseudo-bulbs of epiphytic orchids, the spindle-shaped petioles of Philodendron cannaefolium, and other like structures.

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[1] Schimper, III, p. 42; Haberlandt, Physiol. Pflanzenanat., p. 349.

Comparative culture-experiments have proved that plants liable to desiccation have their epidermis constructed in such a manner as to reduce transpiration. Protective mechanisms, such as a considerable thickening of the outer wall of the epidermis, which is also well cutinized, stomata sunk in pit-like or groove-shaped depressions, air-containing tomentum, mere traces of which appear in cultures under dry conditions, attain a high degree of development in typical xerophytes, and occur quite generally under the most diverse physical conditions. Most xerophytes, also, have the property of closing their stomata when they begin to wilt, and thus of considerably depressing their transpiration; this is, however, not quite universal. Undoubtedly, under direct insolation, the protection afforded by the closing of stomata is much less than is often imagined.

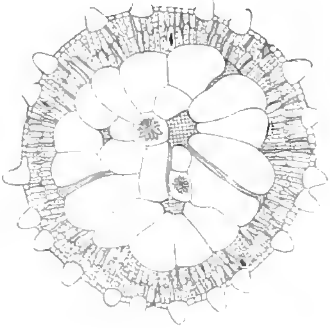


FIG. 13. Xerophilous structure. *Dry climate.* Mesembryanthemum Forskalii, a leaf-succulent of the Egyptian desert. Transverse section of leaf. After Volkens.

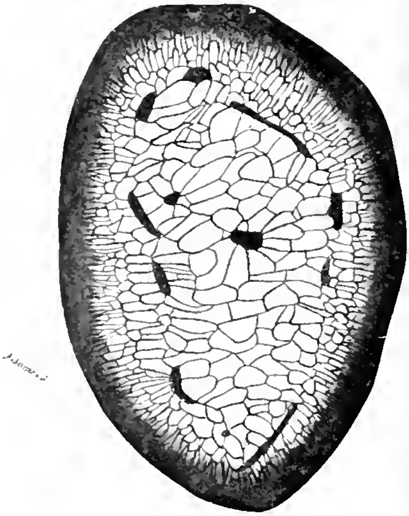


FIG. 14. Xerophilous structure. *Wet saline soil of tropical shores.* Sesuvium Portulacastrum. Succulent plant. Transverse section of leaf.

The organs which serve for absorption in xerophytes are no less well adapted for their purpose than are those for transpiration. A very rich root-system distinguishes the majority of them, and many species, especially epiphytes, possess a highly effective absorbing apparatus, which will be described further on.

Correlations among Xerophytes of Different Habitats.

The contrivances for conserving water, which have been already described, appear to be identical in xerophytes growing in habitats where the danger of desiccation is due to most diverse causes—it may be to physical drought, to coldness of the soil, to abundance of soluble salts or of humous acids in the soil, or to reduced atmospheric pressure. That we have not here merely a case of accidental external resemblance may be safely inferred from the fact that *many xerophytes are satisfied with physiologically dry habitats of the most diverse kinds, but are never found in the much more physically similar habitats of hygrophytes.*

This interchange of physiologically dry habitats may be observed in West Java. The character of the vegetation in this area, as determined by the climate, is decidedly hygrophilous; xerophytes are confined to very limited stations, the physical character of which varies greatly. Such are, for instance:—

FIG. 15. Xerophilous structure. *Wet saline soil of Javanese mangrove-swamp.* Sonneratia acida. Water-storing tracheids from the end of a vascular bundle in the leaf.

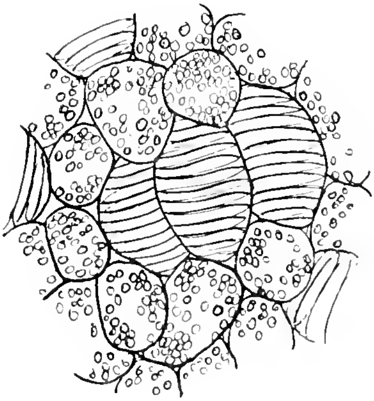


FIG. 16. Xerophilous structure. *Vegetation of dry bark* (epiphytes). Pleurothallis. Water-storing tracheids in the leaf. Blumenau, Brazil.

1. Dry lava-gravels and other stony substrata, as at Gunong Guntur.

2. The bark of trees (epiphytes).

3. The sea-shore, including mangrove-swamps which are still inundated at ebb-tide.

4. Solfataras, with wet clay soil, impregnated with alum and other soluble salts.

5. Alpine highlands with rarefied air and strong insolation.

More dissimilar physical conditions cannot be well imagined than those afforded by the bark of trees in a virgin forest, the solfataras, and the alpine highlands. Yet in West Java the vegetation of these habitats is, to a large extent, composed of identical species of xerophytes, which are completely absent from other habitats that have a greater physical resemblance to those in question but are hygrophilous. Thus, for instance, Vaccinium polyanthum (Agapetes rosea, Jungh.), Rhododendron javanicum, and R. retusum grow as epiphytes in the virgin forest, as terrestrial plants in the treeless alpine region and in solfataras ; Ficus diversifolia is an epiphyte in the virgin forest, a terrestrial shrub in solfataras ; Vaccinium varingiaefolium, Gaultheria leucocarpa, Myrsine avenis, Tetranthera citrata inhabit the treeless alpine region. All these plants have conspicuous xerophilous characteristics. The same agreement is found in Japan between the vegetation of the solfataras and that of the much higher alpine region. The conditions of life on the bark of trees, in the moderately warm virgin mountain-forests, and on the hot saline sea-shore are still much more dissimilar than in the cases cited above. And yet there is at least one plant that grows in both habitats as well as in the solfataras, but nowhere else—the bushy Ficus diversifolia. Forming the first vegetation on the dry lava-fields of Gunong Guntur, which are fully exposed to the sun's rays, at about 1,000 meters above sea-level, I also found the Rhododendron javanicum mentioned above—elsewhere, an epiphyte in the virgin forest, a terrestrial plant only in the solfataras and on alpine highlands—side by side with orchids and ferns which are elsewhere epiphytic.

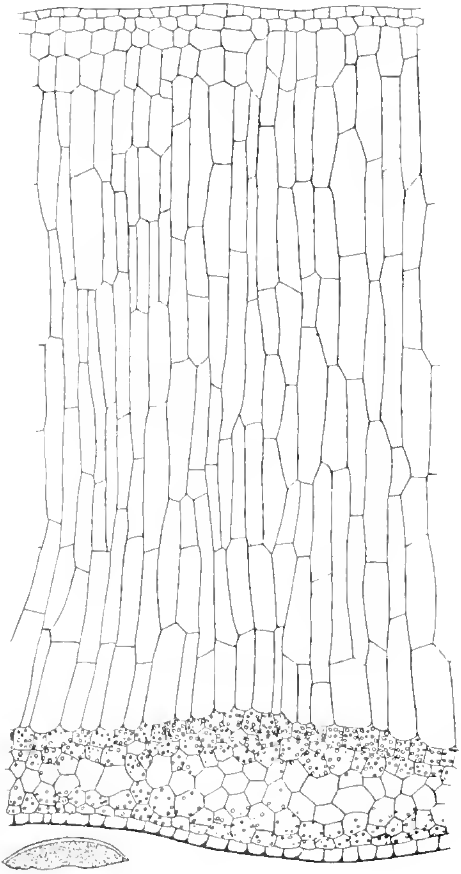


FIG. 16 a. Xerophilous structure. *Dry substratum* (epiphytes). Codonanthe sp. (Gesneraceae). Section of an old leaf with voluminous aqueous tissue. Magnified 55. Natural size shown below. From nature. The lower figure is inverted.

Such manifold interchangeability of habitats among xerophytes, as is found in Java, has not yet been established for other areas, possibly only because the physiological—as opposed to the physical—aspect of xerophily is quite new as a subject of study, and observers have bestowed very little attention on such phenomena. But Battandier had already reported that certain Algerian plants are confined to the alpine summits of the Atlas mountains and to the sea-shore; further, that certain ubiquitous plants, in both these apparently so dissimilar habitats develop exactly similar anomalous forms; and, finally, that the cultivation of alpine and littoral plants in ordinary lowland soil induces similar modifications of structure.

The xerophilous character of the vegetation of peat-moors has hitherto been considered an incomprehensible anomaly, and yet the rich supply of humous acids in the soil furnishes a condition for its occurrence as comprehensible as it is necessary. The presence of Scots pine and heather on both dry sand and on wet peat is thus not more remarkable than is that of Ledum palustre, Vaccinium uliginosum, and other peat-plants on the cold dry soil in the polar zones. All these habitats so very dissimilar in physical character are dry to plants, and therefore suited for the well-being of xerophytes.

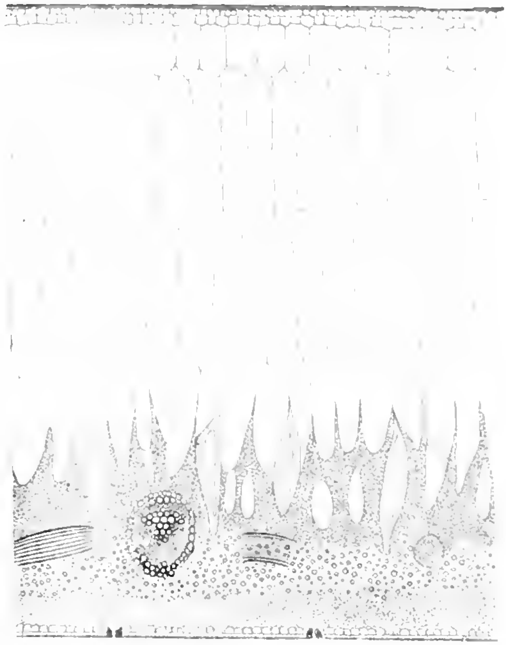


FIG. 17. Xerophilous structure. *Vegetation of wet saline soil of the Javanese mangrove-swamps.* Rhizophora mucronata. Transverse section of leaf with aqueous tissue. Magnified 70.

In spite of all the resemblances in the protective means employed, in spite of the frequent interchange of the precise methods of protection, in short, in spite of all similarity in the vegetation of various physiologically dry districts and habitats, careful examination shows that certain forms of xerophily are favoured by definite external conditions. The connexion between structure and environment is, as a rule, easily intelligible in such cases. Thus succulent plants occur chiefly in hot districts, and there alone attain large dimensions, both in dry and in damp air (plants of deserts, of sea-shores, epiphytes); in districts with cold winters, they fall off both in number and dimensions, and only those species that shrink up considerably in winter appear to withstand low temperature for any length of time. A considerable reduction in the transpiring surface, a formation of thorns, a dense coating with hairs (Fig. 18) are rather characteristic of dry air, whilst in moist air the leaves are more frequently well developed and glabrous. Warm districts with prolonged periods of drought, such as tropical and subtropical deserts, are characterized by the presence of endochylous succulent plants, whereas a perichylous construction indicates a plant accustomed to a more frequent though a scanty water-supply, such as characterizes the sea-shore and the epiphytic conditions within humid forests. Mobile pinnate leaves point to rapid changes in the environment; vertically arranged leaf-surfaces to strong insolation. The leathery foliage of sclerophyllous plants is found indeed in all formations of xerophytes, but is commonest in mild temperate

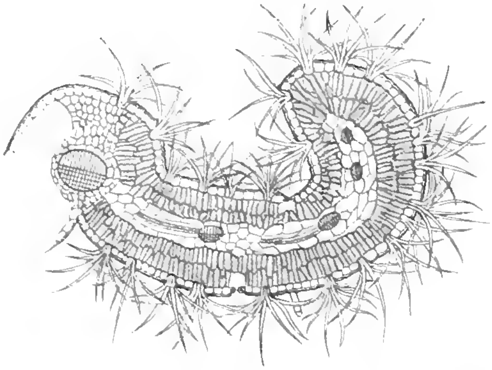
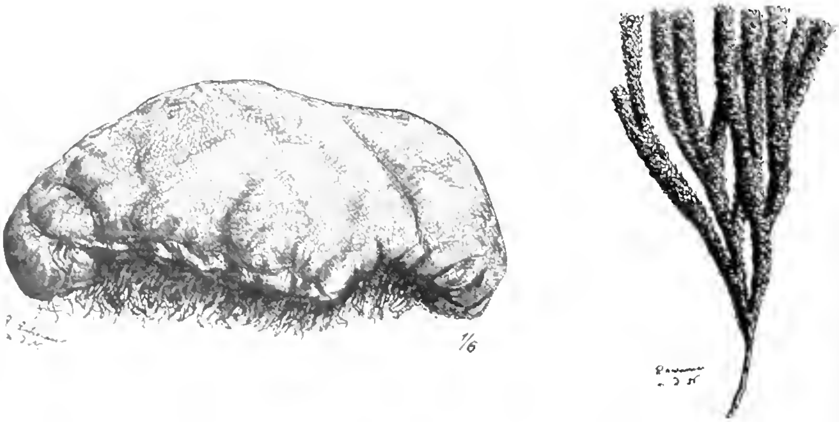


FIG. 18. Xerophilous structure. *Dry climate of the Egyptian desert.* Helianthemum kahiricum. Transverse section of a very hairy leaf. Magnified 40. After Volkens.



FIGS. 19 and 20. Xerophilous structure. Cushion-like growth. Left hand: Raoulia mammillaris from New Zealand. One-sixth natural size. Right hand: Dionysia sp. from the mountains of Persia. Part of a cushion. Natural size.

regions with wet winters and dry summers, like that of the Mediterranean. Finally, according to certain authors, the dense cushion-like growth of certain plants (Figs. 19, 20), which has not yet been mentioned, may also be included among the protective measures against drought; amongst phanerogams this is confined to plants of regions that are cold, or at any rate cool and periodically cloudy, and is chiefly prevalent in those of high mountains. A hard substratum appears to favour it, but is not essential, for cushion-like vegetation is also found on meadows and moorlands.

Such differences often give a varied physiognomy to xerophilous formations; they are however only quantitative and not qualitative, for every natural community of xerophytes includes the most diverse types intermingled in various proportions. For instance, in one locality succulent plants predominate, in another thorny shrubs with pinnate leaves, in still another sclerophyllous or very hairy plants; other forms are however always present as auxiliary species.

iii. *HYGROPHYTES.*

Wiesner[1] cultivated in absolutely saturated air a number of plants of more or less decided xerophilous character, especially some which naturally possess basal rosettes of leaves, and, leaving out of consideration those plants that became diseased, he obtained essential deviations from the normal structure. The leaves attained extraordinary dimensions, the rosettes by lengthening their internodes became converted into long shoots (Fig. 21). Under similar conditions in Lothelier's experiments, slightly foliaged or non-foliaged thorny xerophytes were converted into absolutely or nearly thornless plants with abundant foliage (Fig. 22). *Xerophytes when cultivated in very moist air, provided they can endure it, acquire a quite abnormal structure which approaches that of hygrophytes.*

Typical hygrophytes have weakly developed roots, elongated axes, and large thin leaf-blades. They are hardly ever thorny, as the parts of their vegetative shoots always assume the form of foliaged shoots and of leaves; they may, however, be prickly, as prickles

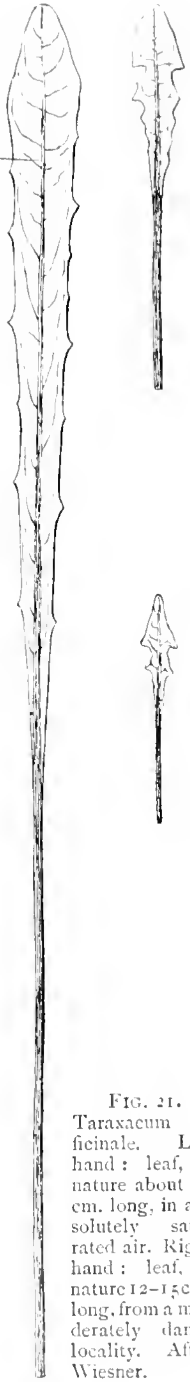


FIG. 21. Taraxacum officinale. Left hand: leaf, in nature about 60 cm. long, in absolutely saturated air. Right hand: leaf, in nature 12–15 cm. long, from a moderately damp locality. After Wiesner.

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[1] Wiesner, III.

do not involve any diminution of the transpiring surface. Their internal structure, like their external form, is specially adapted for promoting the exit of water.

Protective means against the loss of water are not, however, as a rule completely wanting. The Hymenophylleae of moist evergreen forests dry up very quickly in dry air, and are therefore always dependent on an atmosphere that is constantly very damp. This is also true, if to a less degree, of other herbaceous plants of similar habitats. Hygrophilous trees, on the contrary, are at times exposed to a less humid atmosphere, and are partially exposed to direct insolation, by which, even in a saturated atmosphere, their transpiration is materially accelerated. Hence many hygrophilous woody plants, especially in the tropics [1], possess distinct though weakly developed protective devices against the loss of water, apparently similar to those which are strongly developed in xerophytes, such as an epidermis rich in water or a thin aqueous tissue, and in leaves exposed to sunlight a well-developed cuticle.

FIG. 22. Ulex europaeus. *a* In ordinary air. *b* In saturated air. After Lothelier.

By such protective means the palisade-cells are guarded against excessive loss of water during the hot midday hours, the stomata are also closed during the same period. The urgent necessity for such a temporary decrease in the transpiration is proved by the drooping of the foliage of many tropical trees and shrubs under the midday sun. At other hours of the day, or when the sky is clouded, transpiration through the stomata is quite unrestricted [2], and under weaker illumination far exceeds that through the cuticle. Danger to hygrophytes from too much transpiration if it exists at all, is limited to a few hours in the day, and is often nonexistent for weeks; it may, at the worst, cause the foliage to wilt, but cannot cause death from desiccation. Their chief danger is that of stagnation of the transpiration-current, and the existence of this danger is primarily apparent in the structure of hygrophytes.

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[1] Haberlandt, I.

[2] Ibid.

The greatest possible expansion of the transpiring surface is the most general characteristic of hygrophytes. How important this may be has been shown by comparative experiments made by Noll, on a large-leaved hygrophilous plant, Aristolochia Sipho[1], and on a spheroidal Echinocactus. His observations showed that, for equal weights, the Echinocactus possessed a surface 300 times smaller than the Aristolochia. Were it merely a question of the size of surface exposed, the ratio of the transpiration of the two plants would be as 1 : 300. The Cactaceae, however, besides exposing a small surface, have other xerophilous characteristics, in their weakly developed intercellular system, their thick cuticle, and so forth; the Aristolochia, on the other hand, is not only large-leaved, but is also provided with other aids to transpiration, such as large intercellular system, thin cuticle, and the like; so that the ratio of their transpiration is, not 1 : 300, but 1 : 6,000. This latter ratio gives a clearer idea of the efficiency of the means for regulating transpiration than any actual description, and it is not at all an extreme case, for although Cactaceae are typical xerophytes, yet Aristolochia is by no means a decided hygrophyte.

FIG. 23. Hygrophilous structure. Ficus religiosa. Leaf with dripping point. After Stahl.

In many hygrophytes, especially those of damp tropical forests, adaptation in the construction of the thin leaf-surfaces is evident. Where the plant is liable to heavy rainfall the leaves have often the long 'dripping point,' by means of which water is soon drained off[2] (Fig. 23). The leaves of plants living in the deep moist shade of the forest, as well as those growing beside brooks where they may be sprayed by the water, frequently have a velvety surface on which the water spreads out by capillarity into an extremely thin layer that evaporates rapidly (Fig. 24)[3].

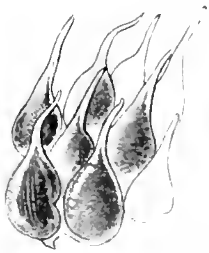

FIG. 24 Hygrophilous structure. Begonia imperialis. Conical papillae on the upper surface of the leaf. Slightly magnified. After Stahl.

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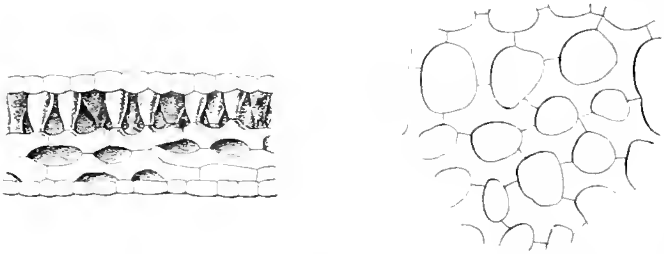
[1] This is tropophilous and therefore hygrophilous during the growing season.

[2] Jungner, op. cit., and especially Stahl, II.

[3] Stahl. IV.

As a means for promoting transpiration the significance of a well-developed air-containing intercellular system, such as exists in the leaves of all hygrophytes (Figs. 25, 26), is self-evident. The very numerous stomata serve as efferent passages, and they are not deeply sunk in the surface, as in xerophytes, but are superficial in position, and sometimes even raised on cones without any protective arrangements.



FIGS. 25 and 26. Hygrophilous structure. Leaf of Fagus sylvatica. Left hand: Transverse section of a shaded leaf. Right hand: Spongy parenchyma of a shaded leaf. After Stahl.

Hydathodes (Fig. 27), which are organs for excreting liquid water, whose wide distribution, variety, and great importance were first revealed by Haberlandt[1], are specially characteristic of hygrophytes in a very damp climate. Early in the morning under such climatic conditions, especially in the tropics, many plants, herbs as well as trees, are so covered with drops of water that not infrequently a drizzling rain seems to be descending from the forest canopy of leaves. This has been incorrectly regarded as dew. It owes its origin much more to excreting hydathodes, the activity of which is greatly increased when transpiration is restricted, but ceases when the air is dry. Hydathodes are epidermal structures of the most varied nature. Sometimes simple, sometimes complex in structure, they appear in the form of hairs, glandular cells,

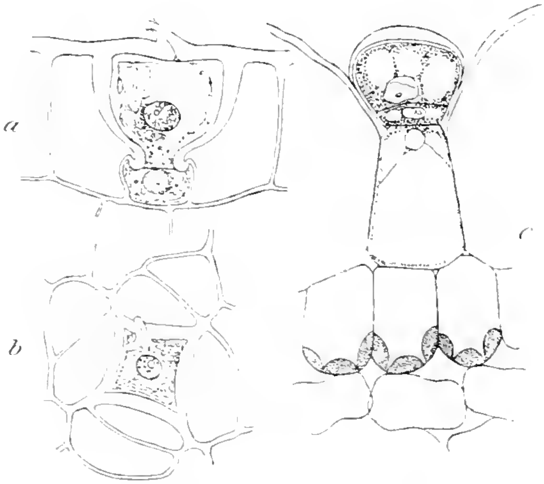


FIG. 27. Hygrophilous structure. Hydathodes of leaves. *a* and *b* Gonocaryum pyriforme. *c* Peperomia exigua. Magnified. After Haberlandt.

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[1] Haberlandt, II and III.

water-stomata, and so forth. They are sometimes active glands comparable to sweat-glands, sometimes passive places of exit associated with a simple process of filtration. In very damp regions hydathodes are often very numerous. Thus Haberlandt found, on an average, fifty-five hydathodes per square millimeter on the upper surface of a leaf of Gonocaryum pyriforme, and fifty-eight on an equal area of its lower surface.

Many other features in the more minute structure of hygrophytes, such as the red and silver spots on variegated leaves, have been regarded as favouring the exit of water. We must leave it to further research to discover how far the ingenious and suggestive explanations of these phenomena are borne out by facts [1].

iv. *TROPOPHYTES.*

The vegetation of districts with climates alternately damp and dry or cold, is alternately of a hygrophilous and of a xerophilous character; it is therefore *tropophilous*. The equivalence of cold and dry seasons as regards the supply of water to plants has caused similar adaptations in both cases.

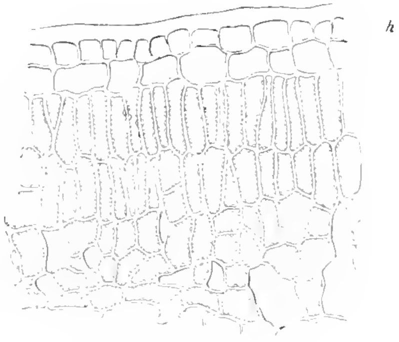

FIG. 28. Xerophilous structure in the perennial leaf of a tropophilous plant. Ilex Aquifolium. After Stahl.

Most tropophytes, whether of an alternately dry and moist climate or of an alternately cold and hot one, sacrifice the greater part of their transpiring organs at the beginning of the physiologically dry season. Many herbaceous plants lose all their subaërial parts, and merely retain their subterranean ones, which transpire but slightly. Others retain only the leafy shoots near the ground, in the form of rosettes or otherwise grouped. Most woody plants shed their leaves.

Periodically foliaged tropophilous woody plants have hygrophilous leaves, but xerophilous axes and buds. Stems and branches are protected against drought by bark or by thick layers of cork, buds by hard and often lacquered scales. In the case of evergreen tropophilous woody plants, xerophily must extend to the foliage, or the latter would perish from want of water in the dry or cold season. Such tropophytes are therefore, except for their young shoots, entirely xerophilous in construction; they are, however, distinguished from xerophytes by their environment. Examples from our own flora are the silver-fir and the spruce (not the really xerophilous Scots pine of dry sandy soil), holly (Fig. 28), cowberry, heather, and others.

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[1] See Stahl, IV.

The change from tints of deep green to greyish brown, from dense masses of fresh foliage to dry loose branches, which the passage from a hygrophilous to a xerophilous mode of life calls forth, gives a very similar appearance to all tropophytic districts, in spite frequently of wide physical differences in climate. Tropical luxuriance of growth is by no means universal in the tropics; extensive regions in the interior of continents remind one by the physiognomy of their vegetation, even in the rainy season, more of Central Europe, than of the overpowering richness of regions near the coast with a heavy rainfall, and the dry season especially is not at all unlike a German winter in its effects upon the covering of vegetation of the soil. On the other hand, many extra-tropical tracts with mild winters and abundant rainfall, such as the West of New Zealand, or South Chili, possess luxuriant evergreen forests like those of the tropics. There the climate is one for hygrophytes.

Periodical foliation and defoliation is indeed particularly characteristic of tropophytic districts, for the defoliation is very complete and foliation very luxuriant; but these phenomena are not confined to such districts. Many xerophytic districts also possess distinct seasons, which are likewise accompanied by the shedding and renewal of the foliage; the periodic change is then however less obvious, partly because the number of evergreen woody plants is greater, partly because the density of the foliage is less. This phenomenon is also common to many hygrophytic districts, but then it is in most cases confined to a thinning of the foliage which is not completely shed. Besides, the phenomenon is limited to a minority of the trees, except in districts which, like East Java, are climatically allied to tropophytic districts and form a transition stage to them. Defoliation is an adaptation to a physiologically dry period. An attempt has been made to assign as the invariable cause of its commencement the beginning of an insufficient water-supply, whether due to the drying up or cooling down of the soil. However obvious, *a priori*, this explanation may appear, it is as yet an unproven hypothesis.

2. VEGETATIVE ORGANS OF AQUATIC PLANTS[1].

The oecological conditions of plant-life in the liquid medium of water are evidently different from those of plants growing in the air, however rich in water-vapour this may be. Aquatic plants in fact exhibit a series of peculiar characteristics that are to be correlated with the physical properties of water in the liquid state. On the other hand, many characteristics that occur in plants growing in a very moist atmosphere are more markedly exhibited in aquatic plants also. The chemical identity of water in the liquid and the gaseous condition has some influence in causing such conformity.

[1] H. Schenck, I–III; Goebel, op. cit.

Many terrestrial plants growing accidentally in water exhibit only slight deviations from their normal structure, for this is too firmly fixed by heredity to yield, in the first generation, to new influences. Other terrestrial plants are more plastic and at once undergo a series of modifications owing to which their structure approaches that of true aquatic plants. Thus H. Schenck found on the banks of a pond, which had overflowed, some submerged specimens of Cardamine pratensis which exhibited the following deviations from the normal terrestrial form. The cauline leaves, normally sessile, had acquired long petioles, their segments were narrower, their mesophyll was thinner and devoid of palisade-cells, their cortex was thicker because their vascular bundles had been displaced towards the centre (Fig. 29), the sclerenchymatous elements richly developed in the terrestrial form were absent, the outer wall of the epidermis had become very thin, the vessels were greatly reduced, and the intercellular spaces enlarged. These modifications are to a great extent very similar to those induced by water-vapour. In very damp air we find lengthening of the petiole, diminution in the thickness of the cell-walls, reduction in the development of vessels and palisade-cells, and an increase in the air-containing spaces. Only two characteristics, which are not very prominent, depend on the liquid condition of the water: these are centripetal displacement of the vascular bundles and the narrowing of the leaf-segments. *This represents the first step towards the transformation of a terrestrial plant into an aquatic plant.*

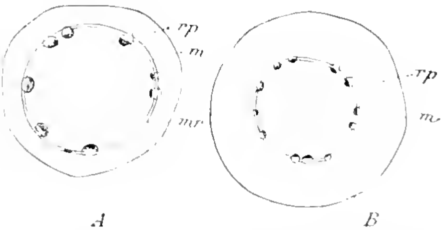

Fig. 29. Cardamine pratensis. Stem in transverse section. *A* Terrestrial form. *B* Aquatic form. *m* pith; *rp* cortical parenchyma; *mr* ring of mechanical tissue. Slightly magnified. After H. Schenck.

The Cardamine does not appear able to hold its own as an aquatic plant. Its plasticity is not sufficient for the purpose. Other so-called amphibious plants, the best known of which is Polygonum amphibium, thrive equally well as aquatic or as terrestrial plants, because, owing to a high degree of plasticity, they become appropriately modified for either medium.

Aquatic phanerogams and pteridophytes, possibly also aquatic mosses, have originated from plastic terrestrial plants that possessed the faculty of establishing themselves as aquatic plants. Excepting the few species that have remained amphibious, their persistence is eventually due to this faculty, for, crowded out by the competition of terrestrial plants, they have taken refuge in the water, where they have gradually become appropriately modified and have lost partially, or completely, the ability to thrive normally upon land.

The directions in which the modifying influence of water has chiefly acted are as follows: enlargement of the external surface of the shoots by the lengthening or subdivision of their members, suppression or diminution of the root-system along with, it may be, its transformation into fixing organs, weak development of the cuticle, absence or reduction in number of the stomata, displacement of the vascular bundles to form a central strand, peripheral disposition of the chlorenchyma. In still waters there is besides, as a rule, a diminution in the mechanical elements and an increase in the air-containing intercellular spaces. These modifications are not so noticeable in actively moving water, where also the relatively large extension of surface is less pronounced. The utility of these modifications is obvious. It is only doubtful whether they are to be attributed to natural selection or to the direct influence of water. The first hint in explanation of some of them comes from the Cardamine accidentally growing in water, in regard to which there can be no question of natural selection. Probably both groups of influences, the direct and the indirect, have acted simultaneously.

FIG. 30. Ranunculus fluitans. 1. Aquatic form. 2. Terrestrial form. Two-thirds natural size.

The modifications which existence in water induced in plants that were originally terrestrial are only in part attributable to the direct action of water. For the rest, it is a question of other factors of plant-life, which are themselves modified by water. Some characteristics of aquatic plants are to be attributed to the weakening of the light in water, and they accordingly reappear in terrestrial plants growing in deep shade; in illustration of this may be cited the peripheral arrangement of the chlorenchyma and possibly the great lengthening of parts in deep water. The considerable extension of the plant-surface, and the abundance of air-containing canals in members (rhizomes, roots) from which such canals are constantly absent in terrestrial plants, is to be ascribed to the risk of want of oxygen owing to the slow diffusion of gas in water; these canals conduct the oxygen set free by assimilation into tissues that are not green. Plants growing in water that is in active movement and consequently richly supplied with air, such as the Podostemaceae of tropical waterfalls and the larger surf-Algae, are distinguished from terrestrial plants neither by a large development of the surface, nor by the possession of special aërating devices. These phenomena will be more thoroughly discussed further on[1].

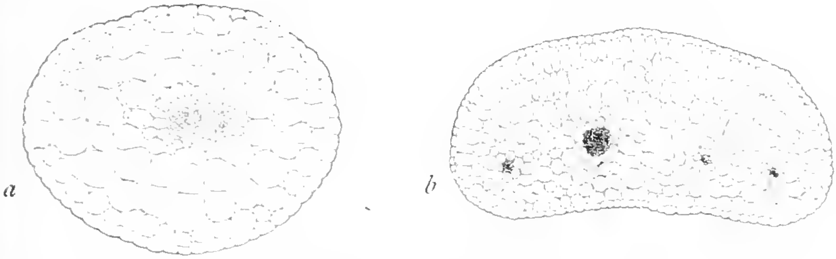

FIG. 31. Ranunculus fluitans. Transverse section of a segment of a leaf. *a* Aquatic form; magnified 90. *b* Terrestrial form; magnified 60. After H. Schenck.

The other characteristics of aquatic plants may be considered as due to the direct action of the water. Three of them are characteristic of liquid water, as opposed to water-vapour: first, the poverty in, or absence of, stomata which no longer function as in air as organs for the interchange of gases, since the whole surface of an aquatic plant absorbs and emits oxygen and carbon dioxide and no transpiration takes place; secondly, the central position of the vascular bundles in correspondence with the necessity for resisting tensile strains; finally, the mucilage, which protects young plants against loss of substance by diffusion[2]. Other peculiarities also occur in a less pronounced degree in damp air, namely, the reduction of the root-system, of the vessels, and of the epidermal tissues, and this reduction is correlated with the absence of transpiration in water and with its diminution in damp air: to this may be added the slight development

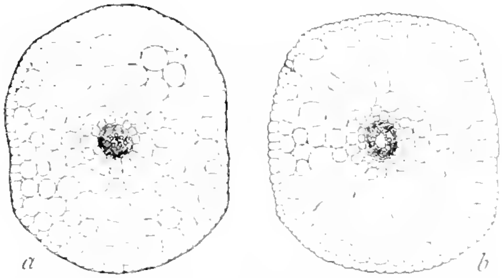

FIG. 32. Callitriche stagnalis. Transverse section of stem. *a* Terrestrial form. *b* Aquatic form. Magnified 67. After H. Schenck.

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[1] See Part I, Chap. IV, and Part III, Sect. V.

[2] Schilling, op. cit.

of the sclerotic elements, which however shows itself only in still water and in still air.

The great plasticity which rendered possible the change of terrestrial plants into aquatic plants has to some extent been inherited by descendants from their ancestors. Most phanerogamous and fern-like aquatic plants can still change into terrestrial forms approaching ordinary terrestrial plants in structure (Figs. 30–32). Shorter axes, less subdivided leaves, palisade-parenchyma, stomata, a well-developed cuticle, and centripetal disposition of the chlorenchyma distinguish such terrestrial forms from aquatic forms. But many of the characteristics acquired during a normal life in water have become hereditary, such as the central position of the vascular bundles. In fact the whole structure shows unmistakably that we have to deal with somewhat modified aquatic plants. Such deserters from the water generally remain weakly, and rarely or never blossom, as opposed to true amphibious plants in which it is precisely the terrestrial form that displays sexual activity more frequently than does the aquatic form.

Terrestrial plants that have been transformed into aquatic plants comprise only a small section of the whole aquatic flora. Algae, which we have not yet considered, preponderate in aquatic vegetation, and are true aquatic plants whose ancestral forms have always inhabited water. Even the few existing terrestrial Algae are more dependent on liquid water than are true terrestrial plants. These qualities render Algae less suitable than more highly organized types for illustrating the difference between aquatic and terrestrial plants.

3. WATER AND REPRODUCTION[1].

A plentiful water-supply, as a rule, favours the development of the vegetative organs; scarcity of water brings about their reduction. On the contrary, *the production of sexual organs is usually impeded by a considerable supply of moisture and favoured by drought.*

This principle, which has long been established by practical operations, has led to various horticultural artifices for the production of a rich supply of blossom. Among these, for instance, is the art of root-pruning, in which a trench is dug around the plant and the exposed portion of the root-system cut off. In Ceylon, in order to cause the vine to blossom, the roots are for a time partially laid bare. Cereus and other Cactaceae bear flowers more plentifully if they have been shrivelled up for some time, than after a period of uninterrupted turgescence. Many plants, for instance certain species of Juncus, blossom only in a relatively dry soil.

Retarded passage of water through the vessels leads to similar results. If a twig of a coffee-plant be broken so that it remains attached to a branch

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[1] Numerous references in Sorauer, Pflanzenkrankheiten, Vol. I, and Moebius, op. cit.

only by a portion of its wood, it produces more flowers and eventually more fruit than an uninjured twig[1]. Sugar-cane infected with the serch-disease having its vessels obstructed by mucilage always blossoms after a short time.

Moebius has devoted some instructive experiments to the question of the influence of moisture on the sexual processes. He cultivated in pots pecimens of Phalaris canariensis, Borago officinalis, and Andropogon schaemum, in some cases watering them plentifully, and in others just ufficiently to maintain life. In every case flowering was signally favoured by drought. Plants that were kept moist did not as a rule produce a single lower during the progress of the experiment.

To the same group of phenomena belongs Wiesner's observation, according to which, in saturated air, Capsella Bursa-pastoris bore only a few tunted blossoms and Taraxacum none at all, whereas the vegetative shoots of both these plants developed with extraordinary luxuriance.

Finally, aquatic plants are highly instructive in this respect. Most quatic phanerogams remain flowerless if a considerable depth of water inders the emergence of fertile shoots. Thus, Alisma Plantago, Sagittaria, snardia, Hippuris, Elatine Alsinastrum, Littorella, and others, remain terile whenever they are completely submerged. Many amphibious pecies, such as Marsilea and Pilularia, develop their sporangia exclusively, r nearly so, on their terrestrial forms. Subularia aquatica is cleistogamous when submerged. On the other hand, vegetative multiplication takes lace in aquatic plants to a very great extent. Thus, in a few years' time, ur waters were overrun by the water-pest Elodea canadensis, developed by neans of its severed branches.

The Algae, forming by far the greatest class of water-plants, complete heir sexual and asexual reproduction under water. They are plants whose ncestral forms were already aquatic plants, and they have always remained withdrawn from the influence of drought. Yet in some of the more mphibious Algae the favourable influence of drought in sexual reproduction as been observed; for instance, by Klebs in Vaucheria.

Those aquatic plants that have sprung from terrestrial forms, as is the ase with phanerogams and the higher cryptogams, have accommodated hemselves fully to water as regards their vegetative activity; but, as egards sexual reproduction, they have with few exceptions remained ubaërial plants, and this condition has induced wonderful adaptations, uch as the oft-described pollination of Vallisneria spiralis, which has ever een a theme for poets. Only a few forms, for example Ceratophyllum, aias, Isoetes, a few mosses, and especially the marine phanerogams, pass very stage of their development under water, for which reason special daptations in relation to the liquid environment are induced. Many

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[1] Ernst after Moebius, op. cit.

plants, also, that form their sexual organs under water are fertile in shallo water. but sterile in deep water where their vegetative growth is luxuriant we see this in Potamogeton rufescens, several of the Podostemaceae, Isoete and other plants. This may be due to the action of light, as the productic of most flowers is arrested when the light is weak [1].

A flowing movement of the water also impedes the formation of flower for instance in Potamogeton pectinatus. From Klebs' researches on variou Algae, it appears impossible that the cause of this should be the weakenir of the light by bubbles of air. The phenomenon has not yet bee explained.

4. WATER AND THE DISPERSAL OF SEEDS.

The species of plants that inhabit waters and shores frequently have co trivances in the construction of their fruits or seeds enabling them to flo for a long time and thus facilitating their dispersal by water-currents. I highly adapted cases such fruits or seeds possess various floating orgar rarely in the form of a *floating bladder* with a wate tight wall, as in Morinda citrifolia (Fig. 33), mo frequently in that of *floating tissue*, formed by a thi husk, the cells of which contain air, often with air-spac intervening, as in fruits of Cocos nucifera, Cerbe Odollam, Barringtonia speciosa, Terminalia Catap (Fig. 34), Calophyllum Inophyllum (Fig. 35), seeds Cycas circinalis. Yet many floating fruits and seec among which are some that remain for a long tin on the water, for instance Heritiera littoralis, altogeth dispense with any particular kind of adaptation and o their low specific gravity to an air-containing water-tig space between the pericarp and the seed, or betwe the seed-coat and the kernel of the seed, as in t case of many inland fruits and seeds which have no connexion wi the water [2].

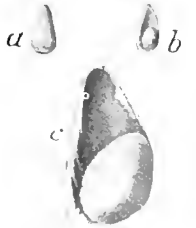

FIG. 33. *a* Morinda umbellata: stone, not floating; natural size. *b* Morinda citrifolia: stone with a floating bladder; natural size. *c* The same magnified.

Fruits or seeds possessed of prolonged floating capacity are freque in the littoral flora, particularly of tropical coasts, where they are oft of considerable size and have great diversity of form, within the fo recorded types.

The great importance of marine currents in regard to the dispers of seeds was first recognized in the case of tropical fruits and seeds Linnaeus, who found some of those belonging to the tropical Americ flora on the Norway coast, whither they had evidently been brought by t

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[1] See Part I, Chap. III.

[2] Schimper, IV. Numerous figures of floating fruits and seeds will be found in t book; see particularly Plate VII.

Gulf Stream from the West Indies. More recently the great importance of marine currents in introducing plants to coasts and islands was proved by investigations relating to the Indian and Pacific Oceans, and carried on by Hemsley, Treub, Guppy, and myself. I wrote on the spot the following description of the appearance of fruits and seeds thrown up by the sea at Tjilatjap, in South Java :—

FIG. 34. Terminalia Catappa. Drift-fruit. Natural size.

'The broad sandy shore is quite free from vegetaion and nearly bare. Except for a few fruits recently hrown up by the surf, together with shells and fragments of pumice coming from the eruption of Krakatoa, t is strewn only with the fruits of Spinifex squarrosus, which are either bounding and rolling along urged by he wind, or lie shortly clipped and half-buried in the sand. Behind the shore, some low dunes stand up sharply, and are overgrown with bluish Spinifex. At he foot of these dunes lies the marine drift, carried hither by the wind or by high tides, in the form of ong sharply-defined strips, resembling heaps of dung, on which many seeds have germinated. The drift consists chiefly of brown herbaceous or woody fragments of various species, which, excepting the Spiniex, are difficult to identify, of pieces of pumice, coral, hells, and finally of fruits and seeds, which, wherever he drift-heaps are specially thick, have partly begun to germinate and cover them with a fresh green verdure. Many of those fruits and seeds come from plants that one might look for in vain in the neighbourhood; some, at any rate, must have come rom the neighbouring island of Noesa Kambangan, but I cannot decide whence he others have come.

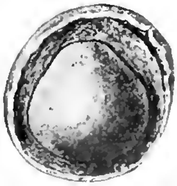

FIG. 35. Calophyllum Inophyllum. Stone of fruit opened and exhibiting the floating tissue. Natural size.

'Many of the fruits look nearly as fresh as if they had just allen from the tree, for instance those of Barringtonia peciosa. Others bear traces of a long journey, and have been rubbed nearly out of all recognition; their husks are overed with Serpicula, or perforated like a sieve, or inhabited y a colony of Cirripedes; many, such as Carapa and Cocos, ave been hollowed out by animals.

'The most numerous of all these fruits are those of Heritiera ttoralis, and they are very conspicuous on account of their reat size. Abundant likewise are the large fruits of Cerbera Odollam, quite stripped of their green husks and partially of heir parenchyma, and displaying the bared tough fibrous oat surrounding the endocarp (here forming the floating tissue) which is almost water-tight. Further arresting the attention are coconuts covered only with the emains of their fibrous husks, and usually with one side perforated by a round hole hrough which some unknown creature has eaten its fill of the seed that has almost entirely disappeared. The ribbed fruits of Nipa fruticans also abound; the wrinkled fruits of a Canarium or merely their remnants in the form of stones; the large mitre-shaped fruits of Barringtonia speciosa, as well as the oblong ones of B. excelsa and the much smaller fruits of a third species not determined; the boat-shaped stones of Terminalia Catappa (Fig. 34), often much worn by friction and with the thick husk infested with several kinds of creatures, especially Cirripedes; the irregularly angled seeds of Carapa obovata looking as if they were cut out of bottle-cork, their husks being also perforated or gnawed; the large angular seeds of Pangium edule; the globular stones of Calophyllum Inophyllum (Fig. 35); fruits of various Pandani; pods of Pongamia glabra and of Cynometra caulifolia; the grey irregularly rounded seeds of Caesalpinia Bonducella, the flat dark ones of a Dioclea, the oblong ones of a species of Erythrina; the seedlings of a Bruguiera. By carefully searching, a number of smaller fruits and seeds may be found, such as the stones of Lumnitzera racemosa or L. coccinea, those of Scyphiphora, and the seeds of Ipomoea Pes-caprae.

'In most cases, even when the fruits are much attrited, the seeds are quite sound, and germination has apparently already commenced in some of them; in this respect there is a striking difference between different species which is probably due to the various degrees of durability of the germinating power. Of coconut palms, oaks or Canarium, there are no young plants, and the seedlings of Heritiera are few in comparison with the vast number of its drifted fruits. Somewhat more numerous are the seedlings of Barringtonia speciosa and another species of the same genus, much more so than of Calophyllum Inophyllum, Cerbera Odollam, and Carapa, and commonest of all are those of Ipomoea Pes-caprae and of various Leguminosae. Seedlings of species, the ungerminated seeds of which I did not discover, are very numerous, especially those of Ricinus communis and of several other Euphorbiaceae.'

The littoral flora includes an extraordinarily high percentage of widespread species, which are often cosmopolitan within their climatic zones, and which owe their extensive area of distribution to marine currents, as is proved by the presence of their seedlings on heaps of drift and by investigations into the floating capacity and germinating power of drift-seeds.

Investigations which I carried out as to the duration of the floating capacity of the seeds of various Malayan littoral plants in water containing 3½ % of salt had to be interrupted before all the seeds had sunk. Seeds of Suriana maritima floated for 143 days, those of Hibiscus tiliaceus for 121 days. Other seeds or indehiscent fruits floated from 10 to 70 days and then sank. Investigations by Guppy at Buitenzorg, which had also to be stopped after 53 days, proved that the germinating power of a considerable number of seeds was unimpaired after 40–53 days.

The dispersal of littoral plants by marine currents has been of considerable importance in establishing plants on islands and coasts not merely in the past but at the present day, as Treub was able definitely to prove when he visited the Krakatoa group of islands about three years after the well-known eruption had completely destroyed their vegetation. Numbers of drift-seeds were then lying on the shore and many plants that had evidently sprung from such seeds were already growing, forming the commencement of a littoral flora agreeing in composition with that found in other islands of the Malay archipelago, which in this respect show a remarkable uniformity.

SELECT LITERATURE

1. Vegetative Organs of Terrestrial Plants.

Altenkirch, G. Studien über die Verdunstungserscheinungen in der trockenen Geröllflora Sachsens. Engler's Jahrbücher. Bd. XVIII. 1894.

Areschoug, F. W. C. Der Einfluss des Klimas auf die Organisation der Pflanzen, insbesondere auf die anatomische Structur der Blattorgane. Engler's Jahrbücher. Bd. II. 1881.

Börgesen, F. Anatomie des feuilles des plantes arctiques. Journal de botanique. 1895.

Brick, C. Beiträge zur Biologie und vergleichenden Anatomie der baltischen Strandgewächse. Schriften der naturforschenden Gesellschaft zu Danzig. Neue Folge. Bd. VII.

Burgerstein, Al. Ueber den Einfluss äusserer Bedingungen auf die Transpiration der Pflanzen. XII. Jahresbericht des Leopoldstädter C. R. und Obergymnasiums zu Wien. Wien, 1876.

Dombois, E. Einfluss der geringeren oder grösseren Feuchtigkeit der Standorte der Pflanzen auf deren Behaarung. Inaug.-Diss. Saarbrücken, 1887. (Reference in Botanisches Centralblatt. Bd. XXXIX. 1889.)

Eberdt, O. Ueber das Palissadenparenchym. Berichte der deutschen botanischen Gesellschaft. Bd. VI. 1888.

Ernst, A. Botanische Zeitung. Bd. XXXIV. 1876. pp. 33-41.

Gain, Ed. Action de l'eau du sol sur la végétation. Revue générale de botanique. Tome VII. 1895.

Géneau de Lamarlière, L. Recherches physiologiques sur les feuilles développées à l'ombre et au soleil. Revue générale de botanique. Tome VII. 1895. p. 481.

Haberlandt, H. I. Anatomisch-physiologische Untersuchungen über das tropische Laubblatt. (I) Ueber die Transpiration einiger Tropenpflanzen. Sitzungsberichte der Wiener Akademie. Bd. CI, Abth. I. 1892.

— II. Bd. (II) Ueber wassersecernirende und -absorbirende Organe. (1. Abhandl.) Ibid. Bd. CIII, Abth. I. 1894.

— III. Bd. (III) Ueber wassersecernirende und -absorbirende Organe. (2. Abhandl.) Ibid. Bd. CIV, Abth. I. 1895.

Hackel, E. Ueber einige Eigenthümlichkeiten der Gräser trockener Klimate. Verh. der zool.-botan. Gesellsch. Wien, 1891.

Heinricher, E. Ueber einige im Laube dicotyler Pflanzen auf trockenen Standorten auftretende Einrichtungen, welche muthmasslich eine ausreichende Wasserversorgung des Blattmesophylls bezwecken. Botanisches Centralblatt. Bd. XXIII. 1885.

Henslow, G. The origin of plant-structures by self-adaptation to the environment, exemplified by desert or xerophilous plants. Journ. Linn. Society. Botany. Vol. XXX. 1894.

Höhnel, F. v. Ueber die Wasserverbrauchsmengen unserer Forstbäume mit Beziehung auf die forstlich-meteorologischen Verhältnisse. Wollny's Forschungen auf dem Gebiete der Agrikulturphysik. Bd. II, Heft 4.

Jungner, J. R. Anpassungen der Pflanzen an das Klima in den Gegenden der regnerischen Kamerungebirge. Botanisches Centralblatt. Bd. XLVII. 1891.

Kihlman, A. O. Pflanzenbiologische Studien aus Russisch-Lappland. Acta soc. pro Fauna et Flora fennica. Bd. VI. 1890.

Kohl, G. Die Transpiration der Pflanzen. Brunswick, 1886.

Krüger, P. Die oberirdischen Organe der Orchideen in ihren Beziehungen zu Klima und Standort. Flora. Jahrg. LXVII. 1883.

Lesage, P. I. Recherches expérimentales sur les modifications des feuilles chez les plantes maritimes. Revue générale de botanique. Tome II. 1890.

—— II. Sur les rapports des palissades dans les feuilles avec la transpiration. Comptes rendus de l'Acad. des sciences de Paris. Tome CXVIII. 1894.

Lothelier. Recherches sur les plantes à piquants. Revue générale de botanique. Tome V. 1893.

Noll, Fr. Vorlesungsnotiz zur Biologie der Succulenten. Flora. Jahrg. LXXVII. 1893.

Pfitzer, E. Beiträge zur Kenntniss der Hautgewebe der Pflanzen. Pringsheim's Jahrbücher. Bd. VII, 1870; Bd. VIII, 1872.

Sachs, J. I. Das Erfrieren von Pflanzen bei Temperaturen über 0°. Botanische Zeitung. Bd. XVIII. 1860.

—— II. Ueber den Einfluss der chemischen und physikalischen Beschaffenheit des Bodens auf die Transpiration. Botanische Zeitung. Bd. XVIII. 1860.

—— III. Ueber den Einfluss der Lufttemperatur und des Tageslichtes auf die stündlichen und täglichen Aenderungen des Längenwachsthums (Streckung) der Internodien. Arbeiten aus dem botanischen Institut zu Würzburg. Bd. I. 1872. (Ges. Abhandl., Bd. II, p. 677.)

Schimper, A. F. W. I. Ueber Schutzmittel des Laubes gegen Transpiration, vornehmlich in der Flora Java's. Monatsber. der Berliner Akademie d. Wissenschaften. Bd. VII. 1890.

—— II. Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze. Flora. Jahrg. LXXIII. 1890.

—— III. Die epiphytische Vegetation Amerika's. Botan. Mittheil. aus den Tropen. Heft II. Jena, 1888.

—— IV. Die indo-malayische Strandflora. Ibid. Heft III. Jena, 1891.

Schröder, G. Ueber die Austrocknungsfähigkeit der Pflanze. Untersuchungen aus dem botanischen Institut zu Tübingen. Bd. II., 1886.

Schwarz, Fr. Die Wurzelhaare der Pflanzen. Untersuchungen aus dem botanischen Institut zu Tübingen. Bd. I. 1883.

Stahl, E. I. Ueber den Einfluss des sonnigen oder schattigen Standortes auf die Ausbildung der Laubblätter. Jenaische Zeitschr. für Naturw. Bd. XVI. 1883.

Stahl, E. II. Regenfall und Blattgestalt. Ein Beitrag zur Pflanzenbiologie. Annales du jardin botanique de Buitenzorg. Vol. XI. 1893.

— III. Einige Versuche über Transpiration und Assimilation. Botanische Zeitung. Bd. LI. 1894.

— IV. Ueber bunte Laubblätter. Annales du jardin botanique de Buitenzorg. Vol. XIII. 1896.

Tschirch, A. I. Ueber einige Beziehungen des anatomischen Baues der Assimilationsorgane zu Klima und Standort, &c. Halle, 1881.

— II. Beiträge zur Anatomie und dem Einrollungsmechanismus einiger Grasblätter. Pringsheim's Jahrbücher. Bd. XVII. 1882.

Vesque, J. I. Études microphysiologiques sur les réservoirs d'eau des plantes. Extract from Annales agronomiques. Tome XII. 1886.

— II. De l'influence des matières salines sur l'absorption de l'eau par les racines. Annales des sciences naturelles. 6e série. Tome IX. 1878.

— III. Essai d'une étude monographique et descriptive de la tribu des Capparidées. Ibid. 6e série. Tome XIII. 1882.

Vesque, J., et Ch. Viet. De l'influence du milieu sur la structure anatomique des végétaux. Annales des sciences naturelles. 6e série. Tome XII. 1881.

Volkens, G. I. Beziehungen zwischen Standort und anatomischem Bau der Vegetationsorgane. Jahrb. des k. botan. Gartens zu Berlin. Bd. III. 1884.

— II. Die Flora der ägyptisch-arabischen Wüste. Berlin, 1887.

— III. Ueber Pflanzen mit lackirten Blättern. Berichte der deutschen botanischen Gesellschaft. Bd. VIII. 1890.

Wagner, A. Zur Kenntniss des Blattbaues der Alpenpflanzen und dessen biolog. Bedeutung. Sitzungsberichte der Wiener Akademie. Bd. CI, Abth. I. 1892.

Westermaier, M. Ueber Bau und Function des pflanzlichen Hautgewebes. Pringsheim's Jahrbücher. Bd. XIV. 1884.

Wiesner und Pacher. Ueber die Transpiration entlaubter Zweige und des Stammes der Rosskastanie. Oesterreichische botanische Zeitschrift. 1875.

Wiesner, J. I. Grundversuche über den Einfluss der Luftbewegung auf die Transpiration der Pflanzen. Sitzungsberichte der Wiener Akademie. Bd. XCVI, Abth. I. 1887.

— II. Der absteigende Wasserstrom und dessen physiologische Bedeutung. Botanische Zeitung. Bd. XLVII. 1889.

— III. Formänderungen von Pflanzen bei Cultur im absolut feuchten Raume und im Dunkeln. Berichte der deutschen botanischen Gesellschaft. Bd. IX. 1891.

— IV. Ueber ombrophile und ombrophobe Pflanzenorgane. Sitzungsberichte der Wiener Akademie. Bd. CII, Abth. I. 1893.

— V. Ueber den vorherrschend ombrophilen Charakter des Laubes der Tropengewächse. Ibid. Bd. CIII, Abth. I. 1894.

2. Vegetative Organs of Aquatic Plants.

Askenasy, E. Ueber den Einfluss des Wachsthumsmediums auf die Gestalt der Pflanzen. Botanische Zeitung. Bd. XXVIII. 1870.

Costantin, J. I. Recherches sur la structure de la tige des plantes aquatiques. Annales des sciences naturelles. 6e série. Tome I. p. 19.

— II. Études sur les feuilles des plantes aquatiques. Ibid. 7e série. Tome III. 1886.

Costantin, J. III. Influence du milieu aquatique sur les stomates. Bulletin de la société botanique de France. Tome XXXII. 1893.

—— IV. Observations critiques sur l'épiderme des feuilles des végétaux aquatiques. Ibid. Bd. XXXII. 1885.

Goebel, K. Pflanzenbiologische Schilderungen. Theil II. Marburg, 1891. VI. Wasserpflanzen.

Karsten, G. Ueber die Entwickelung der Schwimmblätter bei einigen Wasserpflanzen. Botanische Zeitung. Bd. XLIV. 1888.

Sauvageau, C. I. Observations sur la structure des feuilles des plantes aquatiques. Journal de Botanique. 1890.

—— II. Sur la structure de la feuille des genres Halodule et Phyllospadix. Ibid. 1890.

—— III. Sur la feuille des Hydrocharidées marines. Ibid. 1890.

—— IV. Sur une particularité de structure des plantes aquatiques. Comptes rendus de l'Acad. des sciences de Paris. Tome CXI. 1890.

Schenck, H. I. Die Biologie der Wassergewächse. Bonn, 1886.

—— II. Ueber Structuränderungen submers vegetirender Landpflanzen. Berichte der deutschen botanischen Gesellschaft. Bd. II. 1884.

—— III. Vergleichende Anatomie der submersen Gewächse. Bibliotheca botanica. Bd. I. 1886.

Schilling, A. J. Anatomisch-biologische Untersuchungen über die Schleimbildung der Wasserpflanzen. Flora. Jahrg. LXXVIII. 1894.

Vöchting, H. Zur Histologie und Entwickelungsgeschichte von Myriophyllum. Nova Acta Acad. Leopold. Bd. XXXVI. 1872.

3. Water and Reproduction.

Goebel, K. Pflanzenbiologische Schilderungen. Theil II. Marburg, 1891. VI. Di Wasserpflanzen.

Klebs, G. Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen Jena, G. Fischer. 1896.

Moebius, M. I. Welche Umstände befördern und welche hemmen das Blühen de Pflanzen? Biologisches Centralblatt. 1892. The older literature is cited here

—— II. Beiträge zur Lehre von der Fortpflanzung der Gewächse. Jena, 1897.

Schenck, H. Die Biologie der Wassergewächse. Bonn, 1886. The literatur is given here on pp. 130-131.

Wiesner, J. Formänderungen von Pflanzen bei Cultur im absolut feuchten Rau und im Dunkeln. Berichte der deutschen botanischen Gesellschaft. Bd. IX 1891.

4. Water and the Dispersal of Seeds.

Guppy, M. B. The dispersal of plants as illustrated by the flora of the Keelin or Cocos Islands. Transactions of the Victoria Institute. 1890.

Hemsley, W. B. On the dispersal of plants by oceanic currents and birds. I Report on the scientific results of the voyage of H. M. S. *Challenger* durin the years 1873-1876. Botany. Vol. I. Appendix.

Kolpin Ravn, F. Om Flydeevnen hos Frone af vore Vandog Sumpplanter (wit French *résumé*). Botanisk Tidsskrift. Bind XIX. 1894.

Schimper, A. F. W. Die indo-malayische Strandflora. Botan. Mittheil. aus de Tropen. Heft III. Jena, 1891. p. 152. The earlier literature is cited here

Treub, M. Notice sur la nouvelle flore de Krakatau. Annales du jardin botaniqu de Buitenzorg. Vol. VII. 1888.

CHAPTER II

HEAT

1. General Considerations. Heat and the structure of plants. Effects of a cold climate on the form and lie of leaves. The three cardinal points. Phaenology. **2. Zero Points of Plant-life.** i. *Lower Zero Points.* Power of resisting cold. Death by cold often due to drought. The coldest points on the earth. ii. *Upper Zero Points.* Power of resisting heat. Sachs' researches. Hot springs. Highest observed temperatures in soil and air. **3. Cardinal Points of the Functions of Plants.** The harmonic optimum. The absolute optimum. The oecological optimum. Fluctuations of the harmonic optimum during development. The oecological optima of a peach-tree. Cardinal points of germination. Germination, growth, assimilation, and respiration at low temperatures. Useful low temperatures. Effects of cold on sexual reproduction. **4. Acclimatization.** Transference from a warm to a cold climate and the reverse. Schuebeler's and A. de Candolle's researches. H. Mayr on the acclimatization of forest trees.

1. GENERAL CONSIDERATIONS.

In spite of the predominating part played by temperature in regard to the distribution of plants, the action of temperature is not placed in this book at the head of the factors determining plant-distribution, because the existence of such action on vegetable organisms is less clearly recognizable than is that of water. We can directly observe the ingress of water into a plant and its egress, we can explain physiologically the effects caused by these, and we can follow the transpiration-current along its course; whereas the action of heat is carried on in the molecular region of the protoplasm beyond our ken, and is visible to us only in its final consequences, such as the acceleration, retardation or complete cessation of physiological processes. The oecological phenomena display similar differences. Protective adaptations against a want or superfluity of water are within our power of observation, those against cold and heat are entirely beyond them. We can directly see whether any plant naturally inhabits a dry or a moist station, but not whether it belongs to the flora of a cold or warm climate. Indeed plants from hot deserts frequently have a strong resemblance in habit to those of polar zones.

Attempts have, however, recently been made to establish some distinguishing points between individual plants belonging to species growing respectively in high alpine or polar, and in temperate climates. Thus Lindberg writes as follows[1]: 'Most kinds of moss growing here [Spitzbergen] are forms which are more or less imperfect and injured by frost. In fact, they suffer greatly from the rigour of the climate, for the whole plant usually assumes a dark tint; the stems become shorter, more richly branched and more caespitose than usual; the leaves also are modified in shape and direction of growth, and are more crowded, *shorter, less pointed*, and more erect or adpressed and concave; in addition they are frequently white or transparent at the tip, because the chlorophyll is frozen; if in the well-developed plant the midrib of the leaf be continued into a long hair-like termination, here it may be that it seldom protrudes beyond the leaf-tip.' Similar observations were made by Berggren[2]: 'As regards mosses, the characteristics are, that the leaves are broader, very often concave, and have a tendency to form hood-like tips. . . . It is quite the exception to find mosses that are distributed from the temperate zone up as far as Spitzbergen, which have not shorter and, in consequence, relatively broad leaves. . . . Sometimes the margin of the leaf is bent back as well, and its teeth disappear.'

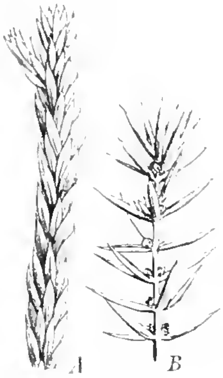

FIG. 36. Juniperus communis. *A* The form nana of a cold climate. *B* The common form. After Warming.

Kjellman gives similar results for several plants of a higher order, and refers to the cones of Picea excelsa and the leaves of a few Ericaceae. There is, he says, the same tendency as in mosses for the leaves to become broader and shorter and to have any irregularity in their margin removed.

Further research must decide how far these modifications depend directly on temperature.

Warming[3] observed in Juniperus communis (Fig. 36), as well as in Lycopodium annotinum and L. Selago, a tendency to bear leaves which are straighter and adpressed and do not stand off from the stem as is elsewhere the case. He considered this to be a method of protection against transpiration. During winter many species of pines resemble such 'cold forms,' as their needles become raised and pressed against the stem. I do not know of any such effects produced by drought[4].

Every plant can live only at temperatures lying between two extreme degrees, which are more or less far apart, and are termed respectively its *upper and lower zero points.* The overstepping of either of these limits sooner or later, but at the latest within two or three days, results in the death of the plant. The zero points vary for different species; on the other hand, individual plants of one species, provided they have grown in nearly similar environments, have the same zero points. *The absolut extremes of plant-life are not identical with those of all its functions. Eac function has its own extremes, and at a certain degree of temperature it optimum.* There are, then, three cardinal points or degrees. Like th

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[1] [illegible]erg, op. cit. p. 536.

[2] Berggren, op. cit. p. 17.

[3] Warming, op. cit. p. 114 and Figs. 12–14.

[4] Johow, op. cit.

extremes, the optimum of each function is characteristic for each species, and stands the higher the more the minimum corresponds to a higher temperature.

The data indicated above form the only basis for research into the influence of temperature on the distribution and mode of life of plant-species.

In opposition to the only scientific interpretation of the effects of temperature which J. Sachs established by careful experiments, *phaenology*[1] assumes much simpler relations between heat and plant-life, as according to its teaching there is a direct connexion between the development of the plant and the degrees of the centigrade thermometer. Thus, in order to ascertain the amount of heat required by an annual plant, the mean temperatures, or also the maximum temperatures, from the sowing to the ripening of the seed on those days on which they exceed zero centigrade, are added together. The sum of these temperatures for one and the same species should be identical for any climate. This theory, as might naturally be expected, is not confirmed by facts. The sum of the temperatures of the individual physiological processes is calculated in a way similar to that of the whole total. For perennial plants the temperatures are usually reckoned from the first of January, and not from the date of germination.

Further discussion is hardly necessary to show that phaenology cannot lead to exact results. Independently of the arbitrary nature of the choice of the degrees of temperature and the date of commencing the calculation, this theory absolutely ignores the facts that degrees of temperature are *not physiologically equivalent*—that in some cases 35° or 30° are less favourable than 25° or 20°, but resemble in their effects 10° or 15°—that different organs and functions require very different amounts of heat, that unfavourable temperatures cause subsequent inhibition, and that other factors besides heat, especially humidity, co-operate and intervene. We need not, then, be surprised if there is very little accord in phaenological observations, and that the utmost one can do is to admit their having a certain importance for purely descriptive geographical botany in the characterization of certain districts. No importance, on the other hand, need be assigned to the theoretical views, nor to the sum total of temperatures.

Physiological researches regarding the influence of temperature on the vital processes of plants are unfortunately not yet numerous. Particularly necessary is it to determine the extremes of temperature and the optima of plants that are much more dependent on definite conditions of heat than are most of the types already investigated. Information on these points, for instance, does not exist in regard to the tropics, polar zones, or alpine heights. Only on the basis of a great number of exact data can we hope to gain a clearer insight into the connexion between temperature and plant-life in different climates. The few observations relating to the subject, and others which throughout require critical confirmation, are given in the following pages.

[1] See Hoffmann, op. cit.

2. ZERO POINTS OF PLANT-LIFE.

i. *LOWER ZERO POINTS OF PLANT-LIFE.*

The different capacity of different species to withstand low temperatures is well known. Thus Molisch found that a number of tropical plants died of cold at temperatures of +2° to +5° C., while, on the other hand, the flora of Yakutsk and Verkhoyansk includes a couple of hundred plants that can withstand −60° C. In fact, different plants appear capable of supporting the freezing of their cell-sap to very different extents, so that there is a strong selective significance attached to temperatures slightly less than 0° C. In the case of tropical plants, freezing generally means freezing to death, whilst the plants of the temperate and the cold zones, at any rate perennials, may be frozen into lumps of ice without dying. In such cases, thawing is more dangerous than freezing, as, if it proceeds too rapidly, it kills more plants or plant-parts than the most intense cold.

Only in a few areas are the climatic conditions such that the vegetation must be able to endure without injury a repeated succession of frosts and rapid thaws. Thus Kihlman described 'the extraordinary power of withstanding severe and rapid oscillations of temperature and thus passing the freezing-point several times within twenty-four hours, as the chief characteristic' of the stunted vegetation of the tundras in Russian Lapland. Similar conditions prevail in very high mountain regions. So alpine plants above the level of perpetual snow in the Alps, for instance Ranunculus glacialis and Gentiana nivalis, whilst in full blossom, pass the nights in a completely frozen state, and during daytime are exposed to the most intense insolation.

Microscopic observation of frozen plant-parts shows that the intercellular spaces, normally filled with air, contain ice-crystals, which were formed at the expense of the cell-sap of neighbouring cells. The loss of water thus occasioned, in very many cases, may be regarded as the cause of death, since, as Müller-Thurgau has shown, it would also cause death if the temperature were favourable. But apart from this, as may be inferred from Molisch's observations, cold exerts a directly injurious influence on the protoplasm.

Those parts of plants that contain little water, as well as plants that can endure great drought without injury, are particularly endowed with the power of withstanding cold. Thus, in some experiments made by C. de Candolle and R. Pictet, certain dry seeds were exposed to a temperature of −80° C. without any injury to their germinating power, whereas seeds swollen in water were killed by temperatures much nearer to the freezing-point. Spores of fungi and of other cryptogams also show a similar power of resistance to cold; so do plants whose vegetative organs can withstand a high degree of desiccation without injury.

Death from cold is undoubtedly in very many cases a result of the *want of water, and not of the low temperature.* H. Mayr[1] states quite correctly: 'One is surprised to find what low temperatures a woody plant sheltered from the wind can endure, provided the air is fairly moist or transpiration naturally restricted, as is the case under dense forest, in an insular climate, in narrow mountain- or river-valleys; on the other hand, most plants are more sensitive to winter frost the drier the air is; nine-tenths of the cases reported of damage by frost during winter are really phenomena due to desiccation, owing to the interference with or stoppage of the movement of water by frost. Thus also perhaps the apparent contradiction may be explained, that many plants have been termed 'hardy' in a notoriously colder climate, yet are considered 'tender' in a notoriously milder one; probably the plants in the former localities were growing in moister air or were sheltered from evaporation, while the tender plants of the warmer climate had to contend against both drought and frost.'

FIG. 37. Cochlearia fenestrata from Pittlekaj. A plant that hibernated in flower and continued its development after winter was over. Natural size. After Kjellman.

Irrespective of seeds and spores, it is not yet known which species of plants are least sensitive to frost and what degrees of cold they can support without injury. But certain observations relating to arctic plants prove that the degree of cold may be extraordinarily low. Thus Kjellman, who as botanist accompanied the 'Vega' expedition, makes the following statement regarding Cochlearia fenestrata (Fig. 37):

'There are few places on earth where the winters are so severe as the spot on which the "Vega" expedition passed the winter. The cold was very persistent, and

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[1] H. Mayr, op. cit. p. 368.

the temperature went below −46° C. The individual in question grew on the top of a fairly high sand hillock near Pittlekaj, exposed to the constant and cutting north or north-east wind. It had commenced to blossom in the summer of 1878, but its blossoming was far from being completed when the winter came on and stopped further progress. Its system of flowers consequently included flower-buds in various stages of development, recently opened flowers, blown flowers, and some more or less ripened fruits. Only an insignificant shrivelled remnant of the basal rosette of leaves remained, but the upper leaves were fresh and vigorous. In this condition the plant was overtaken by winter, and exposed to its utmost rigour. We might well believe that it must have been killed, and especially that the tender flowering parts which were attacked during their development would have been destroyed by the frost and so prevented from developing further. This, however, was not the case. When the summer of 1879 began, the plant continued its growth from the point at which it had been arrested by the approach of winter; the flower-buds opened, and from the axils of the fresh upper stem-leaves fresh inflorescences sprouted forth.'

The fact that the coldest known places on the earth lie within the Siberian forest-district is sufficient to prove, in the first place, that vegetative organs can endure without injury temperatures lower than those observed by Kjellman; and, in the second place, contrary to a widespread but unsupported view, that tree-growth is by no means excluded by prolonged and severe winter-temperatures. Within the district just mentioned is included, for instance, Yakutsk, where the thermometer not infrequently sinks to −62° C., and Verkhoyansk, which is, if possible, still colder. Details concerning the temperature of the latter place are given in the following table:

TEMPERATURE AT VERKHOYANSK (SIBERIA).

67° 34′ N., 135° 51′ E., 107 meters above sea-level.

		Average Extremes.	
	Mean.	Min.	Max.
December	−48·4	−61·9	−28·7
January	−51·5	−64·1	−31·5
February	−46·2	−60·5	−24·3
March	−35·2	−55·7	−16·6
April	−15·8	−33·6	1·9
May	−1·1	−17·2	11·9
June	9·4	−0·7	22·4
July	15·6	5·0	29·8
August	9·3	0·4	30·1
September	0·4	−10·3	12·4
October	−18·1	−36·7	−1·2
November	−39·7	−54·4	−14·0

As far as is known, at no place on the earth is the temperature so low that no plant can withstand it. The alleged complete absence of all terrestrial vegetation in the antarctic polar zones is not due to an absolutely greater cold there—for the thermometer does not fall so low as in the north polar zones—but to the fact that the temperature remains low, and almost constantly under the minimum of the essential functions.

Kjellman was impressed with the fact that contrivances which might be considered as protective against cold are wanting in many arctic plants, for instance in the above-mentioned Cochlearia fenestrata. Indeed, it appeared to him that polar vegetation is externally no better protected against cold than that of temperate zones. We may expand this statement and say: *Our present powers of investigation do not enable us to recognize in plants any special protective means against cold.* The capacity of withstanding intense cold is a specific property of the protoplasm of certain plants, and is quite unassisted by protective means that are external, that is to say, outside the micellae of the protoplasm. In Central Europe the absence of external protective means against the cold may also be demonstrated; it is sufficient to look at any meadow or field during a frost. There we can find such delicate plants as Bellis perennis, Stellaria media, and the like, frozen hard and brittle as glass. These plants are exposed, quite naked as it were, to the inclemency of the weather, and not protected against the attacks of frost by any hairy tomentum, by any corky integument, not even by a thick cuticle. When the thaw comes, the plants continue to grow undisturbed. They are quite hardy in relation to any degree of cold that we experience.

Yet protective means against cold have been ascribed to many woody plants. Bud-scales, corky integuments, the thick cuticle of evergreen leaves, were formerly described as such. But these are actually protective means against drought, as has been shown in the preceding chapter. A cold soil, and especially a frozen one, is, as we already know, physiologically dry, so that any plant rooted in it requires protection against transpiration. Shallow-rooted low herbaceous plants are subjected to approximately the same fluctuations of temperature as the soil on which they grow, and are therefore less exposed to danger from desiccation than are deeply rooted tall woody plants; they are therefore relatively unprotected.

It has often been stated that fatty oil may, in certain cases, be considered as a protection against cold. Hence the phenomenon, which will be discussed further on, of the conversion during winter of starch into oil, is commoner in our northern species of trees than in trees that are more sensitive to cold (A. Fischer). Seeds swollen in water are stated to withstand low temperatures better when they are rich in oil than when they are poor in oil. In such cases, however, we are dealing with mere conjectures, which lack any experimental basis, and seem to be contradicted by other phenomena.

ii. *THE UPPER ZERO POINT OF PLANT-LIFE.*

The power that plants possess of resisting heat, like that of resisting cold, varies with the species, but not nearly to so great an extent. Some plants and plant-parts, however, are remarkable for an extraordinary power of resisting high temperatures; and this power, like that of enduring low degrees of temperature, is generally coupled with an ability to withstand desiccation. Thus, for killing the resting-spores of certain Schizomycetes, a prolonged heating at 130° C. is necessary. Air-dried yeast is killed only at from 115° to 120° C. Air-dried seeds often at only 75° C. lose their germinating power, whereas when thoroughly dried they can withstand 100°, and even for a short time 120° C.

Plants which are in an active condition, and therefore contain much water, possess a much smaller power of resistance to heat than when they are in a resting state, in which they contain less water. Here again bacteria[1] withstand the highest degrees of heat, especially the bacillus of anthrax, which does not lose its infectious qualities even after prolonged heating at 75°-80° C., whereas many other vegetative forms of bacteria are killed by prolonged heating at 45°-50° C. Vascular cryptogams in a vegetative condition perish in a short time when exposed to a temperature of 50°-51° C., as was shown by Sachs and by H. de Vries; Jumelle found by experiment that Cocos Weddelliana, Begonia tuberosa, Pelargonium zonale withstand uninjured a long exposure to a temperature of 35° C., but a rise in the temperature to 40° for a few days, or to 45° for a few hours, was fatal.

Sachs'[2] experiments with Nicotiana rustica, Cucurbita Pepo, Zea Mays, Mimosa pudica, Tropaeolum majus, Brassica Napus—chiefly therefore with plants from warmer zones—showed that none of these plants, when in contact with the air, endured a temperature of more than 51° C., even for ten minutes only, without serious injury or death, but they withstood temperatures of 49°-51° for ten minutes and even longer. On the other hand, organs that had successfully withstood the latter temperatures in the air, when placed in contact with water of the same temperatures, were killed within ten minutes; the highest endurable degree of temperature for the same organs is therefore lower in water than in air.

If we compare natural conditions with experimental results, we find only at a few places of limited area, such as the craters and fumaroles of active volcanoes, that vegetation is entirely wanting because the temperature is too high.

Bacteria and Schizophyceae are the most resistant of all aquatic plants, and also the first to appear in hot springs. 'In a hot spring at Las Trincheras in Venezuela, the temperature of which at its source is 85°-93°, Schizophyceae are stated to thrive at a temperature over 80° C. On the

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[1] [illegible]sch, op. cit.

[2] Sachs, Ges. Abhandl., Bd. I, p. 216.

other hand, in European warm springs they appear only after the water has become much cooler—according to Agardh and Pfeffer, in the hot springs at Carlsbad only when the temperature is down to 57°; according to Hoppe-Seyler, on the edge of fumaroles in water-vapour at about 60° C. I myself saw in Java, on the edge of fumaroles, even plants of a high order, such as Rhododendron javanicum, flourishing vigorously in hot vapour; but I can give no accurate details in regard to the indubitably high temperatures prevailing there.

Under the influence of the sun's rays the temperature of the superficial layers of soil in deserts attains a height which approaches the upper limits for all plant-life, and is endured only by those parts that are poor in water. Kerner says:

> 'The crustaceous lichens, which adhere to the limestone rocks on the shadeless desert of Karst in Istria and Dalmatia, are on cloudless days in summer constantly exposed for many hours to a temperature of 58°-60° C. without suffering any consequent injury, and the manna lichen (Lecanora esculenta), as well as the rock to which it is attached in the desert, is often heated up to 70° C. without perishing. In addition, seeds that are embedded superficially in the desert sand, and there live through the long period of drought, certainly assume the temperature of their surroundings, which at midday is regularly 60°-70° C. The highest temperature in superficial layers of soil has been observed near the Equator at the station Chinchosho on the Loango coast. In very many cases it exceeded 75°, often reached 80°, and once even 84° C. Even in this soil, annuals were not wanting during the rainy season.'

Pechuel-Lösche[1] records a temperature of 69° C. in the sand of the seashore on the Loango coast, close to an Ipomoea in full flower.

Even air-temperatures scarcely lower than those of hot springs have been observed in countries in nowise destitute of vegetation. Thus the absolute maxima given by Blandford[2] for the year 1879 in India are for Calcutta 41·1°, Benares 47·8°, Lahore 50·9°, Multan 52·8° C. As Hann, from whose Climatology these figures are taken, states, air-temperatures of 50° C. are not rare in the Punjab, even when the thermometer is properly set[3]. With such air-temperatures in the shade, parts of plants exposed to the sun's rays have to bear heating up to 60°-70° C., which is a much more considerable degree of heat than the upper zero previously observed. Thus Askenasy observed that with a temperature of 28° C. in the shade the leaves of Sempervivum alpinum exposed to the sun attained a temperature of 52° C. Such differences between the temperatures in the sun and in the shade are exhibited certainly by succulent plants alone, for the same observer found that the leaves of Gentiana cruciata,

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[1] Pechuel-Lösche, op. cit. p. 65.

[2] Blandford, Meteorology of India. Calcutta, 1881.

[3] Hann, Handb. der Klimatologie, ed. 1, p. 265.

exposed to the sun's rays at the same time, were heated only up to 35° C.

Whilst awaiting further investigation, it appears to result from the facts recorded above that the power of enduring high temperatures, like that of withstanding cold, varies more considerably in the different species than is generally supposed. The maximum temperatures determined by Sachs cannot hold for plants living in extreme climates.

Protective means for the prevention of overheating have up to the present time been no better demonstrated than have means for the prevention of overcooling. The subaërial parts of plants in very hot regions, being exposed to the danger of desiccation, in most cases are protected against transpiration, and are thereby deprived of the most important means for keeping the temperature down, as is proved by the high temperatures attained by succulent plants exposed to the sun. Many plants, however, escape from the injurious effects of such high temperatures by leading an exclusively subterranean life during the period of their prevalence. This, however, is by no means true of all species of plants.

3. THE CARDINAL POINTS OF THE FUNCTIONS OF PLANTS.

The life of a plant is made up of thousands of separate actions, each of which is performed within its own ranges of temperature, and exhibits its own optimum temperature. In most habitats—except those which are generally very unfavourable to plant-life—such plants alone can succeed in the struggle for existence as have their functions in a state of equilibrium that corresponds to the external conditions: this condition of equilibrium is termed the *oecological optimum*. This total optimum is not deducible from the separate optima of all the functions taken collectively; indeed many functions, such as respiration or transpiration, when intensely active, are injurious to the plant. In regard to every function we must discriminate between the *absolute optimum*, which corresponds to the *highest intensity* of a function, and the *harmonic optimum*, which corresponds to its *most favourable intensity*. *The oecological optimum is composed of the harmonic optima.*

A knowledge of the extreme temperatures of a function is more important, in geographical botany, than is that of the absolute optimum which it is often difficult to ascertain, and which is often somewhat devoid of significance as regards the natural conditions of life. The absolute optimum is important in geographical botany only when it nearly coincides with the harmonic optimum, as it does, for example, for assimilation and other processes of nutrition.

The corresponding cardinal points, particularly the optima of the individual functions, differ from one another only by a few degrees or fractions of a degree in the case of plants of an equable climate, whereas they may differ greatly from one another in regions with extreme temperatures. Indeed, it may happen in such climates that the curves of temperature of definite functions do not touch those of others. Long ago the practical experienced man grasped these facts, which were ignored by phaenologists, and now he rears tropical plants at a uniformly high temperature, but temperate plants at temperatures alternately high and low.

The oecological optimum temperature does not remain constant during the whole development of a plant—at least in temperate regions—but, as Sachs' investigations prove, shows a rise as development proceeds, so that, for instance, the temperature which is most favourable for the processes of germination does not reach the optimum for succeeding functions. We learn too from the art of fruit-forcing that we must regard the rise not as constant, but as oscillating. Though the harmonic optimum temperature for the successive stages of development is alternately higher and lower, the main curve nevertheless shows a marked rise. Very instructive in this connexion is the following table, prepared by the horticulturist Pynaert, showing the most favourable temperatures (oecological optima) in forcing the peach-tree:

OECOLOGICAL OPTIMA IN THE FORCING OF THE PEACH-TREE
(after Pynaert).

	Day temperature.	Night temperature.
First week	9–10° C.	5–7° C.
Second week	10–12	7–7
Third week	12–15	9–11
To flowering	15–18	11–14
At flowering	8–12 !	6–10 !
After flowering	15–18	11–14
During stoning	12–15 !	9–11 !
After stoning	16–19	12–15
At fruit-ripening . . .	20–22	15–17

Up to the present time only a few satisfactory investigations have been made to fix the cardinal points of the individual functions. The most thorough-going of the available experiments concern germination, a process made up of various distinct processes, such as swelling, the actions of ferments, transport of plastic material, generation of energy, cell-division, cell-growth, &c., each of which possesses its own cardinal points. The data which have been fixed in reference to germination are therefore not very valuable from a purely physiological point of view, but this complexity does not impair their value in relation to oecology and geographical botany, which are chiefly concerned with the oecological optimum. As an example, the following tabular statement prepared by Detmer[1] is here reproduced:

CARDINAL POINTS OF GERMINATION (after Detmer).

	Minimum.	Optimum.	Maximum.
Pinus sylvestris	7–8° C.	27° C.	34° C.
Triticum vulgare	5 *	28·7	42·5
Zea Mays	9·5	33·7	46·2
Alnus glutinosa	7–8	24	36
Lepidium sativum	1·8 *	21	28
Linum usitatissimum	1·8	21	28
Phaseolus multiflorus	9·5	33·7	46·2
Gleditschia triacanthos	9	28	36
Cucurbita Pepo	13·7	33·7	46·2

* Figures too high.

This table shows very clearly that the *cardinal points of germination* ar higher for plants from warm countries than for those from cold ones. Bu these figures are too high in some cases, and by no means properly represent the great inequality of temperatures which are effective during germination in different climates, for, on the one hand, they do not deal with an purely tropical plants, and, on the other hand, some of the minima fo temperate plants are too high. The degrees of temperature given for th minima by F. Haberlandt are more instructive. Sinapis alba, Camelin dentata, Trifolium hybridum, and Medicago sativa not only germinate between 0° and 1° C., but also made considerable further progress i development. Of plants from hot countries, Solanum Melongena, Nicotian Tabacum, and Cucurbita Pepo germinated between 11° and 16° C., bu Cucumis sativa, C. Melo, and Theobroma Cacao only above 16° C. Ulot observed the germination of several grasses, Cruciferae and Papilionacea at 0 C., but the process was very protracted. Kerner placed glass tube containing earth and seeds in a spring, the temperature of which remaine constant at 2° C., and he found that numerous alpine plants germinate even at this low temperature.

Growth depends on conditions of temperature similar to those require for germination, which partially consists of processes of growth. Ther are plants on alpine heights, but especially in the polar regions, that ca grow considerably at a temperature approaching the freezing-point. Thu the flowers of Soldanella alpina break through the snow, and those Anemone vernalis, Crocus vernus, and other species appeared to me t be quite as accommodating, as I found them in half-melted snow; bu owing to direct insolation, even through thin layers of snow, a highe temperature than 0° C. may be reached in such cases. Even more remark

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[1] Lehrb. d. Pflanzenphysiol., p. 269.

able are the seaweeds of arctic seas, for in water whose summer temperature only slightly exceeds 0°, they attain a length up to 20 meters; in winter, however at a temperature never exceeding −1° C., they produce their sexual organs. Among plants growing at very low temperatures are the lower organisms of the snow- and ice-flora, which have been carefully studied by Wittrock.

Assimilation and *respiration* are functions much less complex than germination and growth, and are consequently more readily comparable in the different species of plants; it therefore appears strange that so little attention has as yet been bestowed on the temperature of assimilation in particular. The well-established fact that the two forms of gaseous interchange exhibit remarkably dissimilar temperature-curves is of great interest. The lower zero point for assimilation is lower than that for any other function of the plant. Thus Jumelle could observe a distinct though weak assimilation in Abies excelsa, Juniperus communis, and Evernia prunastri. even at −40° C.; Boussingault and Kreusler had already observed assimilation at about 0° C. According to the few observations available, the maximum is slightly below the lethal temperature, but the optimum is considerably lower. Heinrich places the cardinal points in question for Hottonia at about 31° and 56° C., whilst according to Böhm the optimum for the walnut may be about 30°. Jumelle could not observe any distinct respiration below −10° C. in Abies excelsa, Juniperus communis, or Evernia prunastri, although these plants continued to assimilate distinctly at much lower temperatures. On the other hand. respiration increases in proportion to the temperature up to nearly the higher limit of plant-life. Thus, for instance, Rischawi found in wheat-seedlings the following relationship between temperature and the amount of carbon dioxide expired:

RELATION BETWEEN TEMPERATURE AND EXPIRATION OF CO_2 (after Rischawi).

At 5° C.	3·30 mgr. of CO_2
10°	5·28 ,, ,,
25°	17·82 ,, ,,
35°	28·38 ,, ,,
40°	37·60 ,, ,,

For the functions and aggregates of functions just mentioned, the optima lie among the high temperatures. There are, however, certain physiological processes for which not only the optima, but also the upper zeros are so low that, as a rule, they can take place only in winter, late autumn, or early spring. Obviously this concerns plants of temperate and higher latitudes alone, whilst tropical plants exclusively require high cardinal points.

The category of *functions that are active at low temperatures* only includes among others the obscure processes which are fermentative in nature, according to Sachs' hypothesis, and which awaken into activity hibernating parts of plants; among such processes may be cited the conversion of starch into fatty oil and the reverse. The chapter on Periodic Phenomena in Temperate Regions will include a full account of what is known in regard to this subject. Erikson has shown that, in like manner, the germinating power of certain fungus-spores is markedly increased by cooling them down nearly to zero; according to F. Haberlandt, a similar result follows on cooling down swollen flax-seeds for several days.

Certain movements due to stimuli, such as those of the chlorophyll-corpuscles, are arrested by low temperatures. The needles of certain species of Pinus at a low temperature become adpressed to the axes. Many substances are produced during cold weather; for example, the red drops of oil that cause the brown winter-colour of many conifers. The list of the functions of plants that are called into action at low temperatures only could yet be considerably increased. But only one more of them will be mentioned here, on account of its great importance in geographical botany.

Low temperatures exert a favourable influence on the sexual organs and on the parts oecologically connected with them (perianths, inflorescence-axes) *in many plants of the temperate and frigid zones.* The cardinal degrees for the growth—and perhaps for the inception—of the primordia of flowers are often much lower than for the growth of vegetative shoots, so that the former are favoured by a relatively lower temperature, and the latter by a higher temperature, during development. It is well known that Crocus, Hyacinthus, and other perennial herbs do not send out flowers or inflorescences at a high temperature, but shoot out luxuriantly into leaf. Also in the forcing of fruit-trees the temperature must be kept moderate before, and especially during, the blossoming period. For the same reason many temperate plants seldom blossom in the tropics; for example, most of our fruit-trees. Fritz Müller observed at Blumenau that various European herbs never, or hardly ever, blossomed; amongst them were Carum Carui, cabbage, turnips, parsley, and celery. Echium vulgare blossomed in his garden only once after an exceptionally cold winter. Kurz found in the mountains of Burmah that increased coolness due to increased altitude expedited the blossoming of temperate plants such as Rhododendron and Gentiana, but delayed that of tropical ones. It has been already stated that seaweeds fructify during winter in the arctic seas. Several other isolated observations of the kind might be cited. Consistent, thorough, and comprehensive research is, however, altogether wanting on this question, which is extremely important in geographical botany.

4. ACCLIMATIZATION.

The absolute extremes of temperature of plant-life are constant for ndividual species, but *the cardinal points vary for the separate functions ccording to climatic conditions*; they are susceptible of a limited displacement, either upwards or downwards, so that a plant when transferred from ne climate to another with a different temperature may, provided the tter climate is not too dissimilar, often adapt itself to its new environment nd become *acclimatized.* The possibility of acclimatization always varies ith the species; in some it appears to be unlimited under natural onditions, while in others it takes place only within very narrow limits. omplete acclimatization is therefore only possible when all the cardinal oints change in harmony with the new temperatures. If this is not the ase, or not sufficiently so for certain functions, acclimatization is confined o definite processes, and the plant either is not capable of existing or does ot develop completely. It has already been mentioned that many emperate cultivated plants exhibit vigorous vegetative growth in the ropics, whereas they blossom but seldom; in such cases, the cardinal oints for the growth of flowers, and perhaps also for their inception, re either not raised or not raised sufficiently. On the other hand, many lants from the warm zones do not produce flower or fruit in colder ountries, because the minimum temperature necessary for their production s not attained.

A plant may be cultivated and, as observations in the polar zones and n the Alps show, in cases of rich vegetative propagation, even exist in e wild state, without producing seed. If, however, the cardinal points r such indispensable functions as germination, growth, nutrition, and o forth in a new climate have not been correspondingly displaced downwards or upwards, then the continued existence of the plant is obviously npossible.

If we compare individuals of the same species in climates of different emperatures, we soon become convinced that certain functions in hot limates are associated with higher temperatures than in cold climates. he cardinal points of temperature are therefore not the same everywhere. he difference is first of all hereditary, so that, for instance, seeds from cold climate germinate in a warmer one for some years at lower temperatures than do seeds of the same species that have been produced in this armer zone, and the plants developing from them grow more quickly. ut soon, however, owing to a gradual upward displacement of the cardinal oints, this difference disappears. The reverse takes place when the ansference is from a warmer to a colder zone.

'In the year 1852, maize for poultry (from Hohenheim near Stuttgart) was arvested on September 22, 120 days after the sowing. . . . This maize year after year ripened more and more rapidly, so that in 1857 it was harvested 90 days after sowing. Seed of the same maize from Breslau, sown in the same bed and at the same time as the former, took 122 days to ripen [1].'

Twigs of woody plants behave in the same way as seeds. A. de Candolle kept twigs of Populus alba, Carpinus Betulus, Catalpa bignonioides, and Liriodendron Tulipifera, some of which had grown in Montpellier and others in Geneva, from February 4 onwards, in a frame, the temperature of which varied between 7° and 10° C. The twigs from Geneva produced leaves earlier than those from Montpellier.

By means of such observations as these the existence of a limited acclimatization has been demonstrated beyond doubt. More extended and exact investigations are necessary to determine the amplitude of th possible oscillations of the several cardinal points.

In regard to the acclimatization of important forest trees in Europe North America, and Japan, H. Mayr [2] has collected information, whic may claim wide interest as bearing upon the general question of naturalization. According to this evidence most woody species enjoy good healt when they are transferred to a climate *slightly warmer* than that of thei native home. He says:—

'Broad-leaved trees easily adapt themselves to a warmer climate by prolongin their whole course of development; our native oak (Quercus pedunculata) whe brought from its moderately warm home into the climatically allied region of th subtropical zone, for example into California, at first grows very fast, and in th similar climatic zone of Australia attains a height of 7 meters in nine years. Japanes oaks (Quercus glandulifera and serrata) used for charcoal-making are extensivel grown as coppice in the subtropical area of Japan, where in eight years the become as tall as in fifteen years in their own home. Paulownia imperialis, rar specimens of which grow well in the warm deciduous mountain forests of Japa is cultivated for the sake of its wood in the subtropical region, where in virtue of it extraordinarily rapid growth it produces a very light wood, which neither warps n shrinks. The tree repays cultivation better in the latter place than in its own hom but it is already exhausted after twenty years, becomes hollow and dies, whereas i its home, until recently, trees 6-7 meters in girth and 48 meters up to the crow were not rare.

'In the same way, plants transferred from subtropical zones into the tropic exhibit an increased power of growth in the first decades. The Japanese campho tree, for instance, belongs to the subtropical zone of evergreens; in the tropic of India and Java it grows remarkably fast; its vigour of growth causes the ste to divide into innumerable strong branches, so that the tree loses its ancestral for It is very probable that, owing to this accelerated growth during youth, an earli consumption of vitality and an earlier natural death is brought about: for remar [illegible]ly early and excessive production of seed characterizes all kinds of woody specie

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[1] [illegible] op. cit., p. [illegible]. Many cases of expedited or delayed development are give by [illegible]

[2] H. Mayr, op. cit., pp. 365–368.

that are placed in such circumstances. If in introducing a woody species a zone of vegetation is entirely passed over, as when deciduous broad-leaved trees are brought into the tropics, they grow so feebly, according to experience derived from India and Java, that we must describe them as incapable of cultivation [1].'

According to Mayr, 'Conifers appear to adapt themselves to a new climate with more difficulty than broad-leaved trees. Thus the conifers of the cool area, firs, spruces and larches, whether European or Japanese, are so arrested in growth in the subtropical area, becoming bush-headed and branchy, that they can hardly be considered capable of cultivation there.

'The transference from a warmer to a cooler zone usually yields unfavourable results: all woody species when brought from their home—by which is meant area of distribution—into a cooler area, lose their importance as cultivated plants, at any rate from a sylvicultural point of view, owing to injuries of all kinds, absence or rarity of ripe fruits, production of wood of little value, and so on.

'In the warm subtropical coasts of South California all kinds of palms and trees from the tropical area may be cultivated, but only for ornamental purposes, as they mature no fruits. . . .

'In this transference to a cooler climate some remarkable phenomena are often encountered; woody species become sensitive to frost, a condition not to be expected, judging from their native habitat; others prove to be hardy in relation to frost, though, in their home, they could not have occasion to defend themselves against it.

'It is well known that plants are much less susceptible to frost during their winter rest than during the vegetative season in spring and autumn; we see from their behaviour in relation to late and early frosts how difficult it is for a plant to adapt itself to a colder climate; many species seem to find it quite impossible either to delay the commencement of their development or to hasten its termination, in other words to become frost-hardy. Gleditschia and Robinia are natives of the southern Atlantic States of North America, an area where, as regards summer and winter temperature, the duration of the vegetative period exceeds that of our warmest vine-countries; both trees are cultivated in America, Europe, and Asia far beyond their region of distribution; but during the long period of their cultivation not a single race has been produced that is secured against the frost by a shortening of its vegetative season; moreover, it is well known that the seed of the Robinia is always taken from trees that have already grown in a cold climate; the seedlings retain the peculiarities of the mother-tree unchanged.'

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[1] See also in this book, Part III, Sect. I, Chap. II, Periodic Phenomena in the Tropics.

SELECT LITERATURE.

1. General.

Berggren, S. Musci et Hepaticae spetsbergenses. Öfv. K. Sv. Vet. Akad. Handl. XIII. Bd. VII. 1875.

Johow, Fr. Ueber die Beziehungen einiger Eigenschaften der Laubblätter zu den Standortsverhältnissen. Pringsheim's Jahrbücher. Bd. XV. 1884.

Kihlman, A. O. Pflanzenbiologische Studien aus Russisch-Lappland. Acta Soc. pro Fauna et Flora fennica. Bd. VI. 1890.

Lindberg, S. O. Forteckning öfver Mossor, insamlade under de svenska expeditionerna till Spitzbergen 1858 och 1861. Öfv. K. Sv. Vet. Akad. Forh. 1862.

Warming, E. Om Grönlands Vegetation. Meddelelser om Grönland. Kjöbenhavn, 1888.

Upon Phaenology:—

Drude, O. Deutschlands Pflanzengeographie. This work gives a catalogue of the literature relating to Central Europe and summarily describes phaenological phenomena.

Hoffmann, H. Phänologische Untersuchungen. Giessener Universitätsprogramm. 1887.

The chapter on Periodic Phenomena in Temperate Zones in the third part of this book should also be consulted.

2. Zero Points of Plant-Life.

Askenasy, E. Ueber die Temperatur, welche Pflanzen im Sonnenlicht annehmen. Botanische Zeitung. Bd. XXXIII. 1875.

Boussingault, J. B. Sur les fonctions des feuilles. Annales des sciences naturelles. 5e série. Tome X. 1869.

Candolle, C. de, et R. Pictet. Recherches concernant l'action des basses températures sur la faculté germinative des graines. Archives des sciences physiques et naturelles de Genève. 3e série. Tome II. p. 629.

Cohn, F. Ueber die Flora heisser Thermen. Flora. Jahrg. XLV. 1862.

Detmer, W. I. Ueber die Einwirkung niederer Temperaturen auf die Pflanze. Wollny's Forschungen auf dem Gebiete der Agriculturphysik. 1888.

—— II. Beobachtungen über die normale Athmung der Pflanzen. Berichte der deutschen botanischen Gesellschaft. Bd. X. 1892.

Göppert, H. R. Ueber die Wirkung der Kälte auf tropische Pflanzen. Sitzungsb. d. Schles. Gesellsch. für vaterländ. Cultur. 6. Nov. 1873.

Hoppe-Seyler, F. Pflüger's Archiv für die gesammte Physiologie. Bd. II. 1875.

Kerner, A. v. Alpenpflanzen im Schnee. Botanische Zeitung. Bd. XXXI. 1873.

Kjellman, F. K. Aus dem Leben der Polarpflanzen. In Nordenskjöld, Studien und Forschungen, veranlasst durch meine Reise im hohen Norden. Leipzig, 1885.

Mayr, H. Die Waldungen von Nord-Amerika. München, 1890.

Middendorff, A. Th. v. Die Gewächse Sibiriens. In Sibirische Reise. Bd. IV, Theil I. Lief. 4. 1864.

Molisch, Hans. Das Erfrieren von Pflanzen über dem Eispunkt. Sitzungsberichte der Wiener Akademie. Bd. CV, Abth. I. 1896.

Pechuel-Lösche. Die Loango-Expedition. 3. Abth. 1. Hälfte. Leipzig, 1882.

Rabinowitsch, Lydia. Ueber die thermophilen Bacterien. Zeitschr. f. Hygiene. Bd. XX.

Sachs, J. v. Krystallbildungen bei dem Gefrieren und Veränderung der Zellhäute bei dem Aufthauen saftiger Pflanzentheile. Ber. der math.-phys. Klasse der königl. sächs. Gesellsch. d. Wiss. 1860. (Ges. Abhandl. Bd. I. p. 3.)

—— Die vorübergehenden Starre-Zustände periodisch beweglicher und reizbarer Pflanzenorgane. Flora. Jahrg. XLV. 1863. (Ges. Abhandl. Bd. I. p. 84.)

—— Ueber die obere Temperaturgrenze der Vegetation. Flora. Jahrg. XLVII. 1864. (Ges. Abhandl. Bd. I. p. 111.)

Vries, H. de. Matériaux pour la connaissance de l'influence de la température sur les plantes. Archives néerlandaises. Bd. V. 1870.

Warming, E. Plantesamfund. Kjøbenhavn, 1895. German edition. Berlin, 1896. p. 157.

3. Cardinal Points of the Functions of Plants.

Askenasy, E. Ueber einige Beziehungen zwischen Wachsthum und Temperatur. Berichte der deutschen botanischen Gesellschaft. Bd. VIII. 1890.

Böhm, J. Ueber die Respiration von Landpflanzen. Sitzungsberichte der Wiener Akademie. Bd. LXVII, Abth. I. 1873.

Haberlandt, F. I. Die oberen und unteren Temperaturgrenzen für die wichtigeren landwirthschaftlichen Sämereien. Landw. Versuchsstationen. Bd. XVII. 1874. II. Ueber den Einfluss des Frostes auf gequollene Leinsamen und die daraus gezogenen Leinpflanzen. Ibid. Bd. XXI. 1878. III. Wissenschaftl.-prakt. Unters. auf d. Gebiete des Pflanzenbaues. Bd. I. p. 109.

Jumelle, H. Recherches physiologiques sur les lichens. Revue générale de botanique. Tome IV. 1892.

Kirchner, O. Längenwachsthum von Pflanzenorganen bei niederen Temperaturen. Cohn's Beiträge zur Biologie d. Pflanzen. Bd. III. 1883.

Kreusler, C. Beobachtungen über die Kohlensäureaufnahme und -abgabe der Pflanzen. Dritte Mittheilung. Landw. Jahrb. Bd. XVII. 1888.

Pynaert, Ed. Les serres vergers. Traité complet de la culture forcée et artificielle des arbres fruitiers. 4^{e} éd. Gand, 1888.

Sachs, J. v. I. Physiologische Untersuchungen über die Abhängigkeit der Keimung von der Temperatur. Pringsheim's Jahrbücher. Bd. II. 1867.

—— II. Ueber den Einfluss der Temperatur auf das Ergrünen der Blätter. Flora. Jahrg. LXVIII. 1884. (Ges. Abhandl. Bd. I. p. 137.)

Uloth, W. Ueber die Keimung von Pflanzensamen in Eis. Flora. Jahrg. LIV. 1871. Jahrg. LVIII. 1875.

4. Acclimatization.

Candolle, A. de. Des effets d'une même température sur une même espèce, au nord et au midi. Comptes rendus de l'Acad. des Sciences de Paris. Tome LXXX. 1875. p. 1369.

Hildebrand, F. Die Lebensdauer und Vegetationsweise der Pflanzen, ihre Ursachen und ihre Entwickelung. Engler's Jahrbücher. Bd. II. 1881.

Mayr, H. Die Waldungen von Nord-Amerika. München, 1890.

Moebius, M. Welche Umstände befördern und welche hemmen das Blühen der Pflanzen? Semarang, 1892.

Müller, Fr. Bemerkungen zu Hildebrand's Abhandlung über die Lebensdauer und Vegetationsweise der Pflanzen. Engler's Jahrbücher. Bd. II. 1882.

Naudin, Ch. Huit années d'observations météorologiques faites au Jardin d'expériences de Collioure. Annales des sciences naturelles. 6^{e} série. Tome V. 1877.

Schuebeler, S. Die Pflanzenwelt Norwegens. Christiania, 1873-5.

CHAPTER III

LIGHT

1. **General Considerations.** Importance of light in phyto-geography. 2. **Photometric Methods.** Wiesner's work. 3. **Plant-life in Darkness.** 4. **Intensity and Quality of Light.** Effects of light of various intensities on the different functions. Harmfulness of light of high intensity and the corresponding means of protection. Unequal action of different kinds of rays. Absolute and oecological optima of light. 5. **Sun and Shade.** Full light, light from above, light from the front, light from behind, light from below. Direct sunlight and diffuse light. Wiesner's determination of the actual photic ration of plants. Unequal demands made on light by sun-plants and shade-plants. Contrivances for concentrating light possessed by shade-plants. **6. Day and Night.** Phyto-geographical significance of the unequal duration of daylight. Bonnier's investigations with continuous illumination.

1. GENERAL CONSIDERATIONS.

NEXT to humidity light is the most important external factor affecting plant-form. Whilst heat, which sets the plant-machine in motion and during the whole course of its development and activity has a regulating action of the first importance, yet has no essential influence in determining its conformation, light on the other hand, like water, plays a prominent part in controlling the structure of plants. A plant reared in the absence of light is in form quite different from one that has been normally illuminated and the structure is different at each degree of intensity of light.

The phyto-geographical importance of light, however, in spite of its powerful influence on the conformation and life of the plant, is less than that of heat and rainfall because the supply of light in different climatic regions varies less than that of these factors. Nevertheless until Wiesner recently laid stress on the matter, its importance had usually been underestimated. The unequal intensity of the illumination in the different climatic zones and the increasing duration of sunlight from the equator to the poles do not fail to stamp their mark on the vegetation. The importance of light however remains much greater in regard to botanical topography, since the great diversity of illumination has much influence in determining the characters of the several formations in a region.

In the following pages only such effects of light as have real geographical or topographical significance will be discussed.

2. PHOTOMETRIC METHODS.

The methods for measuring the intensity of light are far less thorough than those that serve to determine the temperature and the humidity of the air. Bunsen and Roscoe have succeeded in inventing a method that in some degree satisfies the demands of exact research; but it is applicable only to the so-called chemical portion of the spectrum, that is to say, to the blue, violet, and ultra-violet rays. The method is as follows:—A photographic paper prepared in a certain way, and termed *normal paper*, is exposed to the action of light and the resulting discolouration is compared with a constant shade of colour, *normal black*, at the same time the period of exposure is noted. Bunsen and Roscoe have clearly proved that in a normal paper changing colour in the presence of light, when a definite shade of colour is attained the product of the light-intensity multiplied by the period of time of exposure is always the same. As unit of measurement of the chemical intensity of light, a darkening of the normal paper is selected agreeing with normal black and produced in one second. If the shade of normal black is produced on the normal paper in 2, 3, 4, 5, . . . n seconds, the intensity of the light is 1 divided by 2, 3, 4, 5, . . . n respectively[1].

The Roscoe-Bunsen method has been further improved and essentially modified by Wiesner, for use in determining the quantity of light available to plants. In its original form, the method is suitable for measuring only weak intensities of light, whilst the determination of higher intensities is faulty, owing to the excessively rapid assumption of the normal tint. To remedy this defect, Wiesner used a scale of several carefully graduated shades of fast colour.

Wiesner's brilliant investigations were in the first place concerned with the ratio between the intensity, i, of the light actually falling upon a plant or its parts or its habitat, and the intensity, I, of full daylight at the same time. The intensity, i, is the *absolute photic ration*[2]. The ratio between the two intensities, $\frac{i}{I}$, *is the relative or specific photic ration*, L. If, for instance, $i = \cdot 252$ and $I = \cdot 756$, then $\frac{i}{I} = \frac{\cdot 252}{\cdot 756} = L = \frac{1}{3}$. When the absolute photic ration approximates to the intensity of full daylight, if for instance $L = \frac{1}{1.5}$ or $\frac{1}{2}$, then, whether the daylight be feeble or intense, the absolute photic ration, i, varies directly with the intensity of full daylight, I, and the relative photic ration, L, remains constant or nearly so. On the other hand, when the absolute photic ration, i, is far below the intensity of full daylight, I, then the relative photic ration, L, has daily fluctuations as the daylight

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[1] Wiesner, V, pp. 301–2.

[2] *Photic ration* is the equivalent of Wiener's term *Lichtgenuss*.

changes, and a maximum, a minimum, and a mean value of L are distinguished from one another.

If, for instance, it is stated that a plant thrives when L is $1/1{\cdot}1 - 1/7$, we should then understand that it will grow under daylight of almost full intensity and also under light one-seventh as strong, but not under less. L (max.) $= \frac{1}{5}$ denotes that, at a certain time of day, the light in the crown of a tree rises up to $\frac{1}{5}$ of the full daylight (I); L (min.) $= \frac{1}{50}$, on the other hand, indicates that at a certain time of day it sinks down to $\frac{1}{50}$ of I.

Wiesner's methods, of which the above is a short sketch, and of which a full account is given in his cited works, ought in course of time to be completed and, if possible, extended to the less refrangible rays. As far as they go at present, they already form an indispensable aid to physiological research that relates to phyto-geography.

3. PLANT-LIFE IN DARKNESS.

As has been already shown, there is nowhere on earth a place too cold for plant-life, and only a few spots of very limited area that are too hot. As regards light, there is no limitation; it is nowhere too dark, nowhere too bright to exclude plant-life of some kind. In the depths of ocean, where light is completely absent, the decaying corpses of animals are decomposed by bacteria. The dung of cavicolous animals becomes mouldy; the shaggiest skin, the thickest hide does not protect an animal's body from the attacks of pathogenic plant-parasites. Vegetation in the dark is, however, limited to plants that are nourished at the expense of organic matter. The reduction of carbon from carbon dioxide by the chlorophyll-containing organs is an operation due to light. Organisms that derive the carbon they require from carbon dioxide thrive in the dark, so long as the organic reserve material suffices, and then perish from want of food.

The reduction of carbon dioxide is not the sole function induced by light in the plant-organisms; on the contrary, the same source of energy is used for numerous other operations. Thus the formation of chlorophyll, except in cryptogams and gymnosperms, demands the presence of light; the same is true in reference to other pigments, especially red and blue ones. The assimilation of nitrates in the higher plants is strongly promoted by light. Foliage-leaves remain very small in the dark. Many movements of plants are excited only by light, others again are arrested by it.

Shoots developed in darkness differ in many respects from normal shoots and are said to be *blanched* or *etiolated*. They are devoid of chlorophyll, and therefore are white or yellowish. Their axes are much longer than they are under normal circumstances; their leaves, on the contrary—except those of grasses and of a few other Monocotyledons—are very small and generally deformed. Flowers are only rarely produced, even when there is a sufficient supply of organic nourishment, and flower-buds that are already formed usually die soon: any flowers that may be formed are usually of abnormal shape and either coloured slightly or not at all.

Etiolated plants are seldom found wild, although they sometimes occur in caves. For instance, in the well-known Guacharo cave near Caribe in Venezuela we found the ground covered with patches of dense etiolated vegetation up to half a meter in height, which had sprung up from the dung of the Guacharo birds, the only inhabitants of the cave.

4. INTENSITY AND QUALITY OF LIGHT.

The action of light on plants is either invigorating or restricting, creative or destructive, according to its intensity and according to the precise physiological function involved. The intensity of illumination, at which one or other action commences, varies, as in the case of heat, in different species of plants; there are however no exact data on this subject.

Growth in length of stems and roots is at its optimum when light is totally excluded. Even light of very weak intensity exercises a retarding influence in this respect, while light of high intensity brings the process to an absolute standstill.

The growth in area of leaves in darkness is very slight, but attains its optimum in light of very moderate intensity. Any further increase in the illumination retards and eventually arrests the process. The optimum intensity of light for growth in thickness of leaves is considerably higher than for the growth of the leaf-surface, so that strongly illuminated leaves are small and thick.

The development of vegetative buds of trees does not commence until the light has reached a definite intensity which is not very low; weak illumination causes the death of branches, the so-called cleaning of the stems of the trees[1].

The action of light on the *origin and development of the reproductive organs*, which has been closely studied by Sachs, Moebius, and Vöchting in the higher orders of plants, and by Klebs in the lower orders, has an important bearing on phyto-geography. Vöchting in particular was able to prove that under a weak illumination the formation of flowers, in numerous phanerogams, was either entirely prevented or only incompletely achieved. In a room with one window looking ENE. flower-buds were produced either very scantily or not at all, whilst vegetative growth remained normal or was even abnormally luxuriant, in the case of Mimulus Tilingi. Buds that were already formed died at early stages; others produced degenerate and malformed flowers: chasmogamous flowers became cleistogamous, for the arrest in development usually affected the perianth

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[1] Wiesner, V.

sooner than the sexual organs. The injurious influence of too feeble illumination was more apparent in sun-plants such as Malva vulgaris under light of higher intensity than it was in shade-plants such as Impatiens parviflora.

Among the *chemical processes affected by light*, the formation of chlorophyll and also that of the pigments of the Brown and the Red Algae are the most accommodating; they attain their optimum under light of very moderate intensity. The minimum light required for the reduction of carbon dioxide is considerably higher than that for the manufacture of the above colouring matter, and the intensity of the process rises proportionally with that of the light. There exists no optimum beyond which the curve for assimilation would descend; the latter appears rather to ascend uniformly till the decomposition of the pigments, by intense light, puts an end to it.

Very intense light acts fatally on protoplasm, and this action is quite independent of the accompanying heat phenomena. Under natural conditions, however, only a few vegetable organisms are sufficiently sensitive to be exposed to danger of death from excessive light. Among these are many bacteria and some of the larger aquatic plants, especially Algae which are attuned to light of feeble intensity and die as soon as their habitat is more strongly illuminated, as for instance by the advancing season. Most usually death from excess of light seems in the first place to be indirect, owing to the decomposition of pigments associated with assimilation; for Algae that are quite decolorized, after exhausting thei reserve material, die from want of nourishment. Terrestrial plants under normal conditions show a much greater power of resistance; in their case the death of entire plants, or even of only separate organs of plants owing to excessive illumination, apparently does not occur. Nevertheless they frequently suffer from a considerable disintegration of their chlorophyll. The vegetation of very sunny spots is never pure green, but always exhibits an admixture of yellow and brown tints due to the products o decomposition of chlorophyll. It will be proved, further on, that intense tropical light may even completely bleach the foliage.

The need for the *protection* of plants, and especially of their chromatophores, against excessively intense light, is shown in many devices which may reach great perfection, especially in the case of aquatic plants that are very sensitive to light[1]. Long and thick coatings of hair cover many marine Algae like an overshadowing cloud; other Algae produce in thei cells special light-absorbing plates which, like window-shutters, cover the peripheral walls during bright illumination, but as the light decreases are forced on to lateral walls (Fig. 38). Finally, the whole form of growth o many Algae is governed by the need for protection against light. All these contrivances are of course better developed in the strongly illuminated seas of low latitudes than in those of higher latitudes, where the light, in itsel

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[1] Berthold, I.

already less intense, by reason of the oblique incidence of the rays, is reflected to a greater extent from the surface of the water. The means of protection against illumination are less marked in terrestrial plants and usually coincide with those that are intended to restrict transpiration, so that it seems hardly possible at present to decide against which of the two dangers a definite protective device originated. Among such, for instance, may be placed the manifold movements and the fixed lie of the leaves in relation to light, by means of which they escape the direct incidence of the sun's rays; in addition there are coatings of hair, smooth strongly reflecting surfaces, various foldings, and so forth[1].

The effects of light on plants depend not only on the amount, but also on the *quality of the illumination*. The different kinds of rays are of unequal physiological significance, and, since they are unequally absorbed by the air and the aqueous vapour, the question of the comparative efficiency of the several parts of the spectrum is not unimportant in phyto-geography.

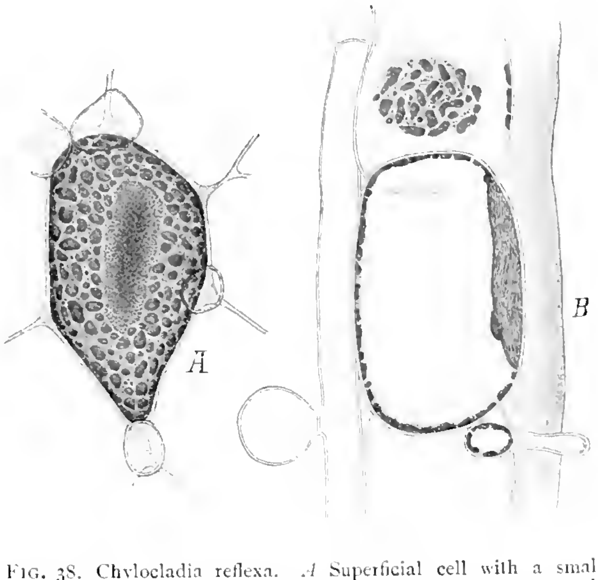

FIG. 38. Chylocladia reflexa. *A* Superficial cell with a small reflecting plate, seen from above. *B* Side view of a similar cell magnified 450. After Berthold.

The less refrangible half of the visible spectrum, from the red to the commencement of the green, contains the rays that are most effective in reducing carbon dioxide by means of the chlorophyll. It is not yet clearly decided whether the efficiency is greatest in the red rays, corresponding to the broadest absorption bands in the chlorophyll, or in the yellow rays, as many investigations render probable, but this uncertainty has no important bearing on the question before us[2]. The manufacture of chlorophyll depends on the presence of yellow or orange-yellow light. The blue and violet rays are the most effective in the assimilation of nitrates[3].

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[1] Wiesner, II; Johow, op. cit.

[2] These questions are thoroughly discussed in all manuals of physiological botany on the basis of the researches of Pfeffer, Reinke, Engelmann, and others.

[3] Regarding the assimilation of nitrates and the formation of organic calcium-compounds depending on this, see Schimper, I and II.

They also exert a retarding influence on growth, and if very intense decompose chlorophyll and kill the protoplasm. According to Sachs, the ultra-violet rays play a prominent part in the production of flowers Investigations on this subject have however hitherto been confined t a single plant, Tropaeolum majus.

Besides *absolute optima* of illumination which for certain function coincide with very unfavourable oecological conditions—the optimum ligh for the growth of axes and certain leaves is zero or darkness—there is also as is the case with heat, an *oecological optimum for light*, which correspond to the normal life of a plant as a whole, and is compounded of th harmonic light-optima of the several functions. A plant strives in variou ways to obtain possession of the oecological optimum of light. Many Algae which are capable of movement by means of cilia collect in place where the light is of a definite and generally moderate intensity, and deser places where another, but to them less favourable, degree of light prevail Fixed plants and plant-parts, that are therefore limited in their power c movement, strive for the same advantage by means of the exposed an changing lie of their foliage-leaves, as well as by means of their heliotropi movements through which, according to the needs of the plant, a stronge or weaker illumination is attained. A similar end is also often achieve by movements of the chlorophyll-corpuscles[1].

In nature these diversified movements would seem to bring the plan usually under the most favourable conditions of illumination; but this i not always the case. Even here perfection is not attained. Among th various functions demanding as they do unequal supplies of light one ofte gains the upper hand to the detriment of the others. Such discords ar still more frequent under artificial conditions of cultivation, in which specie of plants, that in their native habitats may have often received too littl light but hardly ever too much, strive after intensities of light correspondin to their absolute optima, and therein act in a manner so highly inimical t their oecology that they have sometimes to pay for it the penalty of death

5. SUN AND SHADE.

Sun and shade, as terms describing the illumination of habitats occupie by plants, had but vague signification until Wiesner defined them i formulae giving the actual photic ration of plants.

Even plants that are apparently very well illuminated obtain only fraction of the full amount of daylight. The plants occupying flat deser or other horizontal surfaces alone receive an almost intact supply of ligh and that certainly to their own detriment. Trees growing in dense fores and underwood receive *light chiefly from above*, lianes and epiphytes c

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[1] See Stahl, I and II; Wiesner, III; Schimper, III.

he trunks of trees and on rocky cliffs receive *light from the front. Light rom behind or light from below* is usually of only slight importance, though noticed in Venezuela that a small species of Oncidium was always ttached to the lower side of the horizontal branches of the calabash-tree Crescentia Cujete).

Of the two forms of daylight, direct sunlight is of less importance in elation to plant-life than is diffuse light. Most plants either expose only small part of their external surface to the sun's rays or none at all, but eyond that they strive to avoid the sun's rays by appropriate arrangements nd movements of their foliage.

The weakening of the intensity of light by branches and foliage is much nore considerable than one would at first imagine. Wiesner[1], on a sunny March day (27th) in Vienna, estimated the intensity of the full daylight t 0·712, that at one hundred paces from the edge of the still leafless forest t 0·355, and that under the shade of the trees at 0·166.

The weakening of light under trees in full foliage, and especially in woods n that condition, is naturally much more considerable than under bare ranches. Wiesner estimated the intensity of light in Vienna on a sunny lay in March at 0·666, but under the shade of a spruce-tree eight meters igh and branched nearly down to the ground, it was only 0·021; on the ame day, when the intensity of full daylight was 0·518, the intensity of light nder a box-shrub, one meter high, was 0·017. At the beginning of May, he intensities of the full daylight, of the light in the crown of a horse-hestnut tree, and of the light under its shade, were respectively 0·500, 0·070, nd 0·017. These values are in the ratio of 29 : 4 : 1.

How greatly the conformation of plants of sunny or shady habitats is overned by light has been recently proved by comparative cultures ndertaken by Wiesner. Sempervivum tectorum, for instance, is a typical un-plant. With light of mean maximum intensity of 0·04, which is ormal for many shade-plants, it abandoned its characteristic rosette-form. ts internodes became elongated, its leaves diminished in size, and its hlorophyll became reduced in quantity. The optimum for the growth in he surface of its leaves in this case therefore coincides with a pretty high ntensity of light; at still higher intensities of light the superficial growth s decreased. Wiesner cultivated plants of Sempervivum tectorum in some ases with a mean light intensity of 0·305, in others with one of 0·152. Under the first conditions the average maximum length of the leaves was 1 mm. and their breadth 15 mm., whilst the corresponding figures under he second conditions were 26 mm. and 13·5 mm. respectively.

In other sun-plants, such as the potato and the bean, Wiesner observed hat the growth of leaves was favoured by light up to a fairly high

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[1] Wiesner, III, p. 307.

intensity, beyond which light exerted a retarding effect. In the case of shade-plants, the optimum is attained under a much weaker illumination.

Thus the leaf of Scolopendrium officinarum attained in the dark a length of 76 mm. (breadth 11 mm.), when the full light intensity was 0·083 the maximum length of 228 mm. (breadth 25 mm.) was reached, and when the full light intensity was 0·247 it had a length of only 152 mm. (breadth 20 mm.). On the other hand, positive illumination always has a retarding effect on the growth of the stem. Potato-shoots show this reaction plainly even when the full light intensity is 0·0008, whereas diminished leaf-growth is not apparent until the full light intensity is 0·451.

All these values are however in absolutely saturated air, but the effects of light are by no means eliminated in consequence.

The minimum of light for the formation of flowers is lower for shade-plants than for sun-plants; yet the former generally produce fewer flowers than do the latter. The interior of a forest is poorer in flowers than a meadow, and certain regions with intense or prolonged illumination, such as the higher regions of vegetation in mountains, polar countries and many deserts, are characterized by a great abundance of flowers. In such cases however, other factors co-operate.

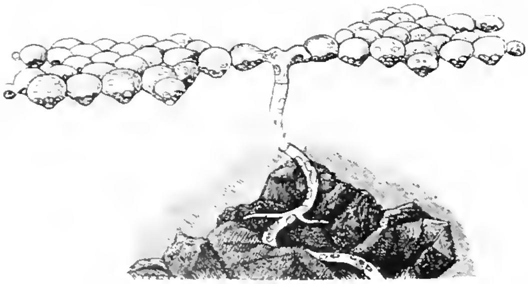

FIG. 39. Schistotega osmundacea. Protonema in its natural position. Highly magnified. After F. Noll.

Apart from their external form, sun-plants and shade-plants respectively differ from one another in their internal structure, and especially in that of their foliage. The formation of palisade-cells is favoured by intense light, just as it is by droughts. Leaves exposed to the sun contain chlorophyll in their mesophyll only, but shaded leaves, over and above this, contain chlorophyll, sometimes even chiefly, in the epidermis.

Of special interest in many plants living in the shade are the *contrivances for concentrating the rays of light on the chlorophyll-apparatus.* The existence of an illuminating mechanism in plants was first demonstrated and its nature carefully studied by Noll, in the case of the protonema of Schistotega osmundacea, the luminous moss that lives in caves (Figs. 39, 40). This protonema, which alone possesses the property of emitting light is tabular in form and consists of a slender foot bearing a flat two-lobed plate. The cells of the latter are lenticular and spheroidal above, but produced conically below; the chlorophyll-corpuscles are aggregated in the narrow basal part of the cells, the upper part of which acts as a completely hyaline glass-like lens. As Noll shows in detail, the incident rays that are in the neighbourhood of the optical axis are so refracted as to be concentrated on to the chlorophyll-corpuscles, which lie just in front of the focus of the lens, near the optical axis, and are consequently intensely illuminated. Each individual chlorophyll-corpuscle, owing to its stronger refractive index, acts again as a small lens and causes the rays, that meet it and are already converging, to converge still more in its interior, so that the intensity of the illumination on its posterior surface is still further increased. The result of the whole process of refraction is a vivid illumination of the chlorophyll-apparatus, which is concentrated in the optical axis near the focus[1]. The luminous property is a physical phenomena that necessarily results, but is devoid of any significance to the plant.

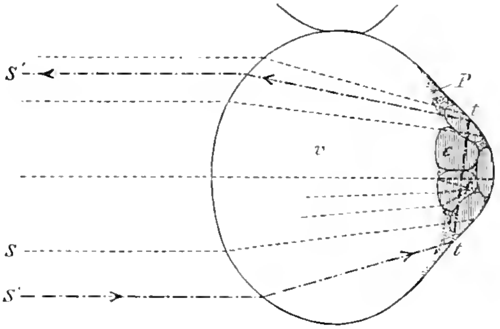

FIG. 40. Schistotega osmundacea. Optical section of a cell of the protonema in which the path of the rays of light is traced. *S'*..*S'* a ray, which is totally reflected by the back wall of the cell *t*. *P* protoplasm. *c* chlorophyll. *v* cell-sap. After F. Noll.

Similar contrivances for illuminating the chlorophyll-containing parts occur, if not in such perfection, in other plants living in shady places. The papillae which cover the velvety surface of many tropical herbs dwelling in shaded habitats serve to concentrate the rays of light[2]. But also in nearly smooth leaves, as Fig. 41 shows, similar adaptations may be noticed. This figure represents a transverse section of the leaf of Argostemma montanum, an herb often found growing in the densest shade of the mountain forests of Java.

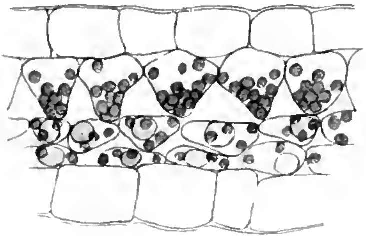

FIG. 41. Argostemma montanum. A Javanese plant. Transverse section through a leaf growing in the deepest shade. Magnified 200.

The bluish metallic lustre of many plants that grow in deep shade remains unexplained. It characterizes to a very intense degree a few tropical species of Selaginella and Trichomanes only, but is pretty widely spread in a less striking manner, and may be observed even at home in Sambucus nigra. This remarkable feature is never seen in sunny spots, and must therefore in some manner be connected with the feeble illumination of very shady places.

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[1] Noll, op. cit., p. 482.

[2] Stahl, IV.

6. DAY AND NIGHT.

The processes of plant-life that depend on light are for the most part strictly confined to daytime; yet in certain cases more or less prolonged after-effects intervene and exercise a disturbing influence. Apart from this the life of a plant at night differs altogether from its life by day. This is clear to the most superficial observer. The leaves of many plants assume a position at night that is frequently, though not always, similar to the profile position resulting from intense illumination. Many flowers gradually close on the approach of darkness, whilst others, less numerous however, then begin to open; many flowers exhale their scent only at night. Careful observation shows that as light decreases in the evening assimilation becomes gradually weaker and eventually ceases, only to recommence at daybreak. The retarding influence of light on growth[1], however, exhibits no such immediate dependence on the intensity of the illumination, but attains its highest effect only in the afternoon or evening, whilst the maximum growth usually occurs not at night but in the early hours of the morning.

The increasing duration of sunlight from the Equator to the Pole certainly acts in a modifying manner on the daily oscillations of plant-life. These would indeed come to an end within the polar circle, if they did not in part, like other periodic phenomena, depend on internal causes, and if they were merely regulated by external influences whenever the latter occur. Apart from this, the more prolonged but less intense illumination in the polar regions is a factor in geographical botany, the importance of which was already recognized by Schuebeler, and more accurately investigated by Bonnier, Flahault, Kjellman, and Curtel.

The works of the above-named investigators will be again referred to in the sections of this work dealing with the polar regions. At present notice will be taken, on account of their general importance, only of the experiments which Bonnier carried out regarding the *effects of continuous electric light* on the development of plants. In order to render the electric light as much as possible like sunlight, the ultra-violet rays were weakened by means of thick glass plates. The electric light used was, at any rate as regards quantity, considerably weaker than daylight, a circumstance which, while indeed influencing the results, did not, as experiments with intermittent electric illumination (twelve hours light, twelve hours darkness) proved, absolutely determine them. The plants experimented on were very varied in character, some woody, some herbaceous, and the cultures lasted for several months. Plants that were continuously illuminated differed most remarkably from those that were cultivated normally, as well as from those grown with intermittent electric light, by possessing a much greater

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[1] Cf. works of Baranetzki and Godlewski.

quantity of chlorophyll ; even deep-lying parts normally devoid of chlorophyll, such as the inner cortex, the medullary rays, and the pith of woody axes, were green. The axes were shorter than under ordinary conditions, the leaves smaller and thicker, the flowers normally developed but more ntensely coloured. The internal structure (Fig. 42) strongly resembled hat of etiolated plants ; thus, the palisade-cells were developed either feebly or scarcely at all, the fibres and woody elements were quantiatively reduced, all the cell-walls were thinner, and the histological tructure generally was less differentiated than in normally grown plants. Even plants that were discontinuously exposed to the electric light showed abnormal ymptoms, but they bore a much loser resemblance to plants grown in ordinary daylight than o those that were continuously luminated. The uninterrupted uration of the illumination must herefore be considered as the ssential cause of the deviations rom the normal structure.

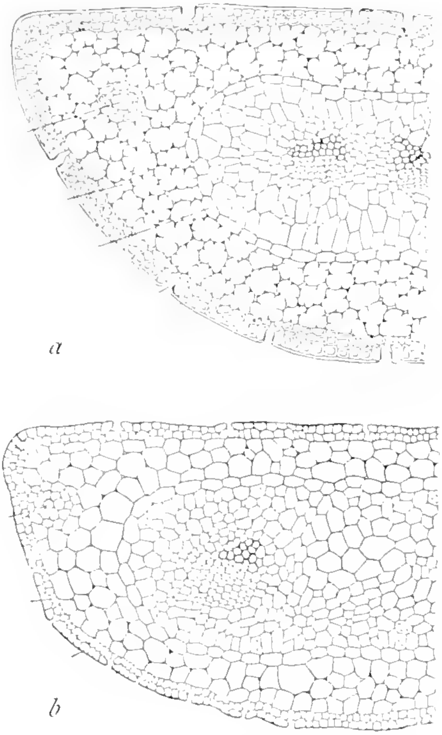

FIG. 42. Pinus austriaca. Transverse section through a needle: *a* in ordinary (intermittent) light, *b* in continuous electric light. Magn. After Bonnier.

Many of these deviations may e explained as being due to wellknown effects of light ; this is specially true in regard to the hortening of the axes, the more ntense colour of flowers, perhaps lso the reduced size of the leaves. Other phenomena have not yet een explained, such as the more lentiful production of chlorophyll and the simplification of the internal tructure. It must be shown by experiments carried on in the polar ones whether or no any significance must be attached to the fact that he electric light differs somewhat in quality from daylight. In favour f the opinion that we have here to deal with effects that would also hold ue in the case of sunlight are the facts stated by Bonnier, that plants rown in the extreme North possess a simpler histological differentiation han the same species on high mountains of Central or Southern Europe, nd that individuals of these species when cultivated in continuous light ecome similar to those grown in the polar zones.

SELECT LITERATURE.

1. General.

Warming, E. Plantesamfund. Kjöbenhavn. 1895. German Edition. Berlin, 1896. Also Wiesner's publications cited below.

2. Photometric Methods.

Bunsen, R., und Roscoe, H. Photometrische Untersuchungen. VI. Abhandl. Meteorologische Lichtmessungen. Poggendorff's Annalen. Bd. CXVII. 1862.

Wiesner, J. Untersuchungen über das photochemische Klima von Wien, Cairo und Buitenzorg (Java). Denkschriften der Wiener Akademie. Bd. LXIV. 1896.

3. Plant-life in Darkness.

Pfeffer, W. The Physiology of Plants. English Edition. Oxford, 1890. The phenomena of plant-life in darkness have little importance in relation to plant-geography, but are of great physiological interest, and an account of them fro this standpoint will be found in Pfeffer's book.

4. Intensity and Quality of Light[1].

Baranetzki, J. Die tägliche Periodicität im Längenwachsthum. Mém. de l'Acad d. Sc. de St. Pétersbourg. 1879.

Berthold, G. I. Beiträge zur Morphologie und Physiologie der Meeresalgen Pringsheim's Jahrbücher. Bd. XIII. 1882.

—— II. Die Vertheilung der Algen im Golf von Neapel. Mittheil. d. botan. Stat zu Neapel. 1882.

Candolle, C. de. Étude de l'action des rayons ultraviolets sur la formation des fleurs Annales des sciences physiques et naturelles. Genève, 1897.

Deherain, P. P. Sur l'évaporation de l'eau et la décomposition de l'acide carboniqu par les feuilles des végétaux. Annales des sciences naturelles. 5e série Tome XII. 1869.

Godlewski, E. I. Die Art und Weise der wachsthumretardirenden Lichtwirkun und die Wachsthumstheorien. Anzeiger der Akademie der Wissenschaften i Krakau. 1890. (Revue générale de Botanique. Tome III. 1891. p. 327.)

—— II. Ueber die Beeinflussung des Wachsthums der Pflanzen durch äusser Factoren. Ibid. 1890.

—— III. Ueber die tägliche Periodicität des Längenwachsthums. Ibid. 1889.

Haberlandt, G. Eine botanische Tropenreise. Leipzig. 1893.

Johow, Fr. Ueber die Beziehungen einiger Eigenschaften der Laubblätter zu de Standortsverhältnissen. Pringsheim's Jahrbücher. Bd. XV. 1884.

Jost, L. Ueber den Einfluss des Lichtes auf das Knospentreiben der Rothbuch Berichte der deutschen botanischen Gesellschaft. Bd. XII. 1894. p. 188.

Kerner, A. v. Natural History of Plants. First English Edition. London, 1894- Vol. II. p. 510.

Klebs, G. Ueber den Einfluss des Lichtes auf die Fortpflanzung der Gewächs Biologisches Centralblatt. Bd. XIII. 1893.

---

[1] From the extremely rich literature only such works are selected as have a bearing on phyt geographic questions.

Lothelier, A. Influence de l'éclairement sur la production des piquants des plantes. Comptes rendus de l'Académie des sciences de Paris. Tome CXII. 1891.

Moebius, M. Welche Umstände befördern und welche hemmen das Blühen? Mededeelingen v. d. Proefstation Midden-Java. 1892. Also Biologisches Centralblatt. Bd. XII. 1892.

Oltmanns, Fr. Ueber die Cultur- und Lebensbedingungen der Meeresalgen. Pringsheim's Jahrbücher. Bd. XXIII. 1892.

Pringsheim, N. Ueber Lichtwirkung und Chlorophyllfunction in der Pflanze. Monatsb. der Berliner Akademie. 1879. Also Pringsheim's Jahrbücher. Bd. XII. 1881.

Sachs, J. v. I. Ueber die Durchleuchtung der Pflanzentheile. Sitzungsberichte der Wiener Akademie. Bd. XLIII, Abth. I. 1860. (Ges. Abhandl. I. p. 167.)

— II. Ueber den Einfluss des Tageslichtes auf Neubildung und Entfaltung verschiedener Pflanzenorgane. Botanische Zeitung. Bd. XXI. 1863. (Ges. Abhandl. I. p. 179.)

— III. Wirkung des Lichtes auf die Blüthenbildung unter Vermittlung der Laubblätter. Ibid. Bd. XXII. 1864. (Ges. Abhandl. I. p. 229.)

— IV. Wirkungen farbigen Lichtes auf Pflanzen. Ibid. Bd. XXIV. 1864. (Ges. Abhandl. I. p. 261.)

— V. Ueber die Wirkung der ultravioletten Strahlen auf die Blüthenbildung. Arbeiten aus dem botanischen Institut zu Würzburg. Bd. III. 1887. (Ges. Abhandl. I. p. 293.)

— VI. Ueber den Einfluss des Lichtes auf die Bildung des Amylum in den Chlorophyllkörnern. Botanische Zeitung. Bd. XX. 1862. (Ges. Abhandl. I. p. 332.)

— VII. Ein Beitrag zur Kenntniss der Ernährungsthätigkeit der Blätter. Arbeiten aus dem botanischen Institut zu Würzburg. Bd. III. 1884. (Ges. Abhandl. I. p. 354.)

chimper, A. F. W. I. Ueber Kalkoxalatbildung in den Laubblättern. Botanische Zeitung. Bd. XLVI. 1888.

— II. Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze. Flora. Jahrg. LXXIII. 1890.

— III. Untersuchungen über die Chlorophyllkörper und die ihnen homologen Gebilde. Pringsheim's Jahrbücher. Bd. XVI. 1885.

Stahl, E. I. Ueber sogenannte Kompasspflanzen. Jenaische Zeitschrift für Naturwissenschaften. Bd. XV. 1881.

— II. Ueber den Einfluss von Richtung und Stärke der Beleuchtung auf einige Bewegungserscheinungen. Botanische Zeitung. Bd. XL. 1880.

Wiesner, J. I. Untersuchungen über die Beziehungen des Lichtes zum Chlorophyll. Sitzungsberichte der Wiener Akademie. Bd. LXIX, Abth. I. 1874.

— II. Die natürlichen Einrichtungen zum Schutz des Chlorophylls der lebenden Pflanze. Festschrift zur Feier des 25jährigen Bestehens der K. K. zool.-botan. Gesellsch. in Wien. 1876.

— III. Ueber die heliotropischen Erscheinungen im Pflanzenreiche. 2 Abtheilungen. 1878 u. 1880. Denkschriften der Wiener Akademie. I. p. 37, II. p. 13.

— IV. Formänderungen von Pflanzen bei Cultur im absolut dunklen Raume und im Dunkeln. Berichte der deutschen botanischen Gesellschaft. Bd. IX. 1891.

— V. Photometrische Untersuchungen auf pflanzenphysiologischem Gebiete. Erste Abhandlung. Orientirende Versuche über den Einfluss der sogenannten chemischen Lichtintensität auf den Gestaltungsprocess der Pflanzenorgane. Sitzungsberichte der Wiener Akademie. Bd. CII. 1893.

Wiesner, J. VI. Beobachtungen über die fixe Lichtlage der Blätter tropischer Gewächse. Sitzungsberichte der Wiener Akademie. Bd. CIII. Abth. I. 1894.

5. Sun and Shade.

Géneau de Lamarlière, L. Recherches physiologiques sur les feuilles développées à l'ombre et au soleil. Revue générale de botanique. Tome IV. 1892. p. 481.

Noll, F. Ueber das Leuchten von Schistostega osmundacea, Schimp. Arbeiten aus dem botanischen Institut zu Würzburg. Bd. III. 1887.

Stahl, E. I. Ueber den Einfluss der Lichtintensität auf Struktur und Anordnung des Assimilationsparenchyms. Botanische Zeitung. Bd. XXXVIII. 1880.

—— II. Ueber sogenannte Kompasspflanzen. Jenaische Zeitschrift für Naturwissenschaft. Bd. XV. 1881.

—— III. Ueber den Einfluss des sonnigen oder schattigen Standorts auf die Ausbildung der Laubblätter. Jenaische Zeitschrift für Naturwissenschaften Bd. XVI. 1883.

—— IV. Ueber bunte Laubblätter. Annales du jardin botanique de Buitenzorg Tome XI. 1893.

Wiesner, J. I. Bemerkungen über den faktischen Lichtgenuss der Pflanzen. Berichte der deutschen botanischen Gesellschaft. Generalversammlungsheft Jahrg. 1894.

—— II. Untersuchungen über den Lichtgenuss der Pflanzen mit Rücksicht auf di Vegetation von Wien, Cairo und Buitenzorg (Java). Sitzungsberichte de Wiener Akademie. Bd. CIV, Abth. I. 1895.

—— III. Photometrische Untersuchungen auf pflanzenphysiologischem Gebiete Erste Abh. Ibid. Bd. CII, Abth. I. 1893.

See also Wiesner's publications cited above under 4. Intensity and Quality o Light.

6. Day and Night.

Baranetzki, J. Die tägliche Periodicität des Längenwachsthums. Mémoires d l'Acad. d. sciences de St. Pétersbourg. 1879.

Godlewski, E. See the citations under 4.

Bonnier, G. Influence de la lumière électrique continue sur la forme et la structu des plantes. Revue générale de botanique. Tome VII. 1895.

Bonnier, G., et Flahault, Ch. Observations sur les modifications des végétau suivant les conditions physiques du milieu. Annales des sciences naturelle 6e série. Tome VII. 1878.

Curtel, G. Recherches physiologiques sur la transpiration et l'assimilation penda les nuits norvégiennes. Revue générale de botanique. Tome II. 1890.

Kjellman, F. K. Aus dem Leben der Polarpflanzen. In Nordenskjöld, Studie und Forschungen veranlasst durch meine Reise im hohen Norden. Leipzi 1885.

Schuebeler, C. I. Die Pflanzenwelt Norwegens. Christiania, 1873-5.

—— II. Nature. 1891.

CHAPTER IV

THE AIR

1. **Atmospheric Pressure.** Growth under decreased or increased atmospheric pressure. Wieler's and Jaccard's experiments. Atmospheric pressure on high mountains. 2. **The Air contained in Water.** Solubility, composition, and diffusion of air in water. Devices for the absorption and transport of oxygen in aquatic plants. Aerenchyma and other aerating tissues. Pneumatophores. G. Karsten's and Greshoff's experiments. 3. **The Wind.** i. *Wind and Tree-growth.* Mechanical influences. Drying influences. Injurious effects of the latter on tree-growth. ii. *Wind and Reproduction.* Anemophilous leaves. Their frequent presence in windy localities. Anemophilous devices for dispersal of seeds. Importance in relation to distribution at great distances apart. Treub's observations at Krakatoa.

THIS chapter will not deal with the endless and manifold relations between vegetation and the atmosphere, but will treat only of some phenomena connected with the oecological character of certain formations of plants or with the distribution of species.

1. ATMOSPHERIC PRESSURE.

As Wieler and Jaccard have shown, the pressure within the stratum of the atmosphere in which plants grow does not at all correspond to the absolute optimum pressure for the growth of plants. On the contrary, *a diminution of the partial pressure of the oxygen*—for the latter only, and not the total atmospheric pressure, comes into question—occasions an acceleration n growth until a certain low pressure is attained, which is constant for each species, and beyond which any further diminution in pressure causes a retardation in the rate of growth. We find this absolute optimum atmospheric pressure for growth to be in the case of Helianthus annuus about 100 mm., but for Vicia Faba about 200 mm. Again, *an increase in atmospheric pressure* above 760 mm. (or the corresponding pressure of oxygen) up to about 2½ atmospheres occasions a retardation, but after that an acceleration in growth. There are therefore for growth two absolute optima of atmospheric pressure, both of which differ considerably from the pressures that prevail in the inhabited stratum of air, the one being at a far ower, and the other at a far higher oxygen-pressure.

According to Jaccard a decrease in the pressure of oxygen occasions not only more rapid growth, but also richer branching in the axes and roots, as well as an increase in the size of the leaves. Jaccard's following tabular statement shows how considerably growth is favoured by rarefaction of the air:—

GROWTH UNDER DIFFERENT CONDITIONS OF ATMOSPHERIC PRESSURE (after Jaccard).

R. represents growth in air at a pressure of 15 cm.; O. at the normal atmospheric pressure.)

	R.	O.
1. Jerusalem artichoke. Tubers with shoots 1 cm. long, in 8 days	40 cm.	4·5 cm.
2. Vicia Faba, 3–4 cm. high, in 8 days	22 ,,	0·8 ,,
3. Oxalis crenata, tubers with two tall shoots	35 ,,	3·5 ,,
4. Bellis perennis, plant 3–4 cm. high, in 15 days	10 ,,	6 ,,
5. Violet, plant 3 cm. high, in 15 days	8 ,,	6 ,,
6. Onions, with shoots 3–3½ cm. high, in 10 days	16 ,,	6 ,,

When air less rarefied than the above is used, correspondingly less marked results follow, but in spite of the greater importance of moderate atmospheric rarefaction in relation to plant-life, this has secured scarcely any attention from Wieler and Jaccard. A pressure of 35 cm. was employed in one solitary experiment conducted by the latter observer on wheat-seedlings. The plants experimented on attained in twenty-three days a length of 20 cm., instead of 17½ cm. at ordinary atmospheric pressure.

Air that is as rarefied as that used in most of Wieler's and Jaccard's experiments occurs in nature only at the highest summits of the Himalayas, for example at an altitude of 8,839 meters on Gaurisankar, where, if we assume that the temperature of the air at the sea-level is 25°, a pressure of 26 cm. prevails. An atmospheric pressure of 35 cm., under which the above-mentioned experiment with the wheat-seedlings was carried out, corresponds to an altitude of about 6,000 meters, at which, in Thibet, a stately flowering plant, Saussurea tridactyla, has its normal habitat: this plant is discussed and illustrated in the section of this book dealing with alpine vegetation. There appears therefore to be no reason why some vegetation, even if only cryptogamous, should not occur at still greater altitudes. In any case however, judging from the information available, there are very few plants occurring at altitudes such that the rarefaction of the air would cause their growth to be appreciably more rapid than in the low land. For a definite reply to the question we must await the results of experiments on typical alpine plants.

The variations in the atmospheric pressure at different altitudes, even if not directly, yet indirectly are of vast physiological importance, since humidity, temperature, and light depend upon their magnitude. The changes that these last-named factors undergo owing to a reduction in atmospheric pressure are responsible for the influences exerted by the alpine climate on vegetation, as will be described further on.

2. THE AIR CONTAINED IN WATER.

Air dissolved in water is richer in oxygen and much richer in carbon dioxide than is atmospheric air. Yet the amount of oxygen at the disposal of a plant is smaller in the former medium than in the latter. According to Forel, a liter of water from the surface of the Lake of Geneva contains:—

	O.	N.	CO_2.
At 5° C.	7·3 c.c.	13·6 c.c.	0·6 c.c.
„ 20° „	5·7 „	10·7 „	0·3 „

As the diffusion of air in water is very slow, whenever the latter remains very still there is a great risk of scarcity of oxygen. Plants growing in still waters are accordingly provided with means for utilizing to the fullest extent the available oxygen, which is not only dissolved in the water but is also produced during the assimilation of carbon dioxide; on the other hand, in very agitated water, where aeration is much more thorough, plants exhibit such adaptations to a lesser degree.

FIG. 43. Caulerpa prolifera from an aquarium, with excrescences. Natural size.

The large size of the surface, when compared with the mass, of aquatic plants is evidently closely connected with their demands for oxygen. I learned from my friend and colleague Noll an interesting illustration of this view. He cultivated Caulerpa prolifera in the still water of an aquarium, and thus obtained plants that were quite healthy but most peculiarly modified (Fig. 43). The so-called leaves, which under normal conditions are tongue-shaped and entire, in such aquarium-grown individuals fray out into numerous thin segments, so that there is evidently a considerable increase of surface. This difference strikingly recalls those existing between the submerged and aërial leaves of many aquatic plants.

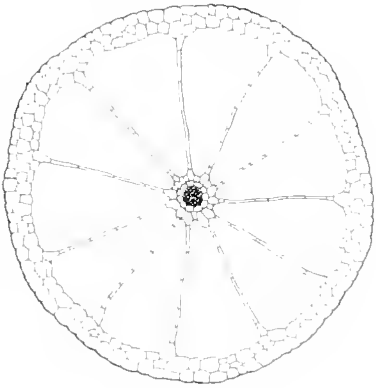

FIG. 44. Elatine Alsinastrum. Transverse section of stem. Magnified. After H. Schenck.

The unfavourable conditions for the supply of oxygen to aquatic plants has led to a considerable increase in the development of the air-passages that were already present in the terrestrial ancestors. In aquatic plants the air-passages are spacious tubes (Fig. 44) which conduct the oxygen set free by the assimilating cells to the points where it is consumed in the non-green parts that are respiring[1].

Woody plants whose roots and stem-bases are in stagnant and therefore badly aerated water, are provided with special means for obtaining oxygen from the atmosphere. Thus the base of the stem of many swamp trees is greatly swollen and, owing to the disruption of the tissues, is hollow in its centre; the cavity serves as an air-reservoir and communicates with the atmosphere by means of intercellular spaces and lenticels. As a rule, however, certain special tissues, or even entire members of the tree, serve to supply oxygen and exhibit an organization suitable for the purpose.

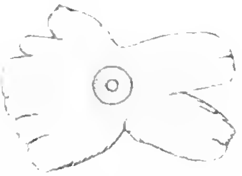

FIG. 45. Caperonia heteropetaloides, Müller Arg. Transverse section through the stem, with a sheath of aerenchyma. Natural size. After H. Schenck.

Aerenchyma[2], which was first accurately described and had its functional significance clearly explained by H. Schenck, is extremely common in woody plants growing in wet soils: this tissue is homologous with cork, but completely differs from it both in histological and oecological characters. In many plants it surrounds those woody portions of the stem and roots that stick into wet soil, with a thick, spongy, fissured mantle (Fig. 45), which occupies the position of the ever-absent cork and is bounded by phellogen. This aerenchyma (Fig. 46) consists of thin-walled, non-suberized cells, loosely united, and bounding broad intercellular passages which form a continuous and much ramified aerating system. The air-passages terminate in the numerous external fissures and open directly to the water, which does not enter them. The aerenchyma is not confined to the wet parts, but extends over parts above the surface of the water. Yet traced upwards into the air it rapidly decreases in thickness and passes over into ordinary cork. Sometimes the formation of aerenchyma is confined to the lenticels, out of which it projects in a cauliflower-like form, whilst the remaining phellogen produces typical cork even under water.

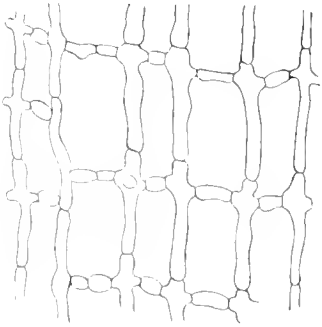

FIG. 46. Caperonia heteropetaloides, Müller Arg. Aerenchyma of the stem in transverse section. Magnified 96. After H. Schenck.

The aerating tissues of woody plants do not always originate in the phellogen. In many cases the greatly developed primary cortex, traversed by broad air-canals, serves for the transport of oxygen, which is partly

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[1] See H. Schenck, I; Goebel, II, Bd. 2, Aquatic Plants.

[2] Schenck, II.

taken from the atmosphere through large lenticels, and partly from the water (Rhizophora, Bruguiera, Avicennia, and others). Less frequently the air-canals are chiefly found in the secondary cortex (Laguncularia)[1]. Lastly, in various Leguminosae the wood is modified into air-containing tissue and consists of thin-walled, air-carrying tracheids, resembling cambium-cells in shape and size, and intercommunicating by means of open pores. Such air-containing wood, if largely developed, causes large swellings at the bases of stems.

In many cases, certain *lateral roots* are differentiated as *oxygen-pumps*, and in accordance with this function differ structurally from other roots.

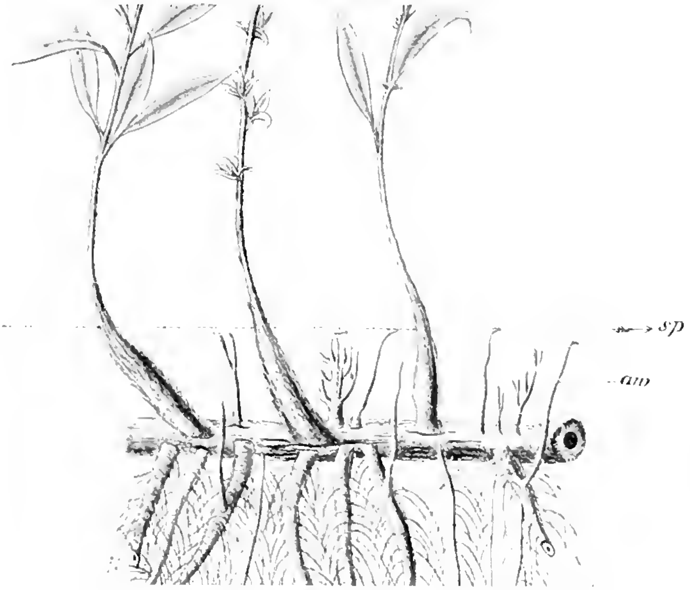

FIG. 47. Jussieuea peruviana, Linn. *aw* pneumatophores under the water-level *sp*. One-third natural size. After H. Schenck.

Such respiratory roots or *pneumatophores* (Jost) have been studied by Schenck in species of Jussieuea inhabiting in numbers, as shrubs or under-hrubs, the shallow waters of warmer districts (Fig. 47). These plants grow n still parts of the water, and from their rhizomes creeping through the mud they develop normal positively geotropic lateral rootlets which penetrate the soil, and also spongy respiratory roots, which are apparently ot geotropic, but, owing to the air they contain, stand upright in the water and conclude their growth in length when they reach the surface. Respiratory roots in contrast with terrestrial roots are simple; less frequently

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[1] See, for example, H. Schenck, III; Schimper; Karsten.

they are branched like coral and surrounded by a thick snow-white coating of aerenchyma.

Lateral roots that serve as pneumatophores of various patterns occur in many other plants. They are not always submerged, but in the majority of cases, at least periodically, project into the air, and accordingly then possess characters other than those of submerged types. These projecting respiratory roots are firm in structure, their aerating tissue is not aerenchyma, but air-containing cork or cortex, and their upright position is not passive, but active and due to negative geotropism. Such pneumatophores frequently attain considerable dimensions, like those of Eugeissona tristis, a palm growing on wet soil, in the case of which they attain a height of 1½ m. and a diameter of 3-5 cm.; or again the peculiar 'knees' of the swamp cypress, Taxodium distichum (Fig. 48), which resembling sugar-loaves in shape and size, project from the frequently inundated southern swamps of North America; or still again the variously modified root-structures of shrubs and trees of the mangrove-swamps. These will be described in a subsequent chapter when the tropical formations are dealt with.

The oecological importance of aerating tissues and pneumatophores has up to the present time been studied chiefly on morphological grounds, and would therefore have remained hypothetical, had not G. Karsten and Greshoff demonstrated it in one case, namely, in the pneumatophores of Bruguiera eriopetala, at the Buitenzorg botanic garden. The pneumatophore on which they experimented exhibited 'an extremely great working-power,' namely, a very strong excretion of carbon dioxide (once, over 45 c.c. in an hour), which, as was shown by a comparison with the respiration of the whole root-system of a young plant, would be quite inexplicable 'if we wished to refer the result obtained only to the part of the root that was exposed to daylight.' Only the assumption that the root, of which the action was investigated, served as an excretory organ for a larger part of the root-system, can explain the high figures obtained.

3. THE WIND.

The vegetation of windy regions exhibits many peculiarities, which may be explained partly as due to direct action of the wind and partly as adaptations to withstand it. These effects of air-currents are apparen both in the vegetative and in the reproductive organs of plants.

1. Wind and Tree-growth.

Areas with an atmosphere almost constantly in active movement, such as flat coasts and islands which experience the first impact of the sea breezes, or elevated unsheltered mountain ridges. are usually characterized

FIG. 48. Florida: margin of a swamp-forest in Monroe County. Taxodium distichum festooned with Tillandsia usneoides; between the trunks are knee-structures (pneumatophores) one meter in height; floating on the water around, Eichhornia crassipes. After a photograph by Webber.

To face p. 74.]

FIG. 49. Banana (Musa Sapientum) in Ceylon. In the foreground: Manihot utilissima.
From a photograph.

by an abnormal tree-growth, if this be present at all, whilst the humbler vegetation exhibits the effects of the wind to a very small extent, or not at all. *This difference between tree-growth and low shrubby and herbaceous growth in relation to the action of the wind, is due to the increasing movement of the air as the distance from the ground increases.*

Some of the results of observations made by Stevenson[1] of Edinburgh upon the increase in velocity of the wind with the height above the ground are shown in the following table:—

Height of Instruments above ground in feet.	Velocity of Wind in miles per hour.	Height of Instruments above ground in feet.	Velocity of Wind in miles per hour.	Height of Instruments above ground in feet.	Velocity of Wind in miles per hour.
½	6·83	½	9·8	1⅓	22·2
2⅓	8·73	3½	12·4	3½	25·6
4⅓	9·77	9	13·8	9	31·9
9½	10·45	14	14·3	14	33·7
14	10·54	25	15·0	25	37·1
25	11·54	51	16·3	51	42·7
50	12·1				

From the above tabular statement it is quite clear that plants that are only slightly raised above the ground experience the effects of the wind much less than tall plants, and especially trees. *The action of the wind on plants is partly direct*, by tensile stresses and by pressure, and *partly indirect*, by increasing transpiration: both these actions are the more energetic, the taller the plants, or the higher the spots they occupy.

The direct effect of the wind on the growth of plants is for the most part strongly exhibited only in places where the wind blows continuously and with considerable strength. It is a common feature in such localities that stems and branches are bent away by the prevailing wind from their normal direction of growth and follow the direction of the wind (Fig. 50). It is also obvious that such trees also suffer direct damage, by breakage of branches, rending of foliage, and so forth. The action of the wind in tearing the leaves of arborescent or lofty plants and tall herbs may, however, prove to be quite a normal and useful feature, as in the case of the banana (Fig. 49) and some other plants, the huge leaves of which when young are quite entire, and remain so in stations that are sheltered from the wind, but are always torn in more exposed ones. The functional activity of the leaves is not thereby in any way prejudiced; on the contrary, owing to

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[1] Stevenson in Journ. Scot. Meteorol. Soc., New Series, Vol. V, 1880, p. 348.

the greater mobility of their segments, the leaves come into contact with larger quantities of air and their interchange of gases is correspondingly increased.

Considerable mechanical damage by exceptionally strong storms is commoner in countries where the weather is usually calm, than in regions that are normally windy, partly because in the latter the form of growth assumed by stem and twigs conveys protection, and partly because, as Hegler proved, a continuous tensile stress occasions an increase of strength and of the mechanical tissue.

FIG. 50. Prunus spinosa to the left, Crataegus Oxyacantha to the right, on the north coast of Zealand in Denmark. Both trees bent and unilaterally branched through the influence of the sea-breeze. From a photograph by Warming.

The mechanical effects of the wind are by no means those most important to the oecology of tall and tree-like plants. They are for the most part markedly exhibited only where very strong continuous air-currents prevail, and then chiefly cause harmless deviations from the normal shape. The destructive influence that in certain areas completely prevents[1] the growth of trees and is chiefly exerted during the winter, is

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[1] Borggreve, for example, states: 'One frequently hears, for example, the assertion made, that afforestation of the west coasts and islands of Schleswig is impossible' (p. 251).

not attributable to the mechanical action of the wind. On the contrary, as Focke was the first to state, the wind must have a power that is directly destructive of life, as is shown by 'the numerous short stiff projecting branches which are to be seen on the tops of shrubs and in the crowns of trees, chiefly on their windward side. in exposed places, and which do not exhibit any trace of external injury[1]' (Fig. 51). The directly fatal influence is, as Kihlman pointed out, the excessive increase of transpiration caused by the wind. When the wind blows during frosty weather—a time when the loss of water cannot be made up by a supply from the soil and from the stem—its action can easily become destructive. Injuries by frost, as has already been shown[2], are not ordinarily attributable to the temperature in itself, but are due to desiccation during the frost.

FIG. 51. Influence of wind on tree-growth: group of trees in a wood on Sylt Island showing branches dried up. After Borggreve.

Evaporation is however universally weaker at low than at high temperatures, yet dry, cold winds possess an extraordinarily strong drying power. A striking example is mentioned by Middendorff. who, on a windy and frosty day, hung outside his tent a leather glove which after being washed had frozen stiff—in an hour's time it was completely dry. The drying action of the wind and its effects are, as will be shown in a later chapter[3], of great geographical importance. since they determine the limits of tree-growth both towards the Poles and in a vertical direction.

[1] Kihlman, p. 68.

[2] Page 59.

[3] Part II, Chap. I, The Formations.

2. Wind and Reproduction.

The flora of open windy tracts of land shows the influence of air-currents no less in its reproductive than in its vegetative functions. *Anemophily in pollination* is much more frequent in exposed localities, where the air is usually in motion, than in the calm interior of forests. The main mass, even if not the majority of species, of the vegetation of grassland and swamps is composed of anemophilous plants, such as grasses, sedges, rushes, species of Plantago, Sanguisorba, Thalictrum, and the like. Lofty trees such as the Coniferae and most Amentaceae are in many cases dependent on wind-pollination. On the other hand, the shrubs and herbs of the forest are chiefly entomophilous. The connexion between the wind and anemophily is most clearly seen in the coast-islands of the North Sea. Thus in Spiekeroog J. Behrens found one-third of the species that blossomed in May had anemophilous devices. Such plants were especially found near the flats, where the winds blow strongly, whilst the entomophilous species, as well as their pollinators, occupied the sheltered spots. In Chapter V (Animals) the connexion between insular stations and method of pollination will be more fully discussed.

Still more evident than in the case of pollination is the connexion between the *means of dissemination* and the amount of wind prevailing in a locality. Anemophilous adaptations in the seeds, or in the fruits that contain them, such as diminutive size, low specific gravity, wings or hairs, are chiefly to be found in wide level grassland (steppe, savannah), in desert, in open swamp, and in the open parts of high mountains. As a rule, it is useless to look for berries in such places. Adaptations facilitating the transport of seeds by animals are, however, not wanting; they are not correlated with birds that eat berries, but with grazing quadrupeds and with carnivorous swamp-birds to whose bodies the seeds become attached. On the other hand, among the shrubs and herbs of the forest or scrub, berries and other adaptations to the animal life of the forest form a common feature. Tall trees and lianes, again, are often provided with anemophilous means of dispersal, and so indeed are many of the epiphytes that grow in the interior of forests. The seeds or spores of the latter are, indeed, so small and light that the weak vertical currents of wind that prevail in forests are sufficient to carry them to their destination among the stem and branches, until owing to their stickiness they adhere to the bark or become caught in its cracks.

The sea-coasts form an exception to the rule that anemophilous means of seed-dispersal predominate in very windy places. The sea is the vehicle for the seeds of most littoral halophytes. Species of plants whose seeds are easily conveyed by the wind, but which sink in sea-water, would with difficulty hold their own on the sea-shore, as their seeds would be either carried inland, where halophytes could not establish themselves, or into the sea, where only floating devices could prevent them from sinking. Weaker breezes which suffice for the transport of pollen are less efficacious for seeds. and all the more so because the smooth loose sand does not arrest anemophilous seeds that have fallen to the ground, but leaves them to the play of the wind.

The work of the wind as a means of seed-dispersal and of spore-dispersal is one of the most important subjects in geographical botany. We cannot say that a conclusive opinion has yet been arrived at regarding it. A. de Candolle and Kerner estimate the efficiency of the wind in this respect at a very low figure in the case of seed-plants. Seeds, they maintain, are conveyed by the wind to short distances only. The former botanist, however. admits the possibility of a longer transport for the spores of cryptogamous plants. According to this view the dispersal of seeds by the wind is merely a local phenomenon and would acquire geographical importance only when frequently repeated in the course of generations. This view is supported by the fact that the transport by the wind of seeds and spores over extensive tracts of water, to oceanic islands for instance, has not yet, in spite of repeated assertions, been positively proved. On the other hand, the presence of various species of plants on such islands can be explained only on the hypothesis of the intervention of the wind.

Treub proved that seeds can be carried by wind over stretches of the sea at least twenty nautical miles in width, for he found in the interior of the island of Krakatoa, which is that distance from Java, three years after the eruption which had covered the island with a thick sheet of lava, eleven ferns, two species of Compositae, and two grasses whose spores or seeds could have been carried thither by means of the wind alone. Accordingly, it is in the first place ferns from the neighbouring islands that colonized the devastated interior of Krakatoa. Ferns also form the chief vegetation of recent volcanic islands that are remote from continents; for instance, the little island of Ascension is almost completely overgrown with ferns Plants that are disseminated by marine currents are not as a rule provided with special means for making their way inland, especially when the interior of the country is mountainous; and berry-eating birds that take long flights do not, excepting for rare accidents, visit islands before trees are established. Only two phanerogamic littoral plants were found inland by Treub upon Krakatoa, Scaevola Koenigii and Tournefortia argentea, the seeds of which are so small and light that the wind might have blown them on to the mountains. Plants disseminated by animals were completely absent.

The significance of anemophilous means of dispersal in relation to the origin of an insular flora has been finally determined by Treub's important observations.

SELECT LITERATURE.

1. Atmospheric Pressure.

Jaccard, P. De l'influence des variations de la pression des gaz sur le développement des végétaux. Revue générale de botanique. Tome V. 1893.

Wieler, A. Die Beeinflussung des Wachsthums durch veränderte Partiärpressung des Sauerstoffs. Untersuchungen aus dem botanischen Institut zu Tübingen. Bd. I. 1881-85.

2. The Air contained in Water.

Bary, A. de. Comparative Anatomy of the Phanerogams and Ferns. English Edition. Oxford, 1884.

Goebel, K. Ueber die Luftwurzeln von Sonneratia. Berichte der deutschen botanischen Gesellschaft. Bd. VI. 1886.

— Pflanzenbiologische Schilderungen. Bd. I. 1889.

Jost, L. Ein Beitrag zur Kenntniss der Athmungsorgane der Pflanzen. Botanische Zeitung. Bd. XLV. 1887.

Karsten, G. Über die Mangrove-Vegetation im malayischen Archipel. Bibliotheca Botanica. XXII. 1891.

Schenck, H. I. Vergleichende Anatomie der submersen Gewächse. Ibid. I. 1886.

— II. Ueber das Aërenchym, ein dem Kork homologes Gewebe bei Sumpfpflanzen. Pringsheim's Jahrbücher. Bd. XX. 1889.

— III. Ueber die Luftwurzeln von Avicennia tomentosa und Laguncularia racemosa. Flora. Jahrg. LXXII. 1889.

Schimper, A. F. W. Die indo-malayische Strandflora. Botan. Mittheil. aus den Tropen. Heft III. Jena, 1891.

Warming, E. Plantesamfund. Kjöbenhavn, 1895. German Edition. Berlin, 1896.

Wilson, W. P. The Production of Aerating Organs on the Roots of Swamp and other Plants. Proceedings of the Acad. of Nat. Sc. Philadelphia. 1889.

3. The Wind.

Bebber, W. J. van. Lehrbuch der Meteorologie. 1890. (Cited by Kihlman.)

Behrens, W. J. Biologische Fragmente. Elberfeld, 1880.

Borggreve, B. Ueber die Einwirkung des Sturms auf die Baumvegetation. Abhandl. des naturw. Vereins zu Bremen. Bd. III. 1873.

Candolle, A. de. Géographie botanique raisonnée. Tome II. 1855. p. 613.

Focke, W. O. Untersuchungen über die Vegetation des nordwest-deutschen Tieflandes. Abhandl. des naturw. Vereins zu Bremen. Bd. II. 1871. p. 412.

Hildebrand, F. Die Verbreitungsmittel der Pflanzen. Leipzig, 1873.

Kerner, A. v. Natural History of Plants. First English Edition. Vol. II. 1895. p. 848. Many good figures.

Kihlman, A. O. Pflanzenbiologische Studien aus Russisch-Lappland. Acta Soc. pro Fauna et Flora fennica. Bd VI. 1890.

Loew, E. Blüthenbiologische Floristik des mittleren und nördlichen Europa sowie Grönlands. Stuttgart, 1894.

Ludwig, F. Lehrbuch der Biologie der Pflanzen. Stuttgart, 1895. p. 301 ff.

Middendorff. A. Th. v. Sibirische Reise : Die Gewächse Sibiriens. 1864.

Pfeffer, W. R. Hegler's Untersuchungen über den Einfluss von Zugkräften auf die Festigkeit und die Ausbildung mechanischer Gewebe in Pflanzen. Ber. der kgl. sächsischen Gesellsch. d. Wissensch. Math.-phys. Klasse. Dec. 7, 1891.

Schrenk, H. v. The Trees of St. Louis as influenced by the Tornado of 1896. Trans. Acad. Sci. of St. Louis. Vol. VIII. 1898.

Warming, E. Plantesamfund. Kjøbenhavn, 1895. German Edition. Berlin, 1896.

CHAPTER V

THE SOIL

1. **The Physical Properties of the Soil.** Water capacity. Conveyance of water by capillarity. Permeability of various kinds of soil. 2. **The Chemical Properties of Soils.** Correlations of physical and chemical properties. Effects of solutions on the absorption of water by plants. Poisonous nature of concentrated solutions. Protective mechanism of plants against increasing concentration of saline solutions in the cells. Various actions of salts on the structure of plants. 3. **Sodium Chloride.** i. *Presence and Function of Sodium Chloride in Plants.* Influence of sodium chloride on the structure of plants. Xerophilous character of halophytes. Influence of sodium chloride on the production of proteids. Its influence on the structure of fresh-water Algae. ii. *Halophytes.* Predilection for salt. Distribution of halophytes among the families of plants. Origin of the halophilous mode of life. Inability to withstand competition inland. 4. **Other easily soluble Salts.** Alum: the solfataras. Saltpetre. 5. **Serpentine.** Plants growing on serpentine. 6. **Calamine.** Calamine-plants. 7. **Calcium Carbonate.** i. *Action of Calcium Carbonate on the Metabolism and Structure of Plants.* Poisonous effects on many plants. Power of accommodation to a calcareous soil. Experiments and observations by Bonnier and others. Nature of the influence of lime on metabolism. Experimental cultures by Fliche and Grandeau. ii. *Character of the Flora on Calcareous Soil.* Calciphilous plants. Calciphobous or silicicolous plants. Instability of the relations of plants towards lime. Thurmann's physical theory. Its refutation. Explanation of the difference between calcicolous and silicicolous floras, and of their instability. Dissimilar relations to lime of closely allied species. Parallel forms on soils rich and poor in lime. Nägeli's theory. 8. **Humus.** i. *The Chemistry and Physics of Humus.* Ash-constituents. Acid humus and mild humus. Leaf-mould and peat. ii. *The Mycorhiza.* Endotrophic and ectotrophic mycorhiza. Thismia Aseroë according to P. Groom. Saprophytes. iii. *Chemical Differences in Humus and the resulting Flora.* Dissimilar nature of the flora on different kinds of humus. Great exclusiveness of certain species of plants. Plants growing on animal humus. 9. **Living Substrata: Parasites.** Dependence on the chemical nature of the substratum.

1. THE PHYSICAL PROPERTIES OF THE SOIL.

The physical properties of the soil[1] that are most important to plant-life depend not so much on the formerly over-estimated forces of cohesion, which offer a more or less considerable resistance to the growth of the subterranean members of plants. as on the forces of adhesion and capillarity which regulate the amount of water and air in the soil. At different spots in one region with uniform rainfall the soil exhibits the numerous stages between a dry and a wet condition, according to its *water-capacity, its*

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[1] See especially Ad. Mayer, op. cit.

power of capillary conduction and its permeability, and these variations occasion variations in the vegetation.

The amount of water that is taken up by the soil is termed by Mayer the *full water-capacity* of the soil, and the amount of water which remains after any excess has been drained away he terms *absolute water-capacity.* The latter, which is most important for plant-life, depends chiefly on the size of the particles of soil. A coarse sand, for instance, has an absolute water-capacity of 13·7 % of its volume, a true clay soil one of 40·9 %. The air-capacity is inversely proportional to the water-capacity, as all pores not filled with water are filled with air.

The *permeability* of a soil is closely connected with its water-capacity. Coarsely grained soils are very permeable, whilst finely grained soils, and especially clay, are characterized by a great resistance to filtration, and take up therefore an amount of water in excess of their absolute capacity.

Capillary conduction of water, or power of absorbing water, a not less important property of the soil, is measured by the rapidity with which dried earth becomes soaked up to a definite height with water when placed in contact with it. Clay possesses the greatest power of conducting water, next come humus and sandy soils, whilst gypsum and chalk exhibit the lowest power of absorption.

The importance of the physical differences in soils in relation to plant-life may be summed up in the following sentences:—

1. *Finely grained soils rich in humus and with a sufficiently permeable substratum* possess a moderate degree of humidity that is generally favourable for plant-life. On such a soil trees and field-plants attain their full development.

2. *A sandy soil poor in humus* with a permeable subsoil such as gravel admits indeed of being thoroughly soaked to some depth at each fall of rain, but dries quickly when the rain is over. On such a soil, therefore, in a climate of medium humidity, only xerophilous plants that require little moisture can grow.

3. *A finely grained calcareous soil that is poor in humus* offers even less favourable conditions, since it has very little power of absorbing water. On such soil, in fact, the vegetation is markedly xerophilous, whilst on a calcareous soil that is rich in humus, if the climate is appropriate, hygrophilous vegetation may appear without risk.

4. Of all soils *clay* absorbs and retains water best. In dry regions, for instance that of the Mediterranean, clay is highly esteemed on account of these qualities, whilst in moist regions like that of Western Europe, soils of exactly the opposite character are preferred, because a clay soil under a heavy rainfall absorbs water beyond its absolute capacity.

5. Absorption beyond its absolute capacity by a soil conduces to *swampi-*

ness, which may also occur in calcareous soils and affords conditions unfavourable to plant-life on account of the stagnation of the oxygen within it [1].

In spite of its great importance, the purely *physical* analysis of soils cannot quite replace a *physiological* analysis that is based on experimental cultures. Indeed only the combination of both methods can explain the connexion between the physical quality of a soil and the physiological process of the absorption of water. The water-capacity of a given soil does not enable us to judge of the quantity of water that a certain plant is capable of taking from it. For instance, in some researches made by Sachs the ratios of the water-capacities of a sandy beech-humus, of a loam, and of a pure quartz sand, were 46 : 52·1 : 20·8, but the ratios of the amounts available in each to a tobacco-plant were 33·7 : 44·1 : 19·3. In other words, that fraction of the force of attraction of the soil for water which the power of suction exerted by the roots could not overcome differed with the kind of soil and varied as 12·3 : 8 : 1·5.

These ratios have recently been more closely investigated by Gain in reference to several kinds of soil, and to three species of plants, namely, Phaseolus vulgaris, Erigeron canadense, Lupinus albus, all of which make unequal demands on moisture. We do not go more closely into the question, as its importance for the topographical distribution of vegetation appears doubtful. However this importance is assumed by Gain, who refers, to a greater extent than is usual, chemical influences of the substratum to the inequality of the force of attraction for water. He assumes, for instance, that the amount of water in the soil of a geographical district might sink to 3 %; then the species of plants with which he experimented could continue to exist in sand or in garden soil, but not in humus, loam, or heath soil. This assumption may be admitted hypothetically, but is without any importance in geographical botany, since in each geographical area numerous qualities of soil occur retaining very different quantities of water.

2. THE CHEMICAL PROPERTIES OF SOILS.

The chemistry and physics of the substratum are in many ways intimately connected. Besides the size of the particles of soil their chemical properties have place in determining the forces of adhesion and capillarity. Soils with equally fine particles, for instance, act differently according as they are composed of clay, lime, or quartz. Physical action is also affected by the salts that are dissolved by the water in the soil, since the salts influence the osmotic processes and consequently the absorption of water. As has been already explained on a preceding page, roots take up more water when it is offered in a chemically pure condition than they do when it is in solutions, and for every species of plant there is a fixed limit of concentration of solutions, rarely exceeding 5 %, beyond which the

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[1] See p. 72.

roots no longer absorb water. A soil that is rich in soluble salts even when thoroughly soaked with water is therefore to a plant a completely dry soil[1].

Nevertheless, by the absorption of salts from the substratum, plants capable of enduring concentrated saline solutions in their cells acquire a certain degree of accommodation, whereby they are enabled to satisfy their demands for water from increasingly concentrated solutions. The importance of this property to the oecology of plants is, however, under natural conditions, less than might be supposed from the results of laboratory experiments, since the concentration of salts in the soil is usually exposed to considerable changes. Thus, for instance, the root-system of a littoral plant, according to the alternations of sunshine and rain, storm and calm, ebb and flow, is bathed in turns by fresh water, or by ordinary or even concentrated sea-water.

The soluble salts in the soil, not only during their absorption, but also, at least so far as they are not consumed by the plant, during their whole passage through it, exercise osmotic actions that greatly affect the processes of development. Thus, merely moderately strong saline solutions cause, as does drought, the closure of the stomata of many plants, especially of those whose natural habitats are deficient in salt, and thereby powerfully affect the assimilation of carbon[2]. The retarding influence on growth of concentrated saline solutions has been frequently observed, and is in all probability primarily traceable to this factor.

The indispensability to vegetable organisms of certain mineral constituents of the soil, especially nitric, phosphoric, and sulphuric acids, potash, lime and magnesia, as well as iron, depends not on their physical, but on their chemical properties. Some of their elements become constituents of protoplasm, and others play a part in metabolism that is indeed secondary but yet quite necessary.

But it is not merely substances which are indispensable to plants that influence their chemical relations. Even those that can always be dispensed with set going, if they are absorbed, both physical and chemical actions which influence vegetable organisms, sometimes favourably, sometimes injuriously, and sometimes in a manner that is quite recognizable but is apparently indifferent oecologically. Above a certain degree of concentration all substances entering a plant in large quantities are poisonous, if they are either not at once, or not at all, assimilated. The degree of concentration at which a solution begins to be poisonous varies with its chemical composition and with the species of the plant. *The inequality of the powers of resistance of different species is to a great extent responsible for the differences in the floras of substrata that differ chemically from one*

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[1] [illegible] p. 4.

[2] Stahl, op. cit.

Besides the relatively simple and direct physical and chemical actions mentioned above, salts exercise a more or less visible but indirect influence on the structure of vegetable organisms. Easily soluble salts evoke protective means against transpiration identical with those accompanying life in a dry soil, and these for the most part are to be ascribed oecologically to the impeded absorption of water[1]. Such protective means are met with both when the soluble salt is nutritive, as for instance saltpetre, and when it is useless and not assimilable, like sodium chloride. Yet in the latter case the salts commence to act in less concentrated solutions and with greater intensity. From this we may learn that protective means against transpiration oppose the increasing concentration of a salt that soon becomes poisonous, and consequently in the case of injurious salts they step in earlier than would be necessary if the salts in the substratum merely rendered difficult the absorption of sufficient water to cover the loss due to transpiration. Whilst the protective means against transpiration appear to be influenced only as to their earlier or later occurrence by the chemical differences in the substances absorbed, these act in a definite specific way, which perhaps resembles the changes induced in their host-plant by certain fungi. Many of the modifications thus caused in the structure of plants have a decidedly pathological character, and rarely, or never, occur under natural conditions. Others, on the contrary, in no way impair the vitality of the plant, and are extremely important in rendering comprehensible the diversities in the floras of soils that differ chemically. To this latter class belong, independently of the protective means against transpiration mentioned above, the modifications caused in the structure of plants by sodium chloride, salts of zinc, serpentine (a silicate of magnesium), and calcium carbonate.

3. SODIUM CHLORIDE.

i. *PRESENCE AND FUNCTION OF SODIUM CHLORIDE IN PLANTS.*

It has been proved by means of cultures in artificial nutritive substrata, especially in culture-solutions, that sodium chloride is of no significance as a nutritive material in the case of most plants. For the normal development of Fagopyrum esculentum this salt has, however, been found necessary, and it is probably necessary for some other plants also, although the number of species with which experiments have been conducted is relatively small.

Plants that require sodium chloride can obtain it in all natural soils, for only a small amount is probably needed in each case. All plants, however, to which chlorides, especially sodium chloride, are offered, actually

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[1] See p. 4.

take them up, and frequently in quantities that are not inconsiderable, even if, as is proved experimentally, the plants can thrive quite normally without them.

Chlorides do not appear to enter into organic compounds, but remain unchanged in the sap of the parenchyma and in the epidermis, where they can be easily micro-chemically recognized [1].

Small quantities of sodium chloride (and of potassium chloride) are apparently endured without injury by all plants. If, however, the ground be watered with a 2–3 % solution of common salt, most species perish in a short time. The only plants to persist are halophytes, which are plants living naturally in saline habitats like the sea-shore, also a few non-halophytes with marked protection against transpiration. Such plants thrive excellently on a soil soaked with sea-water (2·7–3·2 % sodium chloride and store up considerable quantities of salt, chiefly in their stems and leaves. If the concentration of the solution be further increased, however even these species successively die.

According to Wolff's 'Ash-Tables,' the percentages of chlorine in the ash of some sea-shore halophytes were as follows: Armeria maritima, 12·69–15·10: Artemisia maritima, 26·68, though only 1·99 in its root; Aster Tripolium, leaves 43·00, stem 49·90, flowers 19·10; Chenopodium maritimum, 44·06, stem 47·08; Arenaria media 36·55; Plantago media, 43·53. In my own investigations the micro-chemical test for sodium chloride gave intense reactions in a large majority, though not in all, of the littoral plants of Java [2].

The amount of chlorine in the ash of inland plants usually does not exceed 5 % but there are exceptions.

Sodium chloride acts on the vegetable organism in part physically, since like other saline solutions it impedes the osmotic absorption of wate through the roots, and in part chemically, as after its entrance into the cells it affects metabolism.

Systematically conducted cultures investigating the influence of sodium chloride on the structure of plants were first carried out by P. Lesage, with the result that in most cases this salt caused a diminution in the leaf surface, an increase in the thickness of the leaf, a lengthening of the palisade-cells, and a reduction in the intercellular spaces. Also increased hairiness was observed in some cases by Lesage.

Experiments with cultures and a thorough investigation of the Malay littoral flora led me to the conclusion, *that the morphological characteristic which halophytes exhibit agree with those of pronounced xerophytes,* even when the former grow in a wet soil, for example in littoral swamps [3].

There is hardly one of the numerous characteristics capable of being regarded as protective means against transpiration in the xerophytes o a [illegible] climate and a dry soil, that is wanting in halophytes, and this quit

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[1] [illegible] I.

[2] Schimper, II.

[3] See also p. 5 and ff.

irrespective of the fact that the soil is more or less wet, for the quantity of salt in such cases is alone the determining factor. Thus we find in halophytes the *reduction of the transpiration surface* that is so common in xerophytes, as we have already described them, exhibited in their external configuration, and also in their internal structure in the diminution of the intercellular spaces. Moreover in halophytes the following are more or less common: *the profile position of the leaves, abundance of hairs, thick outer walls of the epidermis, storage-tracheids in the leaves, sunken stomata with protective mechanisms, mucilage-cells,* and especially *water-tissues.* This last is specially adapted to guard against injurious concentration of salt in the assimilating cells, and consequently increases in size with the age of the leaves and with the absolute increase within them of salt. All these xerophilous characters of halophytes become weakened in ordinary soil and to some extent completely disappear.

Besides its osmotic effects, sodium chloride also undoubtedly exercises a chemical action on metabolism. Hansteen has shown that it is probable 'that sodium chloride, as well as potassium chloride, stands in a certain relation to the manufacture of proteids from amides and carbohydrates.' This relation is not always the same, as it sometimes consists in a retardation and sometimes in an acceleration in the manufacture of proteids. In any case concentrated solutions of chlorides cause abnormal conditions of nutrition, and finally harmful and considerable disorders. The protective means against transpiration oppose this injurious influence by delaying the increase in concentration during sunlight; the total quantity of salt in the leaves does, it is true, increase with their age, but the water-storing tissues also enlarge simultaneously and with increasing energy depress the concentration of the cell-sap in green cells.

Protective means against transpiration depend on adaptation, and during the course of ages they have been gradually selected as useful devices. Common salt, however, gives rise to more direct and intense structural modifications, which, being exhibited in plants that do not grow naturally in salt water and do not receive any benefit from them, cannot be considered as adaptations. Thus Richter observed in fresh-water Algae, which he cultivated in solutions of common salt of gradually increased concentration, that a considerable increase in the size of the cells was quite a general feature, and in many cases he noted modifications in configuration, in the thickness of the cell-walls, in the cell-division, and in the structure of the chromatophores. It has not yet been ascertained whether this was a case of specific action of common salt, or whether other salts act in a similar way.

At one time I supposed that common salt exercised a retarding influence on assimilation, or at least on the manufacture of starch and glucose. This assumption has become much less probable since Stahl demonstrated that non-halophilous plants, such as those with which I experimented, close their stomata in the presence of large quantities of salt in their nutritive solution and thus experience a materia diminution in their assimilation. Stahl's supposition that halophytes possess stomat that are always rigidly open is not confirmed by O. Rosenberg's more recent investigations. The share taken by stomata in transpiration might therefore be generall less than Stahl believed himself entitled to assume.

ii. *HALOPHYTES*[1].

The amount of salt contained by halophytes is not exclusively determine passively by that of their substratum, but depends chiefly on a craving fo salt in the plant itself, since plants that naturally grow in such localities ar in ordinary soil also in the habit of storing up larger quantities of sodiu chloride than most non-halophytes. There are however, even among th latter, a few species with this tendency, which is always combined with th ability to support larger quantities of salt than other plants can endure Many of these salt-loving species growing in ordinary soils appea occasionally on the sea-shore and in other habitats the salinity of whic keeps other plants at a distance.

Thus the roots of Beta vulgaris, according to several analyses, contain as muc as 35·45 % of chlorine in their ash. In a Cochlearia grown on sandstone 41·70 of chlorine was found: Crambe maritima grown on manured land took from i 15·46 %; Apium graveolens up to 22·14 %; Asparagus officinalis, a facultative halophyte, up to 15 %; Eryngium maritimum up to 19·30 %. In the ash of the horseradish, however, in the root only 1·78 %, in the leaves 5·54 %, of chlorine was found The micro-chemical examination for chlorine in the leaves of Indian halophyte cultivated without salt in the Buitenzorg botanic garden gave an intense reactio in fourteen cases and only a weak one or none at all in seven cases.

It is worthy of note that halophytes are by no means uniformly distributed amon all the families of plants, but rather occur plentifully in certain families, while i others there are few or none. Certain families consist chiefly of halophytes as Chenopodiaceae, Frankeniaceae, Plumbagineae, or contain large numbers o them, as Amarantaceae, Aizoaceae, Cruciferae, Tamaricaceae, Malvaceae, Euphorbiaceae, Umbelliferae, Rhizophoraceae, Lythraceae, Papilionaceae, Convolvulaceae Compositae. Of families and groups which dislike salt may be mentioned Amentaceae, Piperaceae, Urticineae, most Polycarpicae, Rosaceae, Melastomaceae Ericaceae, Orchidaceae, Araceae, and the Pteridophyta and Bryophyta.

According to our present data, it would appear as if the representatives o amilies inclining towards halophily were generally richer in chlorine than thos of salt-avoiding families. The comparison between the contents of chlorine in bot groups of families taken from Wolff's 'Ash-Tables' is in favour of this view. But th material in hand is not yet sufficient to warrant final conclusions.

As has been stated before, halophytes can thrive on ordinary soil, fo [illegible] on garden-soil, without any addition of common salt. Indeed som

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[1] Schimper, II. The older literature is there cited.

f the commonest cultivated trees in the tropics grow under natural onditions only on the saline soil of the sea-shore ; such are Cocos nucifera, yeas circinalis, Casuarina equisetifolia. Terminalia Catappa, Erythrina ndica, Calophyllum Inophyllum, and many others. There can be no oubt that by means of the wind, of animals, of currents of water, seeds of alophytes frequently reach non-saline soil. They would there find con- enial conditions, if their competitors did not hinder them from establishing hemselves[1]. The competition of more vigorous plants, however, excludes alophytes from all localities. except those that are rich in salt.

It is evident that the struggle for space has always been most severe on ils that offer favourable conditions for the majority of plants. In the urse of time many forms have been driven out of specially favoured calities by competitors that have become stronger than they. Many of ese conquered forms have perished, while others have owed their persistence certain characters by means of which they were enabled to colonize healthy territories. Thus, of the expelled plants, those were able to find refuge on saline soil that had already on ordinary soil become accustomed store up plenty of common salt and had thus been rendered immune om its poisonous action. The reduced competition on saline soil permitted em to establish themselves permanently there.

The property of storing salt and existing intact on saline soil does not itself of course render it impossible to continue the struggle in more vourable habitats. There are actually a number of species of plants that cur equally in saline and in non-saline habitats, such as Asparagus ficinalis and Samolus Valerandi.

4. OTHER EASILY SOLUBLE SALTS.

Sodium chloride is the only easily soluble salt which saturates the soil in ncentrated solutions over extensive areas. Other salts of similar solubility pear only locally in large quantities and their action on vegetation is erefore less known. The presence of large quantities of alum in the rm swampy soil of the solfataras of Java and Japan causes the appearance, the centre of hygrophytic regions, of xerophilous plants, which are not, in ordinary saline soil, in part peculiar to the habitat, but are individuals at have emigrated from the nearest habitat of xerophilous plants. Some them are plants that elsewhere grow as epiphytes on dry bark, some are migrants from cool dry alpine regions. The factors which render xero- ilous structure a condition vital to these plants, are evidently the same as ose in the case of common salt, namely, difficulty in absorbing water, and urious action of the salt in the assimilating cells[2].

On page 80 has been described the appearance of elsewhere exclusive littoral halo- ytes in the interior of Krakatoa, where there is not yet any competition.

[2] See Schimper, I.

Saltpetre also induces a xerophilous structure, but only at a higher co centration, and even then less decidedly than common salt. This differen favours the opinion that the decided nature of the xerophilous structure ordinary halophytes, must partly afford protection against poisonous sali action, and therefore appears sooner than in the case of saltpetre, which injurious only when more highly concentrate Such a concentration is not usually attained places rich in nitrates, at any rate not in t case of plants, such as many Solanaceae, Cru ferae, Chenopodiaceae, Fumaria, Sambucus nig, and others, that have a tendency to store sa petre in their tissues, and usually exhibit a ra growth in such places. The nitrate fields America, however, on account of their extrer dryness possess a decided xerophilous flora.

Fig. 52. Asplenium adulterinum. Natural size. After Lürssen.

5. SERPENTINE.

Serpentine, a very slightly soluble silicate magnesium, acts in such a way on two Cent European species of fern, Asplenium viride a A. Adiantum-nigrum, that they are chang into different forms which have for some ti been taken for distinct species. Sadebe succeeded in obtaining a reversion to the o ginal form by cultivating them in ordina soil, but not until the sixth generation; t attempt to induce any corresponding tra formation in the two Asplenia by cultivati them on serpentine however failed. It is the fore evidently a case of an extremely sl progressive action. The deviations from t normal type are apparently purely morp logical without any ascertainable use to t plant.

Asplenium adulterinum, Milde (Fig. 52), the s pentine form of A. viride, assumes in many respe an intermediate form between that species and Trichomanes. For instance, the rachis is bro below and green above. Its peculiar habit is to the extreme convexity of the leaflets and their perpendicularity to the rachis; two allied forms have somewhat long plane leaflets, parallel to the rachis. [illegible] to Lürssen, this characteristic is not constant. Asplenium serpent [illegible] differs from the typical A. Adiantum-nigrum by the segments be edge-shaped at the base and by having more delicate, more herbaceous, dull, eciduous leaves.

Both forms must be considered as fully adapted to their subtratum, for they ourish on it with the greatest vigour and abundance. Asplenium adulterinum lmost entirely suppresses the common A. Trichomanes on serpentine, whilst the riginal form A. viride has been only exceptionally observed. The typical A. diantum-nigrum seems completely absent om serpentine. Kalmus, speaking of the ation of A. adulterinum and A. Trichomanes ear Einsiedel, says that the latter appears to im to be quite a little people which is only llowed on sufferance by its superior neighbours and relatives; and Milde makes the llowing remarks about the same plant: The first thing that struck me was the great ensity of its growth, partly due to the large umber of plants, partly to the immense clumps hich the plant often formed. I have never bserved such vigorous growth in A. viride and nly very rarely in A. Trichomanes[1].'

6. CALAMINE.

The action on plants of large quantities f the slightly soluble zinc ore usually nown as calamine (zinc carbonate and licate) resembles that of serpentine in far as it also induces hereditary modication in some plants, in this case Viola tea and Thlaspi alpestre, the physiogical and oecological connexion of which ith the nature of their substratum has yet obtained no interpretation. The lants thus modified grow on a zinc soil great numbers and luxuriance, and do t overstep its limits.

FIG. 53. Viola calaminaria. Half natural size.

The calamine violet, Viola calaminaria, Lej. . lutea, var. multicaulis, Koch.) (Fig. 53), ffers from other forms of Viola lutea by its rich ramification, its longer stem. d its smaller corolla, which however varies somewhat in size. In the case Thlaspi calaminare, Lej. et Court, the petals are broader than those of the type rm, and are much longer than the sepals, while the filaments are shorter than the pals. The zinc in the soil has induced in the one form an increase, and in e other form a decrease in the size of the corolla.

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[1] Sadebeck, I, II.

Besides its action in producing special varieties, calamine soil is also distinguishe from that of other neighbouring localities by the assemblage of plants composin its flora. Viola lutea is completely absent from the Rhine country, and is first see near Liège. Alsine verna, also common on calamine soil near Aix, is still furthe separated from its other localities. Armeria vulgaris is near Aix confined t calamine soils, and Silene inflata, var. glaberrima, is surprisingly abundant an luxuriant in places that are richest in zinc.

Plants of calamine soils contain zinc in all their parts: Risse found 13·12 % of zin oxide in Thlaspi calaminare: whilst the ashes of the root, stem, and flowers contai respectively 1·66, 3·28, and 3·24 % of zinc. In Viola calaminaria and Armeri vulgaris Risse found the largest quantity of zinc oxide in the root (1·52 and 3·58 respectively of the ash).

7. CALCIUM CARBONATE.

i. *ACTION OF CALCIUM CARBONATE ON THE METABOLISM AND STRUCTURE OF PLANTS.*

Among the compounds of calcium in the soil are some important nutritiv salts, such as salts of nitric, phosphoric, and sulphuric acids; also insolubl completely indifferent substances such as calcium silicate (labradorit andradite, and others): and a salt, calcium carbonate, which although no reckoned as a plant-food, yet affects the metabolism of plants and consequently the character and composition of the vegetation.

Lime combined with carbonic acid occurs in nature as the insoluble an neutral calcium carbonate $CaCO_3$ and as the soluble bicarbonate $CaC_2O_6H_2$[1] The former salt cannot, on account of its insolubility, gain admission t plants; but on the other hand, the acid salt, which results from the actio of water containing carbon dioxide on the neutral salt and therefor constantly accompanies it in the soil, is, as water-cultures attest, taken u by the plant and apparently undecomposed reaches the water-channel the sap of which usually contains calcium carbonate. On the othe hand, it is very probable that the calcium carbonate often richly stored i the cell-walls of active plant organs, for instance in cystoliths, arises a a secondary product from other compounds of calcium, for exampl from the calcium pectate which is always present in cell-walls[2] or b double decomposition from the nutritive calcium salts (nitrate, sulphat or phosphate). The calcareous coatings of many green aquatic plant

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[1] According to another theory, the bicarbonate does not occur in nature, but lime water rather contains the ordinary calcium carbonate and free carbon dioxide. Thi question is without importance in geographical botany.

[2] The formation of calcium pectate in living cells is certainly ascribable to processe similar to those for calcium oxalate, malate, &c.; cf. Schimper, I. II.

are, on the contrary, certainly produced by the decomposition of the bicarbonate and the precipitation of the insoluble neutral salt, resulting from assimilation[1].

Calcium carbonate is present in all soils and in all waters, and in small quantities is endured by all plants. No appreciable action on physiological processes occurs in such cases. On the other hand, *a nutritive solution rich in calcium is poisonous to many plants, whilst by others it is tolerated in different cases to a greater or less extent.* Those plants that tolerate larger quantities of calcium carbonate have their metabolism likewise affected by it, and consequently often undergo visible structural modifications. Calcium carbonate thus acts as do sodium chloride, serpentine, and calamine.

The poisonous action of calcium carbonate on many plants is most easily proved in the case of aquatic vegetation. A supply of water rich in calcium, for instance, suffices, as Sendtner proved, in a short time to kill the species of Sphagnum and is not less poisonous to other aquatic mosses. The same holds true for many Algae that are otherwise common, if we may udge by their constant absence from water that is rich in calcium. Many errestrial plants are scarcely less susceptible. Thus, according to Christ, a mere sprinkling with water rich in lime suffices, in a short time, to kill Drosera and most of the other plants associated with bog-mosses on peat-bogs. According to the same investigator, Lomaria Spicant, Allosorus crispus, Saxifraga aspera, Phyteuma hemisphaericum, Androsace carnea, and many others behave in a similar way. On a substratum rich in lime Kerner cultivated various plants that never appear on a calcareous soil: they at once sickened and died without blossoming.' Among trees, the weet-chestnut and Pinus Pinaster cannot tolerate a calcareous soil; according to Chatin, even three per cent. of calcium in the soil is fatal to the weet-chestnut.

Plants that tolerate large quantities of calcium owe this capacity, as in he case of halophytes in relation to sodium chloride, to a power of ccommodation which is often associated with visible structural modi-cations. The connexion between these variations and the influence of alcium can be explained just as little, either physiologically or oeco-ogically, as the variations induced in Algae by solutions of common salt, r as the production of peculiar varieties of plants on calamine and serpentine soils. Possibly we may also include under the same category of chemical influences certain modifications induced by parasitic fungi in Euphorbia, Anemone, and other plants.

The first experimental investigations into the influence of lime on the ructure of plants were carried out by Bonnier, after he had noticed that Ononis Natrix, on soils poor in calcium, possesses a physiognomy different

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[1] Pringsheim, op. cit.

from that which it exhibits on calcareous soils upon which it usually grows.

In order to ascertain whether this distinction was due to the influence of calcium. comparative cultural experiments were undertaken by Bonnier, in which seeds from one and the same parent were employed, and sown on soil poor in lime (½ sand, ½ clay) and on soil rich in lime (⅔ calcium carbonate, ⅓ sand). The resulting plants differed in appearance according to the nature of the substratum. On the soil rich in lime they formed taller and less spreading tufts, broader leaves, shorter sepals, and possessed a colour different from that of those on the soil that was poor in lime. Even histological differences also were observed. The plants that were poor in calcium possessed a lignified pith, numerous fibres, and thick palisade-tissue in their leaflets, whereas those grown on calcareous soil produced an unlignified pith, less numerous fibres, and looser palisade-tissue.

Numerous observations in the field, especially those by Fliche and Grandeau, have also demonstrated a distinct action of calcium on the structure of plants.

These observers have recorded that Robinia Pseud-acacia, which is a plant indifferent as regards the chemical constitution of the soil, as it grew in the forest o Champfêtu, exhibited the following variations according as it grew on soil that was rich or poor in lime: the wood on soil poor in lime assumes a brown colour after the seventh year, but on calcareous soil not until after the ninth year. The bark is thinner and denser in the former case, the sap-wood bright brown, whilst on calcareous soil it is yellow, and the vessels are more numerous and wider. In wood parenchyma, starch is more abundant on soils poor in lime, albuminates more abundant on the calcareous soil. The pods are longer and much broader in the former case, and more lightly coloured than on calcareous soil.

Masclef examined specimens of Pteris aquilina which were grown side by side on calcareous and clay soils. In the former case. the rhizomes were shorter, provided with more numerous and thicker roots, the reserve parenchyma was more feebly and the protective tissues more strongly developed.

Timbal-Lagrave and Malinvaud discovered that Asclepias Vincetoxicum is represented by different races on calcareous soil and on soil poor in lime.

Hilgard has made extensive observations in North America on the influence of calcium on the configuration of plants. Quercus ferruginea and Q. obtusifolia ar stunted on sand and on black prairie soil, but tall and with a different ramification on calcareous soil. According to Hilgard, an increase of the lime in soils increase the yield of many economic plants, especially of cotton.

There are, up to the present time, only a few observations available a to the nature of the influence of calcium carbonate on plant-metabolism Yet the critically conducted and extensive researches of Fliche and Grandeau[1] have made the first substantial advance in the desired direction.

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[1] Fliche et Grandeau, I, II, III.

The observations were carried on in the forest of Champfêtu near Sens, where, n a small area. calcareous soil (chalk) and silicious soil (sand and sandy clay) lternate, because the clay and sand overlie the chalk, as tertiary strata, forming ometimes a thick deposit and sometimes a thin one, or have been completely ashed away. The area in question had been planted with different species f forest trees, such as Pinus sylvestris, P. Laricio, larch, silver-fir, spruce, oak, birch, hich had for the most part thriven equally well on each of the strata : whereas the aritime pines and sweet-chestnut trees that had also been planted grew luxuriantly n the soil that was poor in lime, but remained stunted on the calcareous soil and on died ; and so much the sooner, the thinner the upper stratum poor in lime. Vherever the sandy soil poor in lime was absent, both trees could scarcely live all.

The chestnut trees and maritime pines on the calcareous soil differed from those n the sandy soil, not only by their stunted growth and by the abundance of their ead twigs, but also by the smaller size and the yellower colour of their leaves, which the case of the chestnut were partly white. Thus on silicious soil the pine needles ere 0·175–0·189 m. long and 2 mm. broad, whilst on calcareous soil the length of the eedles was between 0·092 and 0·111 m. and their breadth 1·5 mm. The chestnut aves on clay and sandy soil were up to 0·253 m. long and 0·072 m. broad, but on lcareous soil at the most 0·149 m. long and 0·056 m. broad ; those at the end of the ig were much smaller, often degenerate and nearly white.

The analysis of the soils from which the specimens of Pinus Pinaster had been ken, the composition of whose ashes will be given below, gave the following sults :—

NALYSIS OF SOILS IN THE FOREST OF CHAMPFÉTU UPON WHICH PINUS PINASTER GREW (after Fliche and Grandeau).

	Silicious clay soil.		Calcareous soil.	
	Surface soil.	Subsoil.	Surface soil.	Subsoil.
Water	1·75	1·66	2·90	2·46
Organic matter	5·50	2·84	6·53	5·39
Lime	0·35	0·20	3·25	24·04
Magnesia	0·38	0·47	0·47	1·31
Potash	0·07	0·03	0·04	0·16
Soda	0·06	0·04	0·03	0·07
Phosphoric acid	0·64	0·42	0·29	0·18
Residue (silica, clay, ferric oxide)	90·55	92·70	83·00	46·80
Carbon dioxide	0·70	1·64	3·54	19·59
	100	100	100	100

In the analysis of the ash of the maritime pine grown on these soils, about equal umes of wood, bark, and leaves were used. For the purpose of comparison, Pinus ricio, which prefers a lime-containing substratum, was taken from the calcareous soil d analysed.

ANALYSIS OF ASH OF PINUS PINASTER ON DIFFERENT SOILS IN THE FOREST OF CHAMPFÉTU (after Fliche and Grandeau).

	Pinus Pinaster.		P. Laricio.
	Silicious clay soil.	Calcareous soil.	Calcareous soil.
Phosphoric acid . .	9·00	9·14	11.33
Silica	9·18	6·42	7·14
Lime	40·20	56·14	49·13
Ferric oxide . . .	3·83	2·07	3·29
Magnesia	20·09	18·80	13·49
Potash	16·04	4·95	13·56
Soda	1·91	2·52	2·24
Total . .	100·25	100·04	100·18
Ash % . .	1·32	1.535	2·45

The analysed sweet-chestnuts grew on the same soil as the maritime pines. In this cas leaves and wood were analysed separately.

ANALYSIS OF ASH OF CASTANEA VESCA ON DIFFERENT SOILS IN THE FOREST OF CHAMPFÉTU (after Fliche and Grandeau).

	Leaves.		Wood.	
	Silicious soil.	Calcareous soil.	Silicious soil.	Calcareous soil.
Silica	5·79	1·46	3·08	1·36
Phosphoric acid .	12·32	12·50	4·53	4·27
Lime	45·37	74·55	73·26	87·30
Magnesia . . .	6·63	3·70	3·99	2·07
Potash	21·67	5·76	11·65	2·69
Soda	3·86	0·66	0·00	0·28
Ferric oxide . .	1·07	0·83	2·04	1·27
Sulphuric acid . .	2·97	0·00	1·43	0·64
Chlorine . . .	0·30	0·52	—	0·08
Total . .	99·98	99·98	99·98	99·96
Ash % . . .	4·80	7·80	4·74	5·71

The most striking point in these tabular statements is the great diffe ence in the quantities of lime and potash. *Trees grown on silicious so are much richer in potash and poorer in lime than those grown o calcareous soil.*

The authors draw from these observations the conclusion that abundanc of lime in the soil *retards the absorption of potash, whereas it accelerat the absorption of lime and thereby produces an anomalous condition tha is prejudicial to the plants.*

The different percentages of ferric oxide in the ashes is perhaps significan although it is less striking on account of the small quantities under considera tion. *Maritime pine and sweet-chestnut on calcareous soil are much poore especially in their leaves, in ferric oxide than on silicious soil.* If we conside in relation to this the smaller amount of chlorophyll that is present in the leaves on the calcareous soil, we may with probability conclude that in calciphobous plants, when they grow on calcareous soil, *the absorption of iron or its transport through the plant is prejudiced, and thus the formation of chlorophyll is checked.* Contejean has also observed that the colouring of Sarothamnus, Ulex, Calluna, Anthoxanthum Puellii is always yellowish when they grow under such conditions.

The physiological causes of the injurious influence of calcium carbonate on certain species of plants are rendered more comprehensible by the researches of Fliche and Grandeau; but, on the other hand, the difference in the behaviour of different species remains quite unexplained. An affinity on the part of calciphilous plants for carbonate of lime, similar to that of halophytes for sodium chloride and of nitrophytes for saltpetre, does not appear to be here in question; the quantities of lime absorbed from the same soil by the different species of plants are indeed as a rule very unequal, but without any perceptible connexion with a greater or less capability the plants may possess of thriving on a substratum that is rich in lime.

In the planted forest of Champfétu, on soil poor in lime (0·35 % CaO), there are found growing together the calciphilous Cytisus Laburnum with 27·15 % CaO in its ash, the calciphobous Ulex europaeus with 5·97 % CaO, the calciphobous Sarothamnus scoparius with 25·03 % CaO, and the indifferent Robinia Pseud-acacia with 58·97 % CaO. If we consider that the laburnum contains only half the quantity of ash contained by the other species it follows that although it is calciphilous it is poorer in lime than its calciphobous allies.

ii. *CHARACTER OF THE FLORA ON CALCAREOUS SOIL.*

The flora of a district the superficial soil of which results, in some parts, from rocks poor in lime, such as granite, sandstone or slate, and, in other parts, from rocks rich in lime, exhibits, in the flora of the two kinds of soil, contrast that at once strikes the eye, although many plants occupy both the soil rich in lime as well as that poor in lime. Of plants in Central Europe strictly confined to a soil poor in lime are, for instance, Calluna vulgaris, Vaccinium Myrtillus, Sarothamnus scoparius, Scleranthus perennis, Rumex Acetosella, Digitalis purpurea: similarly, of species found only on calcareous soil there are Prunus Mahaleb, Aster Amellus, Hippocrepis comosa, Teucrium montanum, T. botrys, Globularia vulgaris, Epipactis rubiginosa. Many species show merely a decided preference for the one or the other kind of soil, without confining themselves to it so strictly. Thus the common bracken is rarely seen on calcareous soil, Anthyllis Vulneraria and Scilla bifolia rarely on soil poor in lime—a soil being considered poor in lime that contains less than 3 %.

Owing to the injurious influence of carbonate of lime on certain species of plants, their absence from a substratum rich in lime is quite comprehensible. It is not less intelligible that many species, although not speciall requiring lime, are restricted to a calcareous soil. As with the halophyte in relation to sodium chloride, it is the fugitives from the struggle fo existence which, on a silicious soil, are unable to maintain themselve against stronger competitors, but endure a calcareous soil better than they.

That the peculiar character of the flora of calcareous soil depends i the first place on its chemical properties would never have been doubte if the same species of plants always behaved in the same manner ; this, however, is only to a limited extent the case. Only those species to which lim is poisonous are always absent from a calcareous soil ; as regards othe species, *the difference between a lime-flora and a silica-flora is not constan as it is between halophytes and non-halophytes, but varies with the localit* In a region with several kinds of soil, but with the conditions determinin the existence of vegetation otherwise the same throughout, there ar always certain species of plants found only on calcareous soil, and other only on silicious soil, whilst a third group is more or less indifferent. List of the three groups in any particular district will be only partially valid i a second district. Many a calciphobous species of the first district is calc philous in the second, or the reverse, and many species that in one district ar selective in the matter of soil appear in another district on any kind of soi

Bonnier, for instance, found that the lists which had been drawn u for the Swiss Alps, of plants more or less confined to a certain kind soil, were no longer completely valid in Dauphiné. Much less do they hol good for the Carpathian mountains or for Scandinavia. Thus the larch i Switzerland and the Tyrol prefers the most primitive rocks, which are poo in lime, and is seldom found on limestone ; whilst in Bavaria and Salzbur it is quite commonly found on calcareous but not on silicious soil ; again, i the Carpathian mountains it grows on all kinds of soil indifferently.

Literature presents a fairly large number of similar cases : 'Pinus montana, Mil in its varieties uncinata and Pumilio, is a decidedly calcicolous plant ; there [in th Swiss Alps] it alternates, markedly according to the substratum, with Alnus viridi The mountain pine produces its dwarf forests on the rubbly slopes of the limeston rocks, whilst the alder clothes the declivities of the primitive rocks. In the Carp thians, on the contrary, the mountain pine is indifferent as to the soil' (Chris The following species are, according to Wahlenberg, confined to calcareous soil the Carpathians, but are indifferent in Switzerland, according to Christ: Dry octopetala, Saxifraga oppositifolia, most of the alpine Leguminosae, Gentia nivalis, G. tenella, G. verna, Erica carnea, Chamaeorchis alpina, Carex capillari Bupleurum stellatum, and Phaca alpina, are confined to calcareous soil in t Carpathians, but prefer silicious soil in Switzerland. Geum reptans, accordi to Bonnier, grows in Savoy (Mont Blanc) exclusively on calcareous soils, in Dauphi exclusively on silicious soils ; in Switzerland it appears to be indifferent.

In the face of such phenomena, which are multiplied by each new investigation, so that the number of species truly characteristic of certain soils becomes more and more reduced, botanists, in the middle of the nineteenth century, gradually began to doubt the chemical influence of the soil on the character of the flora and to trace back the difference between the floras on lime and on silica, respectively, to physical factors. The very able Swiss investigator Thurmann for a time carried the day with his 'physical theory,' which completely denied the chemical influence not only of silica but also of calcium carbonate, and attributed the differences in the flora exclusively to those in the humidity and consistency of the soil.

Thurmann distinguished rocks as *eugeogenous*, which supply an abundant detritus, and *dysgeogenous*, which disintegrate very slightly or not at all into detritus. Hygrophytes are associated with eugeogenous soil and xerophytes with dysgeogenous soil. According to the physical consistence of the detritus, Thurmann further distinguished *pelogenous* kinds of soil, of very fine-grained earthy consistence, and *psammogenous*, of more or less coarse-grained sandy consistence. According to their degree of subdivision pelogenous soils were further classified as *perpelic*, *hemipelic*, *oligopelic*, and the psammogenous, similarly, as *perpsammic*, *hemipsammic*, *oligopsammic*. Transition states between the two groups were termed *pelopsammic*.

According to Thurmann the so-called silicicolous plants are hygrophilous and the calcicolous plants xerophilous. It is not the presence of silica nor of lime, but the presence of larger or smaller quantities of water, that determines their appearance, whilst the other physical differences are said to evoke finer distinctions in the composition of the vegetation.

That this 'theory' so long enjoyed such universal assent and threw the 'chemical theory' almost into oblivion has been explained by Nägeli, who in 1865 wrote a masterly paper in favour of the 'chemical theory,' as due to the fact 'that the principles of the physical theory exhibit a certain want of precision, so that criticism has nowhere a firm basis for refuting them and nothing is more difficult than to correct a vague proposition.' Nägeli, however, did not succeed in making many converts, and this chiefly because the best men were almost entirely occupied with laboratory work, whilst others at that time fortunately kept away from such general questions. Only since 1880 has discussion on this question recommenced, with the result that the 'chemical theory' has now been indisputably maintained, being supported by a correct apprehension of the problem, as well as by better material from field observations, by analyses of soils, and by cultures.

A principal cause for the discredit into which the 'chemical theory' fell is to be found in the then prevailing false conception of the influence of the soil. It was assumed that lime-plants require as food lime but not silica, and that silica-plants, on the contrary, require silica but not lime. It needs no longer to be stated that such ideas, which strange to say are still held by some geographical botanists, are irreconcilable with facts.

The untenability of the 'physical theory' follows most clearly from the fact that even when the physical properties of the substratum are identical, the flora varies with its chemical properties. On the rocks of a stream in granite mountains that are poor in lime, according to Boulay, may be observed, for instance, Hypnum dilatatum, H. ochraceum, Brachythecium plumosum, Amblystegium irriguum, Fontinalis squamosa, Rhacomitrium aciculare, Pterigophyllum lucens. One would look in vain for these species on calcareous mountains. On the other hand, in the waters of such calcareous mountains many species absent from silicious strata may be found, such as those of Cinclidotus. Not less essentially distinct is the algal flora, even the surface flora (e.g. the Desmidiaceae), of water rich in lime and of water poor in lime. In all such cases the difference must depend on the amount of lime in the water, for the physical nature of the substratum is the same in the case of the superficially attached mosses and can have no significance at all in the case of the floating Algae.

The difference between the flora of sphagnum-moors and of grass-moors is also very instructive. In both cases the substratum is peat; in the former, however, it is saturated with water that contains but little lime in the latter with water rich in lime. The flora of the two moors is quite dissimilar. Only on the sphagnum-moors are found Sphagnum, Viola palustris, Spergula pentandra, Drosera, Vaccinium uliginosum and V. Vitis-Idaea, Calluna vulgaris, Rhododendron ferrugineum, Pedicularis sylvatica, Carex dioica, Aira flexuosa, Pteris aquilina; on calcareous moors on the other hand, Spergula nodosa, Pedicularis palustris, Erica carnea Primula Auricula, Carex Davalliana, Sesleria coerulea.

A great dissimilarity is also seen between the mosses and lichens that grow on the surfaces of rocks, according as the latter are poor or rich in lime, whilst to mos species, if not to all, the physical nature of the rock is irrelevant. Thus the species of Andreaea are all calciphobous, also many species of Rhacomitrium, Grimmia Dicranum; whereas the presence of certain other species, especially those of Barbula Pottia, Desmatodon, Encalypta, Gymnostomum, entitles one to infer with certainty the existence of a limestone substratum. Many lichens on rocks show a similar dependence on the chemical nature of the substratum, whilst in regard to others especially those developing very slowly, great durability of the substratum, a physica property in fact, is said to be the determining factor. Lichens of the latter kind are found chiefly on granite or porphyry, but also on very hard crystalline limestone.

A quartz sand possesses physical properties that are quite similar to those o a crystalline calcareous sand, and yet both have their thoroughly characteristic mosses the former for instance Brachythecium albicans, the latter Barbula inclinata Not less dissimilar is the moss-flora of clay, according as it is poor or rich in lime, although the physical properties of the two are very slightly dissimilar Thus Sendtner learned to consider Ephemerum serratum, Phascum crispum, Pleuridium subulatum as so calciphobous, that he believed their presence to indicate a clay suitable for a brick-kiln.

The assumption that forms the basis of the whole 'physical theory' of soils, that calcicolous plants are xerophilous and silicicolous plants hygrophilous, has no foundation. Waters rich or poor in lime are also, physiologically considered, equally wet; sphagnum-moors and grass-moors are equally moist. But even on a substratum of earth, there are hygrophytes on calcareous soil and xerophytes on soils poor in lime. Indeed on basalt the condition is entirely reversed, as silica-plants occupy the slightly disintegrated rock as xerophytes, and lime-plants the fine soils as hygrophytes. Instances of decided hygrophytes on calcareous soil are, for instance, Ranunculus lanuginosus, Arabis alpina, Moehringia muscosa, Bellidiastrum Michelii, Campanula pusilla.

The greatest dependence on the chemical nature of the substratum is frequently most strikingly contrasted with the greatest indifference as regards purely physical conditions. Thus Schultz writes[1]: 'A series of plants are characterized by their ability to live in any habitat, from the driest rocky soil to the swampy peat-meadow. Most of these are peculiarly lime-needing plants; for example, Polygala comosa, P. amara, Astragalus danicus, Phyteuma orbiculare, Gentiana cruciata, Prunella grandiflora, Orchis militaris, Carex flacca.' According to Boulay, Hypnum chrysophyllum grows in all stations that are rich in lime, in swamps, on dolomitic sand, on dry stones, and in meadows. On the other hand, Grimmia eucophaea and G. trichophylla grow on nearly all the kinds of soil as classified by Thurmann, on the one condition that these are poor in ime. Achillea moschata and A. atrata, in the regions where they grow ogether, are markedly confined to one kind of soil, the former to a silicious soil, the latter to a calcareous soil, yet they are quite indifferent as to he physical characters of the soil.

From what has been said it follows that the difference between the ime-flora and the silica-flora must be attributed solely, or at least mainly, o the chemical characters of the soil. Here also must we therefore seek or the key to the enigmatical phenomenon, that, according to the environnent, one and the same species of plant shows an inconstant relation o the chemical nature of the soil. The cause of this different behaviour evidently depends on the fact that, as has been shown above[2], *a plant rown on a substratum rich in lime is an organism of different constitution, and therefore has different physiological qualities and a different oecology rom a plant grown on a substratum that is poor in lime.*

Different plant-organisms differ in their behaviour in relation to external nfluences, and the differences in nearly allied plants are as great as, or nay be greater than, they are in plants which are not allied. Whatever nay benefit the lime-form of a species will therefore frequently favour he silica-form to a less degree, or will even injure it. *External conditions,*

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[1] Schultz, op. cit., p. 43.

[2] See p. 95.

however, change with the area[1]. *In one area the silica-form, in anothe the lime-form, is better adapted to local conditions, whilst in a third are both forms may be able to maintain themselves in the struggle for existenc Accordingly, one and the same species is calciphobous in the first area calciphilous in the second, and indifferent in the third.*

An instructive example of the dissimilar physiological properties o the lime-form and the silica-form of the same species of plant is afforde by Pinus uncinata. This pine in its lime-form, at least in Switzerlan and Bavaria, prefers dry gravel, whilst in its silica-form it avoids ston dry spots and occurs onl on moorlands. In othe regions, with a different climate, probably both form would behave in anothe manner.

Nägeli and Christ hav proved, in the case c closely allied species c Gentiana, Achillea, an Rhododendron, that closel allied plant-organisms be have very differently as re gards the chemical qualit of their substratum. Thu in Switzerland, Gentian acaulis is calciphilous, wher as the closely allied Gentian excisa (Fig. 54), which usually considered as mere variety of the forme is calciphobous; neither them is quite exclusi in its choice. Similar pairs, although less like, are Achillea atrata an A. moschata (Fig. 55), Rhododendron hirsutum and R. ferrugineun Androsace pubescens and A. glacialis, Juncus Hostii and J. trifidu of which pairs the species first named is calciphilous. Kerner has draw up a long list of such parallel species[2].

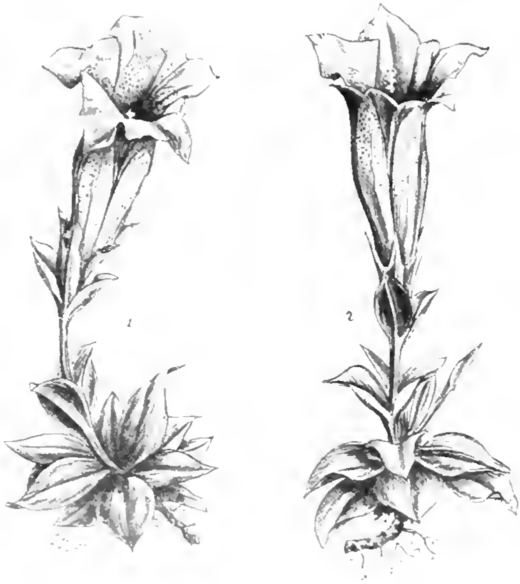

FIG. 54. 1. Gentiana excisa, Presl. Calciphobous. 2. Gentiana acaulis, L. ex p. Calciphilous. Two-thirds of natural size.

The parallel forms are usually confined to their respective soils in th regions where both occur, but are indifferent as regards their choice soil, wherever one of them is absent. Nägeli[3] has ingeniously indicate

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[1] The remarkably great susceptibility of a plant-organism to insignificant external i ence follows from Wettstein's brilliant researches on Gentiana and Euphrasia.

[2] Kerner, l. c.

[3] Nägeli, op. cit.

this dissimilar relation by means of the example of Achillea atrata and A. moschata.

Achillea moschata excludes A. atrata from a silicious soil and is itself excluded by the latter from a calcareous soil. On the other hand, either of them grows equally well in the company of A. Millefolium. Evidently the two first-mentioned plants, as hey are externally extremely alike, make analogous demands on the environment. A. Millefolium, however, which systematically is further removed from either, does not compete with them, because it is dependent on other conditions of existence. f either of the two species be absent, the other becomes indifferent as regards its hoice of soil.

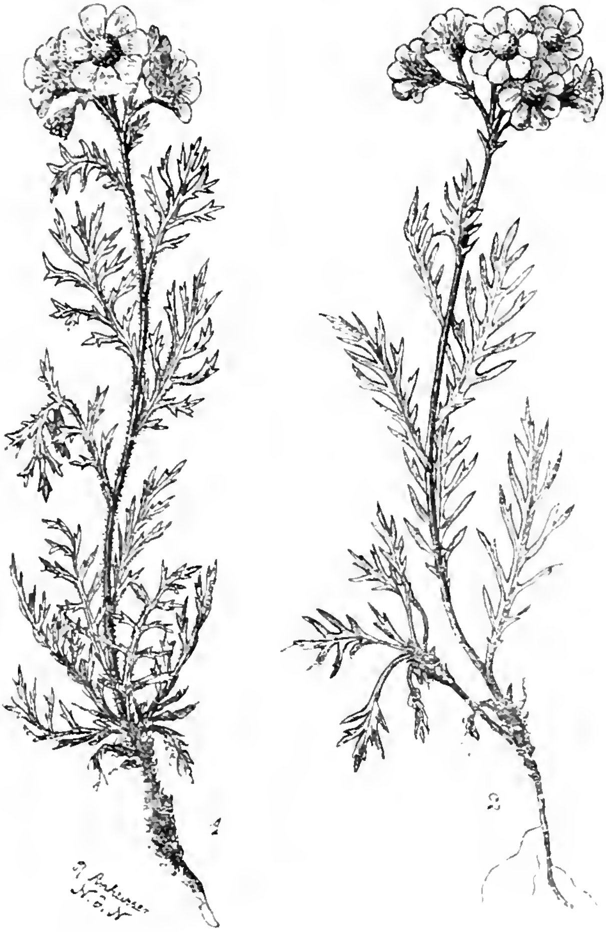

FIG. 55. 1. Achillea atrata. Calciphilous. 2. Achillea moschata. Calciphobous. Natural size.

'In Bernina-Heuthal (Upper Engadine), A. moschata, A. atrata, and A. Millefolium, all abound; A. moschata and A. Millefolium on slate, A. atrata and A. Millefolium on lime. Wherever the slate passes into limestone, A. moschata at once stops and A. atrata begins. Both species are here therefore strictly confined to one soil; and this I have also observed in several places in Bündten, where the two species occur. If one of the species be absent, the other becomes indifferent as regards its choice of soil. A. atrata then inhabits both lime and slate indifferently; the same fact also applies to A. moschata: although, as it appears, this species does not thrive so well on limestone as the other does on slate, yet, besides occurring on the primary mountains, it is also found on pronounced lime formations, along with the usual characteristic vegetation. In Bernina-Heuthal, I found in the midst of the slate that was stocked with A. moschata a large fallen block of limestone with a layer of soil on it hardly an inch thick. A colony of A. moschata had settled on it, as there all competition with A. atrata was excluded.'

8. HUMUS.

i. *THE CHEMISTRY AND PHYSICS OF HUMUS*[1].

Only a few natural soils consist exclusively of mineral matter, only those in fact that are quite devoid of vegetation. As soon as plants have settled on a mineral substratum, even if they be only bacteria, unicellular Algae, or slowly growing lichens, they produce by their death and decomposition a finely grained organic substance, which, by the action of the rain and of underground animals, becomes gradually and closely intermingled with the mineral matter, so as to form dark *earth*, or ordinary soil, which is at once distinguishable by its nearly black colour from purely mineral detritus.

The organic products of decomposition of animals and plants are called *humus*. During the process of humification dead animal and vegetable remains produce by oxidation carbon dioxide and water, the latter however in much greater quantity than the former, so that the residue is much richer in carbon than were the living organisms. If sufficient air be admitted a formation of ammonia and nitric acid takes place at the expense of the proteids; nevertheless the greatest part of the nitrogen remains combined in organic compounds that are decomposed with difficulty. What follows here is chiefly concerned with the universal and important vegetable humus only: animal humus is of mere local importance in determining the distribution of natural vegetation, and will be discussed separately.

As appears from the foregoing, humus is rich in two of the most important constituent elements of plants, carbon and nitrogen, which occur in an inorganic nutrient medium only in a condition of extreme dilution. These nutritive substances, in the form in which they are present in humus however, cannot be utilized by green plants, nor indeed by any of the higher plants. Only certain bacteria and fungi can assimilate them to [illegible] or less extent, or resolve them into simpler compounds. Many

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[1] See especially Ad. Mayer and P. Müller.

hanerogams and ferns have utilized this property of lower plants, and are hus able to absorb indirectly from humus both carbon and nitrogen; in eneral, however, these substances are taken, not from humus, but from he carbon dioxide of the air and from the nitrates of the soil.

Of more general importance than carbon dioxide and nitrogen to most lants are the ash-constituents, which humus contains in a more con- entrated form and in a better state of mechanical subdivision than do the urely mineral deeper layers of the soil. The wealth of humus in useful sh-constituents depends partly on the amount of such matter in the ecomposing plant-parts, and partly on the activity of earthworms, which ring up from below the constituents of the soil, reduce them to a fine tate of division. and mix them with humus in their alimentary canals. If o the above properties of humus be added the power of absorption, we can horoughly understand its beneficial effects on vegetation. However, as ill be shown later on. not all kinds of humus possess these properties, or orm a good substratum for plant-life.

The organic constituents of humus are as yet imperfectly known. Some ave an acid character, and form with alkalis soluble. and with alkaline arths insoluble, dark-coloured compounds. Brown humus-substances are omprehended under the collective name *ulmic acid*, and the blacker ones nder that of *humic acid.* The neutral constituents of humus that are nsoluble in alkalis are termed *humus*, if they are black, and *humin*, if they re brown. A deficient supply of oxygen favours the formation and ccumulation of acid compounds and hence the formation of *acid humus*. hich, in contrast with *mild humus* resulting from an abundant supply of xygen, does not permit the development of a luxuriant vegetation that is ch in species.

Mild humus is usually loose in texture and is then termed *mould.* It is ntimately mixed with mineral constituents, and by the gradual increase of ese it insensibly passes over into the purely mineral subsoil. Mould ccurs on moderately damp fresh soil only, and attains its most complete evelopment in shady forests, where the earthworms pass it continually rough their alimentary canal and eject it in the form of separate pellets ose in texture. The mould in forests actually consists of worm- xcrements, and its excellent qualities are due to this circumstance. The ch aeration of mould leads to the formation of highly oxidized neutral ubstances; acids form only about a sixteenth of its organic substance.

Acid humus is usually matured in the form of *peat.* The latter, in ontrast with mould, forms a cohesive compact crust, which lies superposed n the mineral layers of the soil, without gradually passing over into them. nly the abundant humous acids that are soluble in water penetrate the ineral soil and give to it a dark colour. In opposition to mould, which in iny weather rapidly becomes saturated, peat is only slightly permeable, so that rain-water collects on it in puddles. With persistent rain, however, it becomes full of water like a sponge, but without yielding any water to the underlying mineral soil.

Acid humus arises whenever the supply of oxygen is only slight, namely on soils below stagnant water, but also in dry sunny stations, where earthworms are rare, for these animals would prevent the humus from caking into a solid mass. For the same reason, peat does not contain the minera constituents of the subsoil which are intimately mixed with the humus by the burrowing activity of the organisms inhabiting mould.

Wet peat, or peat in the ordinary sense of the word, is characteristic o moors, dry peat of heaths. The latter may be differentiated from moor peat, as heath peat. Dry peat is also found in forests, as soon as the soil has dried after a clearance of the wood and the worms have died out; in this way the first step is taken towards the conversion of a forest into a heath. Except for the amount of water they contain, the difference between the heath peat and moor peat does not seem to be very noticeable. The elevated and drier parts of moors bear essentially the same vegetation as true heaths on dry soil.

ii. *THE MYCORHIZA.*

Mould and peat are penetrated in all directions by an extraordinary tangle of mycelial threads belonging to various forms of fungi, hitherto rarely identified and appearing to differ from one another in the differen kinds of humus. These fungi can exist not only as parasites but also as saprophytes, and form, as they envelop the roots of the higher plants, the so-called *mycorhiza*, which appears to possess a high significance in the physiological processes of the nutrition of many forest and heath plants it is in fact probable that the fungus acts upon the organic components o the humus and partly transfers them in an assimilable form to the roots.

Mycorhiza was discovered by Kamienski in Monotropa Hypopity (Figs. 56, 57) and in Fagus sylvatica (Fig. 58) and its importance recognized Later, Frank as well as Wahrlich, Johow, Schlicht, Oliver, Groom, Janse and others demonstrated the constant appearance of mycorhiza on many other phanerogams and on pteridophytes, some of them green and some not green, and it was assumed that these plants required the mycorhiza fo their normal existence. The name mycorhiza was invented by Frank.

The fungus of mycorhiza forms either, as a mere epiphyte, a thick coating round the root, which in such cases is devoid of root-hairs, or i lives within the root as an endophyte. In both cases the hyphae are connected with the mycelium ramifying in the soil and belonging in certain established cases to recognized species of fungi. Wahrlich recognized species of Nectria (N. Vandae and N. Goroschankiniana) in the mycorhiza of several orchids, whilst Noack, Reess, and Fisch recognized in Elaphomyce granulatus, and Noack also in species of Geaster, Agaricus, Lactarius and Cortinarius, and in the well-known Agaricus muscarius, the mycorhizal fungi of our forest trees.

The relations between fungus and root are symbiotic, that is to say, useful to both organisms, at least in the case of endophytic fungi, for P. Groom's observations on Thismia lead to the conclusion that the presence of the fungus promotes the elaboration of proteids in the root-cells, and that between both organisms an exchange of nutritive matter occurs, although the nature of this is unknown.

The relations between fungus and root are very simple in epitrophic mycorhizae; n those that are endotrophic, on the contrary, they are often very complicated. As an instance of the latter, the mycorhiza of Thismia Aseroë, which has been studied in detail by P. Groom, may be described somewhat more minutely (Fig. 59). The

FIG. 56. Monotropa Hypopitys. Portion of a young plant. After Kamienski.

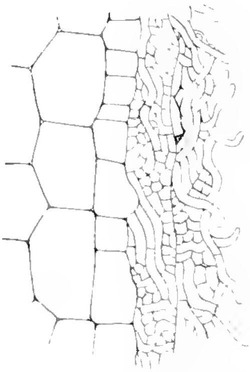

FIG. 57. Monotropa Hypopitys. Epidermis and mycorhiza-fungus. Magnified 450. After Kamienski.

coral-like branching root-system has a fine papillose surface. The thin-walled eripheral tissues free from starch, which the author termed the sheath (*sh.*), are raversed longitudinally by a few fine mycelial hyphae. Within the sheath next ccurs a sharply differentiated layer of cells (*e.c.*), all of which contain swollen yphae, wound round in a kind of coil. These hyphae are externally coated with cytoplasm. Inside the exocortex (*e.c.*) comes the limiting layer (*l.l.*), in the cells f which fine, delicate hyphae here and there dilate into thick vesicles filled with roteids. An inner part of the cortex (mediocortex *m.c.*) is composed of two or hree layers rich in starch and characterized by possessing dead, yellow masses of mycelium in all its cells, except those containing raphides. The endodermis and entral cylinder are free from the fungus.

On entering from the sheath into the deeper lying cells the terminal point of the mycelial thread grows directly towards the nucleus. In the medullary layer of he cortex (mediocortex), where the relations are clearest, the starch of the infected ells is at once dissolved, but reappears on the death of the fungus. The latter however forms, as soon as it comes into contact with the nucleus, a vesicle that i egg-shaped or pear-shaped and becomes filled with cytoplasm and nuclei (Fig. 60 After a time the contents of the vesicle become disorganized and transformed int a yellow, granular mass. The nucleus in the meantime has changed its position i the cell, but the terminal point of the mycelial thread follows it, and, in contact wit it, repeatedly forms fresh vesicles. In the outer region of the cortex the hyphae liv longer and exhibit less connexion with the nucleus or (in the sheath) none at al Groom attributes, without doubt correctly, the growth of the terminal point of th

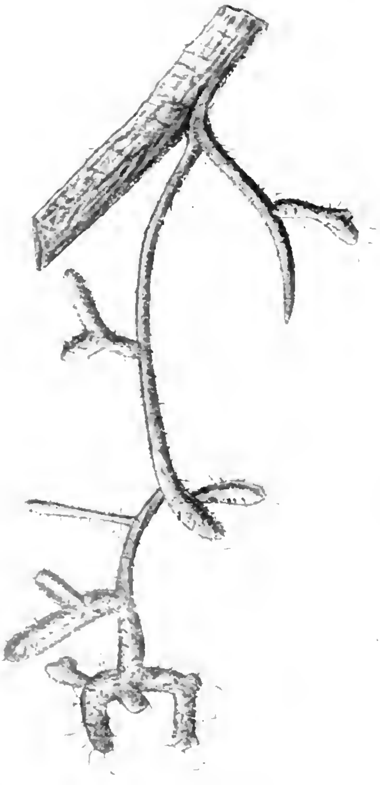

FIG. 58. Fagus sylvatica. Mycorhiza with fungal hyphae. Magnified 9. After Kamienski.

FIG. 59. Thismia Aseroë. Cortex of the myc rhiza. After P. Groom.

hyphae in the direction of the nucleus, to chemotropism. The same thing occur in the case of undoubtedly parasitic fungi, for instance in Puccinia asarina ar Hemileia vastatrix, the fungus of the coffee disease, and is quite general in end trophic mycorhiza. It is clearly due to a product near the nucleus arising chiefly in th inner cortical layers. The swelling is due to vigorous nutrition, for a similar phenomenon also occurs in cultures of fungi in nutritive solutions, if the concentratio of the latter be increased. That the solution of the starch is to be associated with th formation of proteids in the vesicles is obvious from what has been said before.

There can be no doubt that the fungus derives certain nutritive materials from its host. That, conversely, matter passes from the fungus into the cells of the host, is proved at the death of the vesicles, which shrivel up as they give out a liquid. It was not possible to determine what the latter contains in solution, or what is the composition of the granular mass that remains in the dead vesicle and is not utilized by the host.

Most plants provided with a mycorhiza obtain from it, in any case, only a portion of the carbon that they need. Some plants however, especially those growing in deep forest shade, are entirely dependent on the mycorhiza and have lost their chlorophyll. They, like fungi that nourish themselves directly on humus, are termed *saprophytes*. Plants that contain chlorophyll but nevertheless require the organic constituents of humus are *hemisaprophytes*, an intermediate stage between true saprophytes (*holosaprophytes*) and completely autotrophic plants. Saprophytes will be discussed in a future chapter.

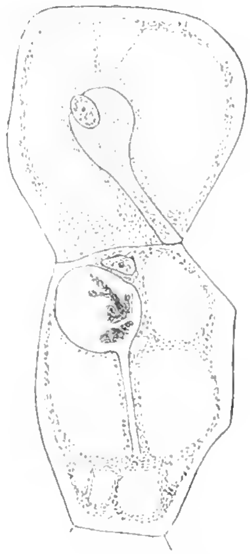

FIG. 60. Thismia Aseroë. Two cells of the mycorhiza. After P. Groom.

iii. *CHEMICAL DIFFERENCES IN HUMUS AND THE RESULTING FLORA.*

The floras of mild and of acid humus are quite dissimilar. Many species may be at once described as characteristic of the one or the other kind of humus; for instance, for mild humus, Asperula odorata, Mercurialis perennis, Milium effusum, Melica uniflora, Stellaria nemorum; for acid humus, Aira flexuosa, Maianthemum bifolium, Melampyrum pratense, and several mosses, such as Hylocomium triquetrum, Polytrichum formosum, Leucobryum. *On the very acid humus of moors the vegetation assumes a decidedly xerophilous character, because the humous acids impede the absorption of water by the roots.*

Mild and acid humus are collective terms for numerous kinds of humus hat vary according to the nature of the decomposing plants. The differences between them are more easily discovered by the fine chemical analysis of plants than by the rough chemical analysis of our laboratories. Each kind of humus has its characteristic species of plants. There are plants depending on the different kinds of humus, as on the mineral onstituents of soils—some confined to one kind of humus, others that are ndifferent. Many species of plants grow only on the humus of coniferous orests; for instance, Goodyera repens and the North American saprophyte Schweinitzia odorata. Monotropa Hypopitys occurs in broad-leaved orests almost exclusively in its glabrous form, in coniferous forests in its hirsute form. Thus we have here a case parallel to that of the calciphilous Gentiana acaulis and its calciphobous ally, Gentiana excisa.

The choice of the substratum goes even further with many humus-plants, especially among the lower cryptogams. Phanerogams and pteridophytes are less exclusive, yet I always found Trichomanes sinuosum widely spread in tropical America and growing exclusively on tree-ferns, and the North American Epidendrum conopseum preferring the bark of magnolias to that of other plants.

Among mosses growing on humus, all intermediate forms are found between those making a promiscuous choice of any kind of humus soil to others showing quite a decided and often highly peculiar exclusiveness. Decaying tree-stems have their characteristic species of mosses, such as Plagiothecium silesiacum and Buxbaumia indusiata, which do not occur on living trunks of trees. The latter have again a rich moss-flora (for instance Leucodon sciuroides, many species of Orthotrichum), the components of which do not appear in other habitats. Most epiphytic mosses are not strict in their choice, although many are limited to definite kinds of trees. Thus Orthotrichum leucomitrium occurs only on conifers, whilst species of Zygodon. and Barbula latifolia, appear on broad-leaved trees only. More strict in their selection are, for instance, Ulota Drummondii, which has been observed only on Pyrus aucuparia; Orthotrichum gymnostomum, which is attached only to Populus tremula; the rare Anacamptodon splachnoides, which hitherto has been found only in cavities on the beech left by fallen boughs. The Splachnaceae almost exclusively frequent animal humus, and are generally very strict in their choice; thus Tayloria splachnoides occurs on decomposing bodies of several animals, and Tetraplodon mnioides on various excrements; Tayloria serrata, on the other hand, only on decomposing human excrement, Tayloria Rudolphiana on the dung of birds of prey as it lies on the boughs of trees, Tetraplodon urceolatus on the dung of sheep, goats, and geese, Splachnum ampullaceum on cow-dung, Splachnum luteum and S. rubrum on that of reindeer.

Saprophytic fungi comport themselves like mosses. Many of them are seen wherever the remains of plants and animals are decaying, others again are confined to definite substrata. Thus species of Marasmius only occur on fallen spruce needles, Antennatula pinophila only on fallen silver-fir needles, Hypoderma Lauri only on fallen bay-leaves, Septoria Menyanthis only on the submerged decomposing leaves of the buckbean, Poronia punctata only on cow-dung, Gymnoascus uncinatus only on decomposing excrement of mice, Ctenomyces serratus only on rotting goose-feathers, Onygena corvina only on the down of birds of prey, Onygena equina only on rotting hoofs.

9. LIVING SUBSTRATA: PARASITES.

Many plants grow purely as epiphytes on living substrata without taking ny material from them. This is however not the case with *parasites*, the node of life and nutrition of which will be described in a later chapter. Iere merely the relations of parasites to the chemical nature of the substratum will be considered.

Plant-parasites occur on animals as well as on plants, but the species are listinct in the two cases. In other respects, parasites, like plants growing n humus, are sometimes very strict, and sometimes less so, in their hoice as regards the chemical nature of the substratum. The common istletoe, Viscum album, occurs both on conifers and on broad-leaved trees, sually, however, in distinct varieties; the typical form with white berries refers broad-leaved trees, a form with yellow little fruits (V. laxum) is, on he other hand, more or less confined to conifers. Loranthus europaeus ttacks oaks and chestnuts; Arceuthobium Oxycedri, in Europe, is onfined to Juniperus Oxycedrus, but in North America to certain species f Pinus.

The different species of Orobanche comport themselves very differently. hus O. minor was found by G. Beck on fifty-eight different species of lants, O. ramosa on thirty-five, whilst many other species of this genus are onfined to certain definite hosts; for example, O. Rapum to Sarothamnus coparius.

Many fungi attack indifferently plants or animals belonging to natural rders wide apart, others have a larger or smaller circle of nearly allied osts, such as Claviceps purpurea on grasses, Cordyceps cinerea on species f Carabus. Others are strictly confined to one species of host, such as eronospora Radii on Pyrethrum inodorum, Laboulbenia Baeri on the ouse-fly.

So far as is known, such exclusive relations are limited to natural nditions. Brefeld succeeded in growing several strictly parasitic fungi as prophytes and Möller in cultivating lichens without Algae, just as it has en found possible to rear in the garden halophytes that in nature are nfined strictly to a richly saline soil.

On the whole, in their choice of a substratum, parasites and saprophytes xhibit differences similar to those among plants that are rooted in a ineral soil, and a comparison between the two classes is very instructive regards the significance of the chemical nature of the substratum. mong the plants that grow on mineral soil we have learned to distinguish me that behave themselves quite indifferently as regards soil, some that ow a more or less decided preference for certain chemically definite kinds soil, and some that appear always dependent on the presence of large quantities of definite mineral substances, such as common salt or carbonat of lime. *Mutatis mutandis*, the same holds good, but with a greate diversity, for plants growing on an organic substratum.

We found in particular among lime-plants the phenomenon, at firs sight puzzling, that one and the same species in different localities mad quite different demands as to the chemical nature of the substratum. Th same phenomenon also occurs in relation to many parasites. The mistleto in many districts attacks only the silver-fir, in others only broad-leave trees. Loranthus europaeus in Bohemia grows only on the oak, in th East on the chestnut also. Puccinia sessilis on Convallaria majalis, P Digraphidis on Polygonatum multiflorum and Maianthemum Convallaria P. Paridis on Paris quadrifolia, are in many regions strictly confined t their usual hosts; in other regions, however, they grow indiscriminatel on Convallaria, Polygonatum, Maianthemum, or Paris, and are thus indifferent as to substratum (Magnus). A similar condition holds good fo many other fungi. There cannot be a doubt but that, as in the case o plants in relation to lime and other mineral salts, here too differences i organization come into play, which differences in turn correspond to dissimilar requirements as regards the conditions of life. Such changes i organization are not always open to ocular demonstration, as in many case they are confined to the most minute structure of the protoplasm and ar beyond the reach of our means of observation. There are, however, specie of rust-fungi that in certain stages of their development agree with on another completely, but in other stages distinctly and constantly differ an are purely 'physiological' species: they can be distinguished from on another by no morphological character, and yet show a decidedly specifi character in that they are connected with different host-plants and lack an power of reciprocal interchange (Eriksson).

SELECT LITERATURE.

1. The Physical Properties of the Soil.

Gain, Ed. I. Action de l'eau du sol sur la végétation. Revue générale de botaniqu Tome VII. 1895.

—— II. Recherches sur le rôle physiologique de l'eau dans la végétation. Annale des sciences naturelles. 7^e^ série. Tome XX. 1895.

Hoffmann, H. Untersuchungen zur Klima- und Bodenkunde mit Rücksicht auf di Vegetation. Botanische Zeitung. Bd. XXIII. 1865. Beilage.

Mayer, Ad. Die Bodenkunde. 4. Auflage. 1895. (Lehrb. der Agriculturchemi Zweiter Theil. 1. Abth.)

Sachs, J. v. Ueber den Einfluss der chemischen und physikalischen Beschaffenhe des Bodens auf die Transpiration der Pflanzen. Landw. Versuchsstatione [illegible] Ges. Abhandl. Bd. I. p. 417.)

Thurmann, J. Essai de phytostatique appliquée à la chaine du Jura. Berne, 1849.

2. The Chemical Properties of the Soil in General.

Burgerstein, A. Einfluss äusserer Bedingungen auf die Transpiration. Wien, 1876.

Schimper, A. F. W. I. Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze. Flora. Jahrg. LXXIII. 1890.

— II. Ueber Schutzmittel des Laubes gegen Transpiration vornehmlich in der Flora Java's. Monatsberichte der Berliner Akademie. Juli 1890.

Stahl, E. Einige Versuche über Transpiration und Assimilation. Botanische Zeitung. Bd. LII. 1894.

Stange, B. Beziehungen zwischen Substratconcentration, Turgor und Wachsthum bei einigen phanerogamen Pflanzen. Botanische Zeitung. Bd. L. 1892.

Vesque, J. De l'influence des matières salines sur l'absorption de l'eau par les racines. Annales des sciences naturelles. 6e série. Tome IX. 1878.

3. Sodium Chloride.

Battandier, A. Quelques mots sur les causes de la localisation des espèces d'une région. Bulletin de la Société botanique de France. Tome XXXIV. 1887.

Brick, C. Beiträge zur Biologie und vergleichenden Anatomie der baltischen Strandgewächse. Schriften der Naturf.-Ges. zu Danzig. Neue Folge. No. 7.

Hansteen, B. Beiträge zur Kenntniss der Eiweissbildung und der Bedingungen der Realisirung dieses Processes im phanerogamen Pflanzenkörper. Berichte der deutschen botanischen Gesellschaft. Bd. XIV. 1896.

Heinrich. Die Zusammensetzung der Asche der oberirdischen Theile von Chrysanthemum segetum. Landw. Annalen des Mecklenburg. Patriot. Vereins. Jahrg. XXIV. 1885.

offmann, H. Ueber Kalk- und Salzpflanzen. Landw. Versuchsstationen. Bd. XIII. 1870.

esage, P. Recherches expérimentales sur les modifications des feuilles chez les plantes maritimes. Revue générale de botanique. Tome II. 1890.

ichter, A. Ueber die Anpassung der Süsswasseralgen an Kochsalzlösungen. Flora. Jahrg. LXXV. 1892.

osenberg, O. Ueber die Transpiration der Halophyten. Oefversigt af Kongl. Svenska Vetenskaps-Akademien Förhandl. Stockholm, 1897.

chimper, A. F. W. I. Ueber Schutzmittel des Laubes gegen Transpiration, vornehmlich in der Flora Java's. Monatsberichte der Berliner Akademie. Juli 1890.

— II. Die indomalayische Strandflora. Botan. Mittheil. aus den Tropen. Heft II. Jena, 1891.

— III. Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze. Flora. Jahrg. LXXIII. 1890.

chultz, A. Die Vegetationsverhältnisse der Umgebung von Halle. Halle, 1888.

ahl, E. Einige Versuche über Transpiration und Assimilation. Botanische Zeitung. Bd. LII. 1894.

4. Other easily Soluble Salts.

nghuhn, F. W. Java, deszelfs gedaante, bekleeding en invendige structuur. German edition by Hasskarl. 1852. Bd. I. p. 453. (Fumaroles.)

ayr, H. Aus den Waldungen Japan's. 1891. p. 27. (Fumaroles.)

chimper, A. F. W. I. Ueber Schutzmittel des Laubes gegen Transpiration, vornehmlich in der Flora Java's. Monatsberichte der Berliner Akademie. 1890. (Fumaroles.)

— II. Die indo-malayische Strandflora. Botan. Mittheil. aus den Tropen. Heft II. Jena, 1891. (Fumaroles.)

— III. Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze. Flora. Jahrg. LXXIII. 1890. (Nitrates.)

5. Serpentine.

Lürssen, Ch. Die Farnpflanzen oder Gefässkryptogamen. Rabenhorst's Kryptogamen-Flora. Bd. III. Leipzig. 1889.

Milde, J. Filices criticae: Asplenium adulterinum. Botanische Zeitung. Bd XXVI. 1868.

Sadebeck, R. I. Ueber Asplenium adulterinum. Verhandl. des botan. Vereins fü die Prov. Brandenburg. Bd. XIII. 1872.

—— II. Ueber die generationsweise fortgesetzten Aussaaten und Culturen de Serpentinformen der Farngattung Asplenium. Berichte über die Sitzunge der Gesellschaft für Botanik in Hamburg. Heft III. 1887. p. 4.

6. Calamine.

Baumann, A. Das Verhalten von Zinksalzen gegen Pflanzen und im Bode Landw. Versuchsstationen. Bd. XXXI. 1885. p. 1.

Hoffmann, H. I. Culturversuche. Botanische Zeitung. Bd. XXXIII. 1875.

—— II. Untersuchungen über Variation. Ibid. Bd. XXXV. 1877.

Sachs, J. v. Handbuch der Experimentalphysiologie der Pflanzen. Leipzig, 186

Wirtgen, Ph. Une petite excursion dans les terrains calaminaires de la Vieil Montagne. Extr. des Bulletins de la Société royale de botanique de Belgiqu Vol. IV. 1865.

7. Calcium Carbonate.

Bonnier, G. I. Quelques observations sur les relations entre la distribution d Phanérogames et la nature chimique du sol. Bulletin de la Société botaniq de France. Tome XXVI. 1879.

—— II. Etudes sur la végétation de la vallée de Chamonix et de la chaîne du Mo Blanc. Revue générale de botanique. Tome I. 1889.

—— III. Remarques sur les différences que présente l'Ononis natrix cultivé s un sol calcaire ou sur un sol sans calcaire. Bulletin de la Société botanique France. Tome XLI. 1894. p. 59.

Boulay, N. Étude sur la distribution géographique des Mousses en France. Par 1877.

Candolle, A. de. Géographie botanique raisonnée. Tome I. 1855. p. 422.

Chatin, Ad. Le Châtaignier. Étude sur les terrains qui conviennent à sa cultu Bulletin de la société botanique de France. Tome XVII. 1870. p. 194.

Christ, H. Das Pflanzenleben der Schweiz. Basel, 1879.

Contejean, C. H. Géographie botanique. 1881.

Drude, O. Ueber die Standortsverhältnisse von Carex humilis Leyss. bei Dresd als Beitrag zur Frage der Bodenstetigkeit. Berichte der deutschen botanisch Gesellschaft. Bd. V. 1887. p. 286.

Fliche, P., et Grandeau, L. I. De l'influence de la composition chimique du sol s la végétation du pin maritime (Pinus Pinaster, Soland). Annales de chimie de physique. 4e série. Tome XXIX. 1873.

—— II. De l'influence de la composition chimique du sol sur la végétation du chât gnier. Ibid. 5e série. Tome II. 1874.

—— III. Recherches chimiques sur les Papilionacées ligneuses. Ibid. 5e sér Tome XVIII. 1879.

—— IV. Influence de la composition minéralogique des roches sur la vég tation. Colonies végétales hétérotopiques. Bulletin de la Société botanic de France. Tome XLI. 1894. p. 41.

Hilgard, E. W. Ueber den Einfluss des Kalkes als Bodenbestandtheil auf die Entwickelungsweise der Pflanzen. Wollny's Forschungen auf dem Gebiete der Agriculturphysik. 1888.

Ivolas, J. Les plantes calcicoles et calcifuges de l'Aveyron. Bulletin de la Société botanique de France. Tome XXXIII. Session extraord. 1886. p. xxxv.

Kerner, A. I. Ueber das sporadische Vorkommen sogenannter Schieferpflanzen im Hochgebirge. Verh. d. K. K. Zoolog.-botanischen Gesellschaft in Wien. Bd. XIII. 1863.

—— II. Natural History of Plants. First English Edition. Vol. II. 1894.

Kohl, G. Ueber Kalk und Kieselsäure in der Pflanze. Marburg, 1889.

Magnin, Ant. La végétation de la région lyonnaise et de la partie moyenne du bassin du Rhône. Lyon, 1886.

Masclef, A. Sur l'adaptation du Pteris aquilina aux sols calcaires. Revue générale de botanique. Tome IV. 1892.

Mohl, H. v. Ueber den Einfluss des Bodens auf die Vertheilung der Alpenpflanzen. Vermischte Schriften botanischen Inhalts. 1845. p. 393.

Nägeli, C. v. Ueber die Bedingungen des Vorkommens von Arten und Varietäten innerhalb ihres Verbreitungsbezirkes. Sitzungsberichte der bayrischen Akademie. Bd. I. 1865. p. 367.

Parisot, L. Sur l'herborisation faite le 21 juillet au Kaiserstuhl. Bulletin de la Société botanique de France. Tome V. 1858.

Pfeffer, W. Bryogeographische Studien a. d. rhätischen Alpen. Chur, 1869.

Planchon, J. E. Végétation spéciale des dolomies. Bulletin de la Société botanique de France. Tome I. 1854.

Pringsheim, N. Über die Entstehung der Kalkincrustationen an Süsswasserpflanzen. Pringsheim's Jahrbücher. Bd. XIX. 1888.

Richard, O. D. Note au sujet des voies romaines. Bulletin de la Société des antiquaires de l'ouest. Poitiers, 1891.

Röthe, C. Ueber das Vorkommen der Herniaria glabra auf Dolomitsand. Ber. des naturhistorischen Vereins in Augsburg. 1869.

Schimper, A. F. W. I. Ueber Kalkoxalatbildung in den Laubblättern. Botanische Zeitung. Bd. XLVI. 1888.

—— II. Zur Frage der Assimilation der Mineralsalze durch die grüne Pflanze. Flora. Jahrg. LXXIII. 1890.

In both these papers the literature relating to the rôle of calcium in plant-life is cited.

Schultz, A. Die Vegetationsverhältnisse der Umgebung von Halle. Halle, 1888.

Sendtner, O. Die Vegetationsverhältnisse Süd-Bayerns. 1854.

Unger, Fr. Ueber den Einfluss des Bodens auf die Verteilung der Gewächse, nachgewiesen in der Vegetation des nordöstlichen Tirols. Wien, 1836.

Vallot, J. Recherches physico-chimiques sur la terre végétale et ses rapports avec la distribution géographique des plantes. Paris, 1883.

Weddell, H. A. I. Remarques sur le rôle du substratum dans la distribution des lichens saxicoles. Annales des sciences naturelles. 6^{e} série. Tome I. 1875. p. 394.

—— II. Sur le rôle du substratum dans la distribution des lichens saxicoles. Comptes rendus de l'Académie des sciences de Paris. Tome LXXVI. 1873.

8. Humus.

Bary, A. de. Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria. English Edition. Oxford, 1887.

Boulay, l'Abbé. Études sur la distribution géographique des Mousses en France. 1877. p. 30.

Burgerstein, Alf. Ueber den Einfluss äusserer Bedingungen auf die Transpiration der Pflanzen. Wien, 1876. (Humus-compounds.)

Christ, H. Das Pflanzenleben der Schweiz. Basel, 1879. p. 186.

Frank, A. B. Ueber die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze. Berichte der deutschen botanischen Gesellschaft Bd. III. 1885.

—— Neue Mittheilungen über die Mycorhiza der Bäume und der Monotropa hypopitys. Ibid.

—— Sind die Wurzelanschwellungen der Erlen und Elaeagnaceen Pilzgallen Ibid. Bd. V. 1887.

—— Ueber neue Mycorhiza-Formen. Ibid.

—— Ueber Ursprung und Schicksal der Salpetersäure in den Pflanzen. Ibid.

—— Ueber die physiologische Bedeutung der Mycorhiza. Ibid. Bd. VI. 1888.

—— Ueber den Einfluss, welchen das Sterilisiren des Erdbodens auf die Pflanzen Entwickelung ausübt. Ibid.

—— Lehrbuch der Botanik. Leipzig, 1892. Bd. I. pp. 260 and 548.

Groom, P. I. On Thismia Aseroë, Beccari, and its Mycorhiza. Annals of Botany Vol. IX. 1895.

—— II. On a new saprophytic Monocotyledon. Ibid.

Janse, J. M. Les endophytes radicaux de quelques plantes javanaises. Annales du jardin botanique de Buitenzorg. Tome XIV. 1896.

Kamienski, Fr. Les organes végétatifs du Monotropa hypopitys. Mémoires de la société nationale des sciences naturelles de Cherbourg. 1882.

Mayer, Ad. Die Bodenkunde. 4. Auflage. 1895.

Müller, P. E. Studien über die natürlichen Humusformen und deren Einwirkung auf Vegetation und Boden. Berlin, 1887.

Noack, Fr. Ueber mykorhizenbildende Pilze. Botanische Zeitung. Bd. XLVII. 1889

Schlicht, A. Beitrag zur Kenntniss der Verbreitung und der Bedeutung der Mykorhizen. Inaug. Dissertation. Berlin, 1889.

Vogel, A. Zur Charakteristik der Hoch- und Wiesenmoore. Sitzungsberichte de Bayrischen Akademie. Bd. I. 1865. p. 104.

Wahrlich, W. Beitrag zur Kenntniss der Orchideenwurzelpilze. Botanisch Zeitung, 1886.

See also the literature cited in this book under
Part II, Chap. II, The Guilds. 3. Saprophytes.
Part III, Sect. II, Chap. VIII, Edaphic Formations in Temperate Zones.

9. Living Substrata: Parasites.

Bary, A. de. Comparative Morphology and Biology of the Fungi, Mycetozoa an Bacteria. English Edition. Oxford, 1887.

Eriksson, J. Der heutige Stand der Getreiderostfrage. Berichte der deutsche botanischen Gesellschaft. Bd. XV. 1897.

Laurent, Em. Influence de la nature du sol sur la dispersion du gui (Viscum album). Bullet. de la société royale de botanique de Belgique. Tome XXIX 1890.

Magnus, P. Die systematische Unterscheidung nächst verwandter parasitische Pilze auf Grund ihres verschiedenen biologischen Verhaltens. Hedwigia Bd. XXXIII. 1894. p. 81.

See also the literature cited in this book under
Part II, Chap. II, The Guilds. 4. Parasites.

CHAPTER VI

ANIMALS

1. **Geographical Distribution of the Arrangements for Pollination.** i. *Orni-hophilous Flowers.* Fritz Müller's and Belt's discovery of humming-bird flowers. Sun-birds as pollinators. Scott-Elliot's observations in South Africa. Ornithophily n New Zealand. Feijoa, a plant with sweet petals. ii. *Entomophilous Flowers.* Different pollinators in lowlands and in mountain ranges. Hermann Müller's observa-ions. Decrease of entomophily in arctic countries. Insular floras and their pollinators. Long-tubed Lepidopteron-flowers characteristic of the tropics. Special adaptations. Yucca and its pollination by moths. Species of Bulbophyllum near Singapore. 2. **Plants and Ants.** i. *Ants as cultivators of Fungi.* Leaf-cutting ants in tropical America. Their nests and fungus-beds. Other ants that cultivate fungi. ii. *Myrmecophily.* Belt's discovery of myrmecophilous plants. Acacia cornigera and A. sphaerocephala. Cecropia Adenopus. Proof of the utility of ants as protectors of plants. Other plants with axial habitations. Plants in which leaves produce the habitations. Extra-floral nectaries.

THE adaptations of plants to the animal kingdom form an extensive nd largely investigated domain of oecology; the geographical and opographical aspects of the question have been, however, only slightly onsidered, although there can be no doubt, and it has been actually proved in certain cases, that differences in the animal world cause differ-nces in the plant world. In the matter of the pollinating mechanisms nd the relations between plants and ants a very promising start has uite recently been made in the direction just mentioned. As regards he mechanism for the dispersal of seed, a connexion between the istribution of certain animals and plants has been affirmed in certain ndividual cases, but the question of the relations of size, form, taste, olour, and other properties of fruits, to the requirements of the animals hat feed on them has not yet been touched upon. The multifarious rotective means of plants against destruction by animals, so far as they nay characterize districts and their separate formations, have been at best pproached quite hypothetically, except in the case of ants: and the henomena regarding them have hitherto only exceptionally formed the ubject of serious scientific inquiry. Stahl's admirable work on 'Plants nd Snails[1]' will, it is hoped, stimulate further research, which, if attention e paid to geographical questions, will certainly lead to valuable results.

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[1] Pflanzen und Schnecken, Jena, 1888.

1. GEOGRAPHICAL DISTRIBUTION OF THE ARRANGEMENTS FOR POLLINATION.

By the investigations of K. Sprengel and Darwin, which have been so well supplemented by those of Fritz and Hermann Müller, Delpino, Hildebrand, and many others, it has been definitely proved that many flowers require for their pollination the assistance of certain animals, sometimes insects, more rarely birds, and that they owe many of their peculiarities to this circumstance.

Numerous flowers are robbed and pollinated by the most varied visitors, as their pollen and nectar are offered freely to all, or are easily accessible. Other flowers are, in a greater or less degree, adapted to certain definite visitors, either because their allurements presuppose characteristic tastes, or the access to their nectar is only possible to visitors possessed of a certain bodily shape or of certain faculties. When adaptations of the latter kind are connected with animal forms of restricted distribution, the presence or absence of such adaptations is characteristic of the vegetation of definite districts.

i. *ORNITHOPHILOUS FLOWERS.*

The greatest phytogeographical interest, at least from the present point of view of our knowledge, is attached to the adaptations of flowers to pollination by birds, because birds that visit flowers are restricted to certain definite districts. Chiefly three classes of birds come thus under consideration—humming-birds (Trochilidae), sun-birds (Nectariniidae), and honey-suckers (Meliphagidae), although individual birds of other families also play the part of pollinators.

Humming-birds are restricted to America. Only in the fantasy of certain flower-biologists are they ever seen swarming round flowers in Africa and Asia. Their importance as pollinators was first hypothetically mentioned by Delpino, but first proved in 1870 by Fritz Müller, who observed humming-birds as pollinators on species of Combretum, Manettia, and Passiflora, in Santa Catharina. Belt then wrote[1], as a result of careful observations in Nicaragua, the first complete descriptions of humming-bird flowers.

> 'Higher up the valley more trees were left standing, and amongst these small flocks of other birds might often be found, one green with red head (Calliste laviniae, Cass.); another shining green, with black head (Chlorophanes guatema-[illegible]) and a third, beautiful black, blue and yellow, with a yellow head

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[1] Belt, I, p. 128.

Calliste larvata, Du Bus.). These and many others were certain to be found vhere the climbing Marcgravia umbellata expanded its curious flowers (Fig. 1). The flowers of this lofty climber are disposed in a circle, hanging downvards, like an inverted candelabrum. From the centre of the circle of flowers s suspended a number of pitcher-like vessels, which, when the flowers expand, n February and March, are filled with a sweetish liquid. This liquid attracts nsects, and the insects numerous insectivorous birds, including the species I ave mentioned and many kinds of humming-birds. The flowers are so disposed, vith the stamens hanging downwards, that the birds, to get at the pitchers, must rush against them, and thus convey the pollen from one plant to another. A econd species of Marcgravia, that I found in the woods around Santo Domingo, as the pitchers placed close to the pedicels of the flowers, so that the birds must pproach them from bove; and in this pecies the flowers re turned upwards, nd the pollen is rushed off by the reasts of the birds.' he ornithophily of a ecies of Erythrina as also established y Belt: . . . 'Many owers, like the Marcavia, are specially dapted to secure the d of small birds, parularly humming-rds, for this purse. Amongst these, e "palosabre," a ecies of Erythrina, small tree, bearing d flowers, that ew in this valley, ar the brook, ten drew my attention. The tree blooms in February, and is at the ne leafless, so that the large red flowers are seen from a great distance. ich flower consists of a single long, rather fleshy petal, doubled over, flattened, d closed, excepting a small opening on one edge, where the stamens protrude. ly minute insects can find access to the flower, which secretes at the base a ney-like fluid. Two long-billed humming-birds frequent it; one (Heliomaster llidiceps, Gould), which I have already mentioned, is rather rare; the other haethornis longirostris, De Latt.) might be seen at any time when the tree was bloom, by watching near it for a few minutes.'

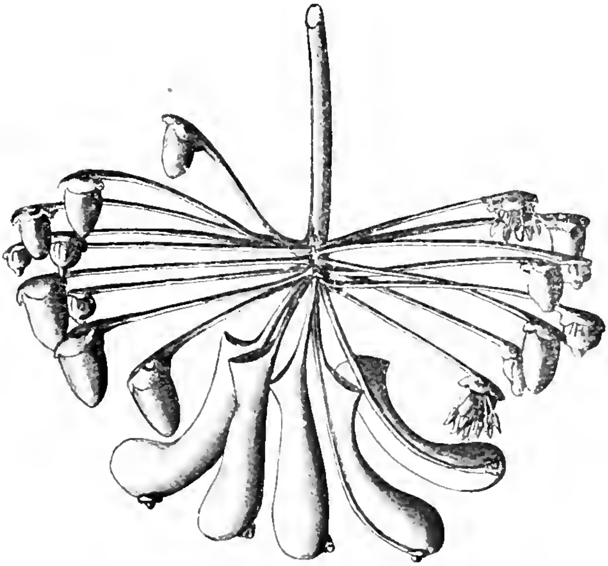

FIG. 61. Marcgravia umbellata. Inflorescence adapted for pollination by humming-birds. Natural size. After Flora Brasiliensis.

Since Belt's classical description and the unfortunately very short communications of F. Müller, the knowledge of humming-bird flowers has not made any considerable progress. for the surmises of severa biologists formed far away from the home of humming-birds cannot be considered as such. The share taken by humming-birds in causing the peculiarities of many American flowers can be ascertained only by carefu and critical investigations on the spot. Undoubtedly these brilliantly coloured pollinators show a preference for red, especially for fiery red colours ; in regions where humming-birds abound, for instance the Antilles. I have rarely seen a woody plant resplendent in the sun with the beauty of its red flowers without also being able to detect, with a little patience, humming-birds on it. I vividly remember having seen, in Trinidad. Norantea guianensis resplendent with scarlet nectaries and with humming-birds swarming round it. I have even observed these visitors on the peculiar. large, deep carmine flowers of Couroupita guianensis In the garden of a house on the coast of Massachusetts, where I lived in the summer, every day I could see the single indigenous species of humming-bird (Trochilus colubris) frequenting the deep carmine flowers of a shrub of Weigela. This preference for red does not, however exclude visits to flowers that are differently coloured ; for the flowers of the species of Marcgravia that I know are of a dull brownish colour.

Kerner endeavours to establish an essential connexion between, on the on hand, the wealth of the American flora in plants with red blossoms, and on th other, the presence of humming-birds. But what is the nature of this wealth Certainly an uninitiated person landing at a tropical American port and seein the "Flame of the Forest" (Poinciana regia) in a blaze of blossom would, afte a well-known example, be inclined to conclude that in tropical America th trees have red flowers. But this most brilliant of all red-flowered trees is East Indian origin, as are many other plants which make a scarlet display flowers and are commonly cultivated in warm countries as ornamental plant I did not receive the impression that the red colour is more prominent in th American than in the Malayan flora.

Since sun-birds, which live in the greatest part of Africa, in tropical Asia, ar in Australia, have also proved to be flower-pollinators and have a similar preferen for red tints, the question at any rate may be asked, whether the actually great wealth in bright red flowers and bracts, that distinguishes the warm zone fro the north temperate zone, is connected with ornithophily. To the flowers th are so distinguished belong, in America, among others, those of numero Bromeliaceae. especially species of Aechmea and Vriesea ; in the Malay Archipelag the Zingiberaceae. I have never seen any birds close to these flowers. Th Bromeliaceae with coloured bracts. so far as I have seen them in their nati habitats. live only in shady places. where the sun-loving humming-birds a seldom seen, and the Malayan Zingiberaceae do not appear outside the deepe forest shade. where sun-birds would be sought for in vain.

A rôle quite similar to that of humming-birds in the New World is layed by the Nectariniidae, or *sun-birds*, in the warm zone of the Old Vorld, but only in tropical and Southern Africa do they appear in comparable number of species and individuals. The relations of sunirds to flowers were investigated in South Africa by Scott-Elliot, whose xcellent works have first opened out for us a closer insight into the tructure of ornithophilous flowers. The South African sun-birds, accordig to Scott-Elliot, are excellent pollinators, since they, like bees, confine hemselves to the flowers of one species.

Nectarinia chalybea, N. bicollaris, and Promerops caper are the most important pecies near Cape Town; Promerops Gurneyi replaces P. caper in the eastern art of Cape Colony and in Natal; Nectarinia famosa lives from December till pril in the Karroo, at other times in the districts of Knysna and East ondon.

Like humming-birds, the South African sun-birds also show a preference r red flowers, and indeed a certain red tint, which appears in the reast feathers of several species of these birds, also characterizes everal ornithophilous flowers. Labiates, species of Aloe, Irideae, and eguminosae assume this otherwise rare floral tint, when they are adapted pollination by sun-birds. Characteristic features of the ornithophilous owers of South Africa are also, in many cases, a brushlike polyandrous ndroecium and a protruding style. Similar features are observable also humming-bird flowers, for example in those of Marcgraviaceae and f Couroupita.

To ornithophilous flowers moreover belong many species of Protea, hose large capitulate inflorescences are surrounded by rigid bracts at e base of which the honey accumulates; the birds sit on the edge the cups and rub the protruding style that is covered with pollen ig. 62). Many of the Cape species of Erica are also adapted for ollination by birds, as well as many Leguminosae, such as Erythrina ffra, which possibly has no other visitors than sun-birds. The banana Natal, and Ravenala madagascariensis in its native home, are mainly, t not exclusively, ornithophilous.

The most remarkable of the South African ornithophilous floral echanisms occurs in Strelitzia reginae (Fig. 63), which is frequently ltivated in our greenhouses. Its three external perianth-leaves are a bright orange colour; of the three inner ones, one is differentiated a large azure-blue arrow-shaped labellum, while the two others are nall and form an archway over the entrance to the nectar-cavity. groove traced along the labellum encloses the stamens and the style, e tip of which, with the stigma, projects freely. The bird hovers near e edge of the labellum and sucks the nectar which is under the archway.

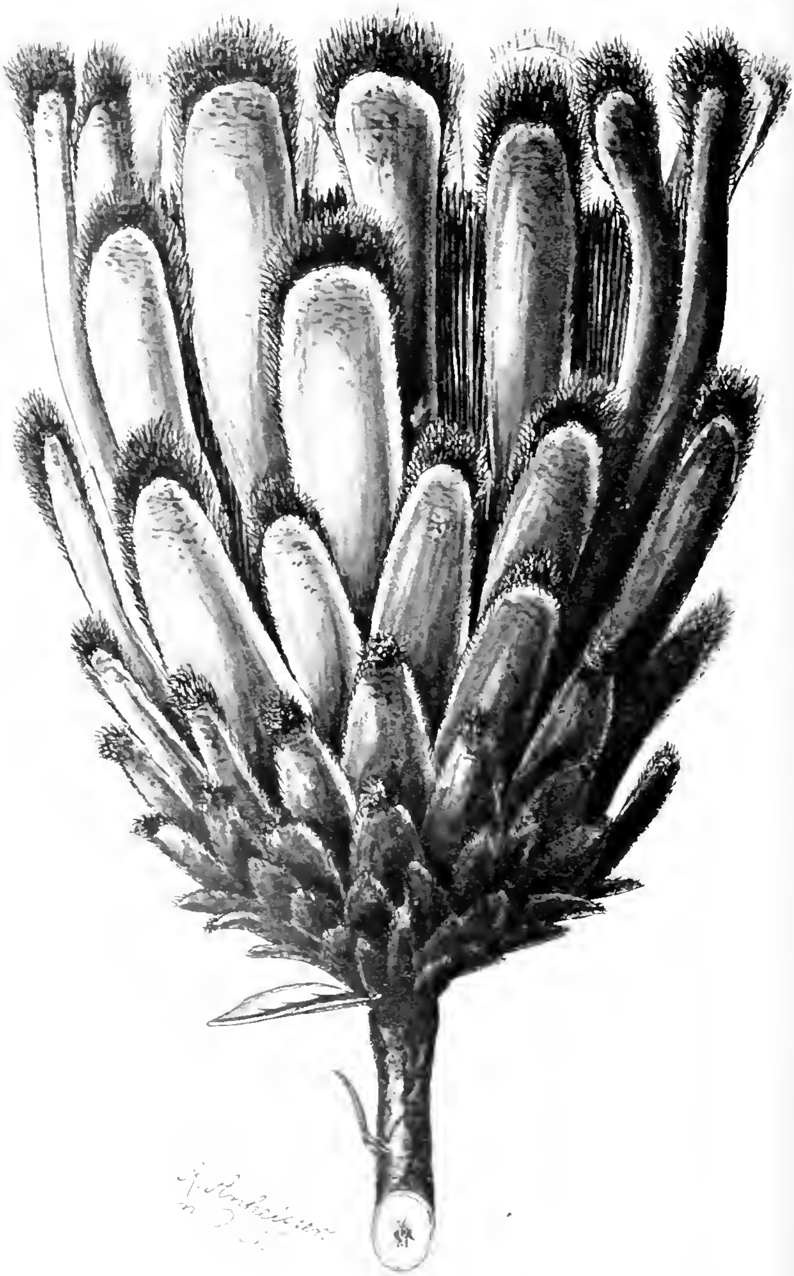

FIG. 62. Protea speciosa, Linn. Capitulum. Pollination by sun-birds. Natural size.

hus rubbing first the stigma and then the stamens. The beautiful colours of the flower fully correspond to those of its pollinator, Nectarinia Afra.

In New Zealand also pollination by birds has been observed, especially by Thomson, in Clianthus puniceus, Sophora tomentosa, Metrosideros ucida, Fuchsia exorticata, Loranthus Colensoi, Dracophylum longifolium, Phormium tenax. These flowers are in part red-coloured.

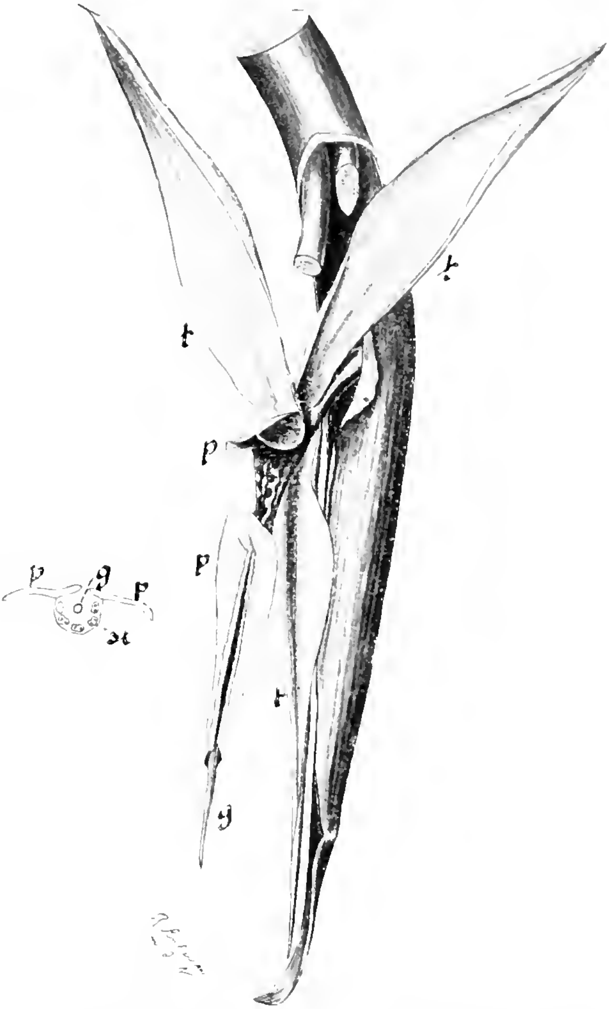

Fig. 63. Strelitzia reginae. A South African sun-bird flower. *t* sepals, *p* petals, *g* style and stigma, *st* stamens Two-thirds of natural size.

Adaptations to ther families of birds as been proved in he case of one plant nly, namely Feijoa Schenckiana (Fig. 64), n arborescent myraceous plant, which Fritz Müller discoverd in the table-land of Santa Catharina and lanted in his garden t Blumenau, where I ad an opportunity of seeing it in blossom. he structure of the ower has been excellently described by Fritz Müller. Highly eculiar are the four now-white petals, hich are rolled inards so that only a arrow slit remains sible when looking om above or somehat from the side. hese petals are fleshy, juicy, and sweet to the taste. As with most nithophilous flowers, the stamens also are of a beautiful red colour, umerous, like a stiff brush, and exceeded in length by the style. The nly pollinator that has been as yet recognized with any certainty is a rather large black bird, unfortunately undetermined, which eats th petals greedily.

ii *ENTOMOPHILOUS FLOWERS.*

The number of flowers adapted for pollination by insects is far greate than that of flowers adapted for pollination by birds, even in place where there are excellent pollinator among the bird Whilst however ornithophily shows a restricted range o distribution, entomophily has been prove to exist in all flora even up to the limit of phanerogamic vegetation. Only thre classes of insects ar specially active a pollinating agent Diptera, Lepidopter and Hymenopter whereas other insect are either of no importance or of merel subsidiary importanc in this respect, an appear to have calle forth no speciall adapted form of flowers. The three mos important groups o pollinating agents ar however presen wherever flowers exis and have everywher caused adaptation through natural selection; but their relative numbers are often ver unequal, and this inequality repeats itself in the relative number o flowers specially adapted for pollination by Diptera, Lepidoptera, an Hymenoptera respectively. A comparison between cold, temperate, an warm districts, or between islands and continents, is often very instructiv in this respect.

FIG. 64. Feijoa Schenckiana. An ornithophilous myrtaceous plant from Santa Catharina, Brazil. Natural size.

The high regions of the Alps are indeed poorer in insects than the urrounding lowlands; yet, as Hermann Müller has shown, flowers are ot less frequently visited by insects there than in the plains. More nportant than the reduced total number of insects is the quite altered umerical relation among the different groups. Thus, according to Iermann Müller, Apidae, except humble-bees, fall off rapidly in numbers s the altitude increases. Lepidoptera, on the contrary, show a considerble increase. Accordingly bee-flowers decrease and lepidopteron-flowers icrease. The latter, according to Loew, number in the Alps 53 species, ut only 36 in the Westphalian lowlands.

Many genera are represented in the plains by bee-flowers, in the Alps y lepidopteron-flowers; for example, Gentiana, Rhinanthus, Viola. One nd the same species may even xhibit corresponding variations. The owers of Viola tricolor (Fig. 65, 2) e short-spurred in the plains, correponding to the short proboscis of ie bees, their pollinators; the variety pestris is long-spurred, corresponding the long proboscis of Lepidoptera. he purely alpine Viola calcarata is long-spurred lepidopteron-flowers 'ig. 65, 1). Primula farinosa, accordg to Hermann Müller, has in the ains, where its pollinators are bees, considerably wider entrance to its ower than it has on alpine heights. here it is practically visited by epidoptera only.

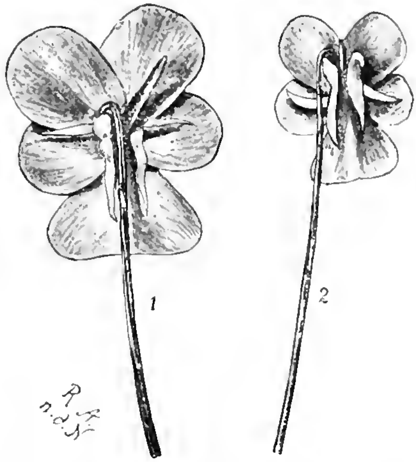

Fig. 65. 1. Viola calcarata. Lepidopteron-flower; long-spurred. 2. Viola tricolor. Bee-flower; short-spurred. Natural size.

The Pyrenees are poorer in Lepiptera than are the Alps, but on the other hand are richer in insects at have not produced through natural selection definite forms of flowers; pidopteron-flowers are accordingly feebly represented (MacLeod).

The Norwegian plateau is poor in insects owing to the shortness and etness of the summer; adaptations for cross-pollination have therefore ndergone a considerable reduction.

Of the 76 alpine and arctic species of the Dovrefjeld, according to a compilan by Loew, there are 2 anemophilous species (Oxyria digyna and Thalictrum pinum), whilst the 74 entomophilous species exhibit the following arrangements: lf-pollination is invariably or usually prevented in 12 species = 16·2 %; self-llination as well as cross-pollination occurs in 40 species = 54 %; self-pollination regular or easily accomplished in 22 species = 29·7 %. In comparison with the ps of Central Europe the alpine plants of Norway show a distinct falling off in allogamous flower-mechanisms (about 10 %), as well as a much more considerable increase in autogamy (about 15 %).

The conditions of pollination in *extreme arctic* countries have bee investigated in Greenland by Warming. Insect-visits appeared to b very rare. Anemophily and autogamy are correspondingly strongl and entomophily is weakly developed. Many flowers that are markedl entomophilous elsewhere show a strong tendency to self-pollination; fo example, those of Mertensia maritima, the flowers of which are smalle in Greenland than in Scandinavia, of Azalea procumbens, Vacciniur Vitis-Idaea var. pumila, Bartsia alpina, Thymus Serpyllum, Menyanthe trifoliata, Pyrola grandiflora. In spite of the scarcity of insects, th allurements are not more strongly marked than when a rich insec fauna exists, although this is contrary to an opinion that has bee repeatedly expressed.

Vegetative multiplication is strongly developed in Greenland, especially plants in which self-pollination takes place with difficulty or to a slight exten 'In Greenland, which is poor in insects, the more entomophilous a species ma be, the more it adapts itself to multiplication by vegetative means, where autogamous plants can dispense with this kind of propagation, and actually dispense with it' (Warming).

The conditions of pollination have often been cited in explanation the peculiarities of *insular floras*. Wallace, especially, has tried to conne the presence, absence, or rarity of brightly coloured flowers on islan with the fauna. Thus on the islands of the eastern part of the Sou Pacific Ocean, for example in Tahiti, insects, especially Lepidoptera a bees, are rare: to this circumstance the poverty of the local flora entomophilous flowers, especially in brightly coloured ones, and t prevalence of ferns have been ascribed. On the western islands, f example in Fiji, butterflies are more numerous and have produc through selection a greater number of brightly coloured flowers. T flowers of the Galapagos have such inconspicuous flowers, that Darw could only after a long time convince himself that they nearly blossomed during his visit. As a matter of fact small Diptera a Hymenoptera are the only representatives of the insect-world on the islands.

Such tentative explanations are certainly interesting and suggestive; b yet it need hardly be stated, that the above peculiarities are explicable, merely by the conditions of pollination, but by taking into considerati also historical and climatic factors. Moreover, Wallace's views chie rest on the incomplete information and collections of other biologi whose investigations scarcely lay in this direction, and they have alrea been refuted in many very important cases. Thus Wallace has describ e New Zealand flora as consisting of almost exclusively inconspicuous, eenish, scentless flowers, and he connected the supposed absence of ightly coloured or scented flowers with the supposed rarity of insects. ctually however neither beautifully coloured flowers, nor insects with ell-developed senses of colour and smell, are so rare in New Zealand Wallace assumed.

Of 433 flowering plants of New Zealand, according to G. M. Thomson, hardly lf (49 %) have inconspicuous flowers, and 22 % are scented. Over 23 % of the species e adapted for cross-pollination by insects, 48 % are fertile when self-pollinated, d 29 % are anemophilous. Diptera are here the most important pollinators; e inconspicuous entomophilous flowers are hardly ever, if at all, visited by other ects. In addition many of the numerous beetles (about 1,300 species) take rt in pollination. Among Lepidoptera the numerous Noctuidae are of greater portance than the few butterflies (18 species). There are only 10 species of es. Finally, birds are the chief or exclusive pollinators of many large flowers. e sole inference to be drawn from this description is that the relatively large mber of inconspicuous flowers possibly may be connected with the predominance Diptera.

Whilst most insular floras are remarkable for their poverty in plants th beautiful flowers, the small archipelago of Juan Fernandez, on the ntrary, is distinguished by the splendour of its flower-tints; frequently e flowers of indigenous species are even more conspicuous than those allied continental species. According to Wallace, the beautiful colours of e flowers have been induced through selection by two endemic species of mming-birds. Johow, who was able to study on the spot the oecology the vegetation of Juan Fernandez, considers as highly probable the llination of many species by humming-birds, for instance Rhaphithamnus, callonia, Myrceugenia fernandeziana; he however states, on the other nd, that the scarcity of insects is not nearly so great as Wallace pears to have assumed. Thus, various Lepidoptera are extraordinarily merous, and Diptera were observed by Johow on the flowers of ndroseris, Robinsonia, and Eryngium bupleuroides amongst others. allace's view, although generally adopted, should not command scientific ceptation until it has been confirmed by observations made on the spot. Only careful and prolonged observations will be able to demonstrate e significance of the pollination of flowers in regard to the composition d physiognomy of insular floras. In the case of some islands of the rth Sea, near the coast, observations have recently been made by hrens, Verhoeff, Alfken, and Knuth, from which there is a promise useful results. These islands indeed have no indigenous forms, and , in many respects, less interesting than oceanic islands; but their ent formation, their proximity to the continent, and the obvious origin their flora and fauna, appear to fit them for explaining many differences between insular and continental conditions of life, and for paving the wa towards an explanation of the more complex relations that affect ocean islands. As on oceanic islands, so also on coast-islands, the relative numb of entomophilous species is smaller than on continents: the mere separa tion of the coast-island from its adjacent mainland has consequentl caused the disappearance of a portion of these species. At the sam time, a reduced number of insects is also noticeable. Both phenomen are to be attributed to the strong winds, which on the one hand lesse the number of insects and the species of plants associated with the, and on the other hand favour anemophilous flowers[1].

FIG. 66. Angraecum eburneum, Thouars, in its native habitat. Seychelles. To the right zingiberaceous plant. From a photograph by Brauer.

Up to the present time observations on the pollination of flowe, with few exceptions, have been made only in temperate regions; in t tropics, only a few and generally fragmentary observations have be recorded, although many tropical forms of flowers appear to be adapt to quite definite pollinators. From this point of view it is only necess

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[1] See p. 79.

o mention orchids. The beauty and
cent of many tropical Lepidoptera
lenote correspondingly developed
enses of colour and smell, and the
irge blue Morphos of South America
nd the brilliant bird-like Malayan
)rnithoptera are very common in
heir native countries. But some
dditional characteristics of many
ropical Lepidoptera may be con-
idered here. Thus many tropical
owers have enormously long tubes
Fig. 66), at the base of which there
; nectar, which can be reached only
y moths with a correspondingly
ng proboscis. The longest struc-
ures of this kind are the spur-like
ockets of the labellum of Macro-
lectrum sesquipedale, Pfitzer, a
Iadagascar orchid, which are five
ecimeters long (Fig. 67). Some
opical Rubiaceae cultivated in the
otanic garden at Buitenzorg at-
acted my attention by the unusual
ngth of their corolla-tubes (Fig.
8); moths with a proboscis suffi-
ently long to be able to suck the
ectar that is at their bases do not
ccur in Europe, and possibly not
any part of the north temperate
ne.

Macroplectrum sesquipedale may
one of these species whose very
stricted geographical distribution
connected with that of a genus
species of insect that pollinates
em. An indubitable case of this
ture is exhibited by several North
merican species of Yucca, which
e exclusively pollinated by moths
the genus Pronuba. Thus Yucca
amentosa, which is frequently grown
our gardens but always remains

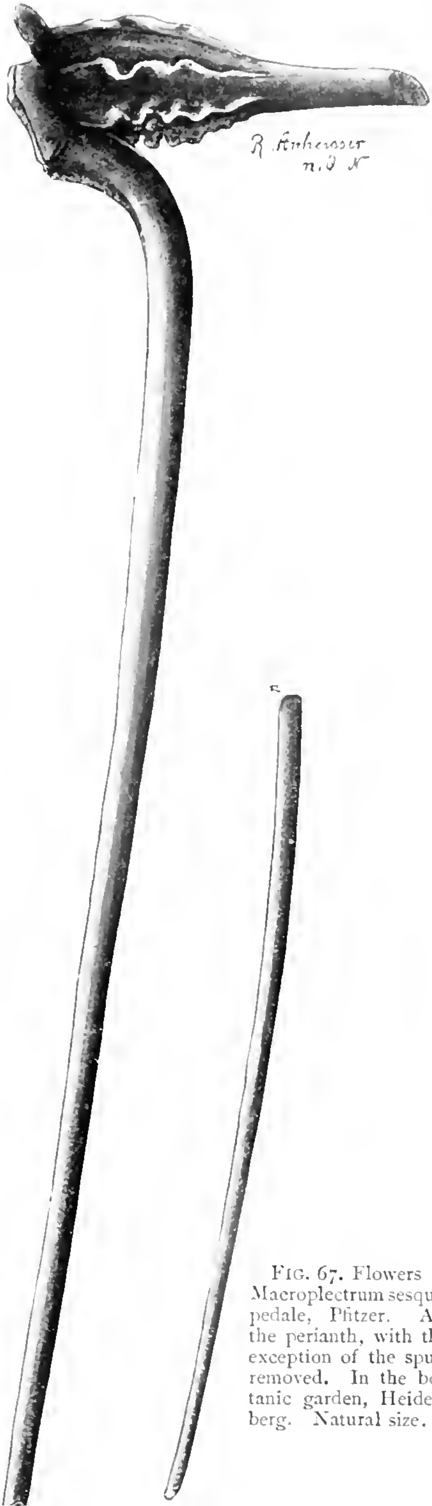

FIG. 67. Flowers of Macroplectrum sesquipedale, Pfitzer. All the perianth, with the exception of the spur, removed. In the botanic garden, Heidelberg. Natural size.

FIG. 68. Tropical rubiaceous moth-flowers with long corolla tubes. 1. Exostemma floribundum, Röm. et Schult. 2. Posoqueria hirsuta. 3. Oxyanthus hirsutus. In the Buitenzorg botanic garden. Natural size.

terile, depends on Pronuba yuccasella for its fertilization (Fig. 69). As he insect is just as dependent on the Yucca for its multiplication, it is lifficult to say which of the two organisms determines the geographical listribution of the other.

The process of pollination in the Yucca is extremely peculiar. The moth lays s eggs in the ovary, in which the larvae have to develop at the expense o he young seeds. In order to render the development of the seeds possible, the oth effects pollination by introducing pollen into the stigma. Since many seeds e produced and only a few larvae, both organisms profit equally. Other species Yucca are pollinated by other species of Pronuba; for example, Yucca Whipplei California by Pronuba maculata, Yucca brevifolia in the Mohave desert by onuba synthetica.

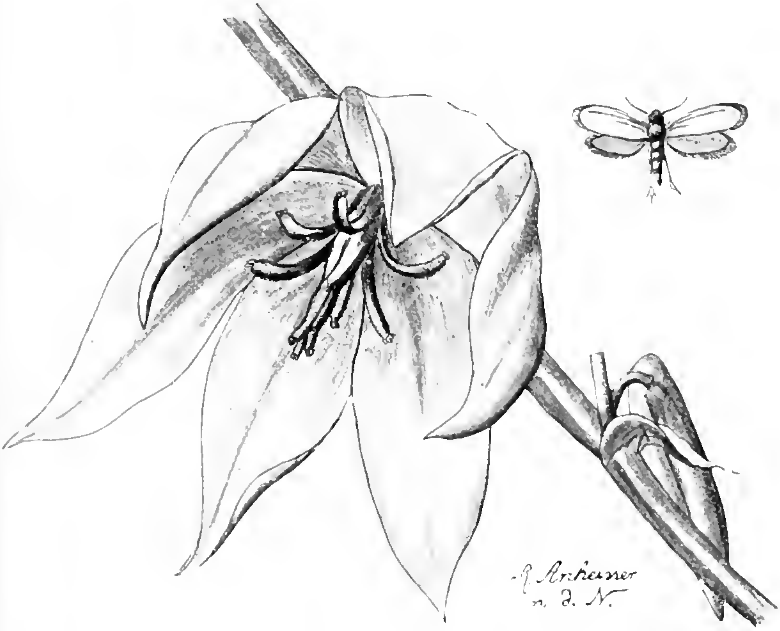

FIG. 69. Yucca filamentosa flower and (after Kerner) the moth (Pronuba yuccasella). Natural size.

The dependence of certain plants on their pollinators is also strikingly hibited in red clover. This plant is pollinated exclusively by humble-es. In New Zealand there are no humble-bees, and red clover therefore mains sterile. In recent times, therefore, humble-bees have been im-rted to New Zealand in order that pollination and consequent seed-mation may take place[1].

Further observations, especially in any countries that have remained

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[1] Belt, II.

as much as possible unchanged, will without doubt in numerous cases prove the connexion between the occurrence of certain definite forms of insects and the flowers specially adapted to them. Interesting in this respect is the fact, established by Ridley, that species of Bulbophyllum near Singapore are adapted for pollination by a certain fly with a very specialized taste, and that, of the orchids that are not indigenous, only Dendrobium superbum is visited by this fly.

2. PLANTS AND ANTS.

Ants in the temperate zones play an unimportant part in the economy of nature, but in the tropics a leading part. They are the most numerous and the most industrious representatives of the tropical insect-world. They abound everywhere. Untiring in their search for food, and usually quite fearless, they are ever ready for attack, in which they employ either their sharp jaws or poisonous stings. In the eastern part of the tropics they do but little harm to vegetation, for, as in temperate countries, they are for the most part satisfied with the dead parts of plants or with sweet exudations from the nectaries on leaves, to which subject further reference will be made. In tropical America, however, the so-called leaf-cutters, or parasol-ants, of the genus Atta may be reckoned as the most dangerous foes to vegetation.

i. *ANTS AS CULTIVATORS OF FUNGI.*

The foraging expeditions of parasol-ants in tropical America are well known to every traveller, and have frequently been described. Straight across the forest path moves a green stream—travelling pieces of leaf, each as big as a farthing and borne upright on the head of ar ant. In some species, large-headed soldiers without any load accompany the procession. The pieces of leaf come from a plant on which the bold little creatures may be easily observed at work. A piece is cu from the margin of a leaf, in a few minutes, by their shear-like mandible and placed on their heads by a kind of jerking movement. Thus laden the ant follows the homebound troops (Figs. 70–72).

The attacked plant is frequently, though not always, abandoned onl after all the foliage, except the hard ribs and petioles, has been carrie away. It is remarkable that parasol-ants so frequently bring their boot from a great distance, although suitable plants are near at hand; Bel frequently found them engaged half a mile from their nest. This wa probably due to the fact that, as Alf. Möller proved, they reject an select the same species of plant in turns; a fact that seems explicabl only upon the assumption that it relates to the preparation of a certai mixture or to the replacing of components of a mixture that have becom

FIG. 70. Cut pieces of Cuphea leaves severed in four or five minutes by Atta discigera. Natural size. After Alf. Möller.

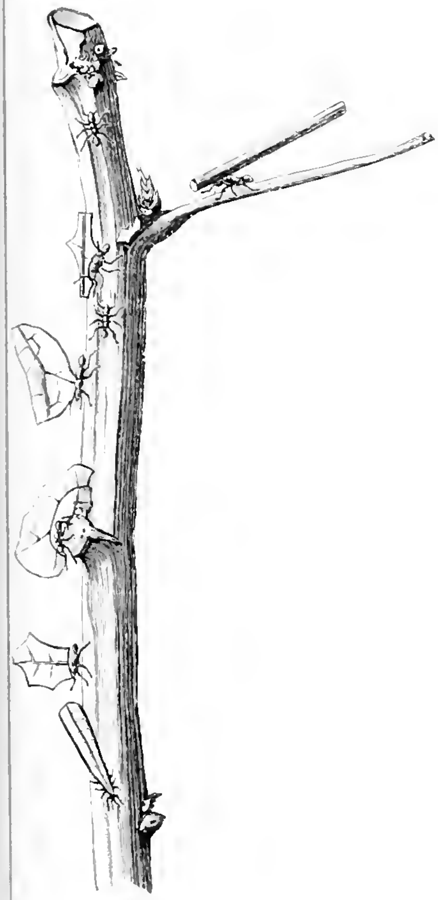

FIG. 71. Atta discigera descending a plundered Aipim plant with severed pieces. Natural size. After Alf. Möller.

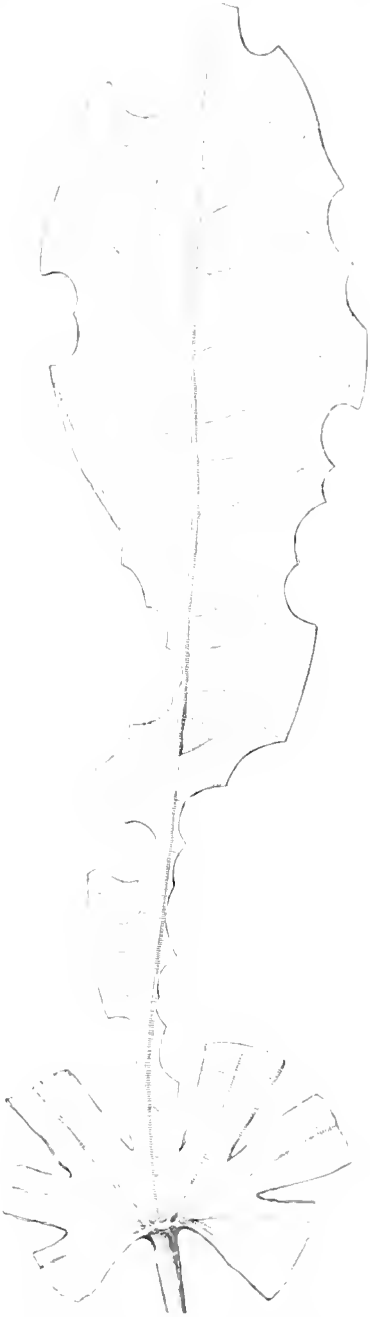

FIG. 72. A leaf of the Aipim plant on which Atta discigera was engaged. The whole leaf would have been eventually reduced to the same condition as on the right hand near the base of the midrib. Natural size. After Alf. Möller.

unserviceable. Not only leaves, but also flowers, fruits, and seeds, o portions of them, are carried home.

The parasol-ants disappear with their booty through the entrance-hole to their nest, which lies either in a shallow natural cavity, as in the cas of the very carefully investigated Atta discigera and A. Hystrix of Sout Brazil, or is dug in the ground, as in the case of Atta coronata an probably of most species. What becomes of the pieces of leaves tha are brought home in such large quantities has until recently remaine an unsolved problem. Bates considered that they were used for linin walls; MacCook thought they were for the preparation of a kind o paper for internal constructions; Belt, however, advanced the darin hypothesis that the ants cultivated fungi on the decomposing masse of leaves. The sagacious 'Naturalist in Nicaragua' had, as usual, hi on the right explanation. Alf. Möller, in a research that presents rare instance in the domain of oecology of acuteness combined wit the critical faculty, has definitely proved the correctness of Belt's often disputed and derided statement, 'I believe ... . that they are in realit mushroom-growers and eaters.'

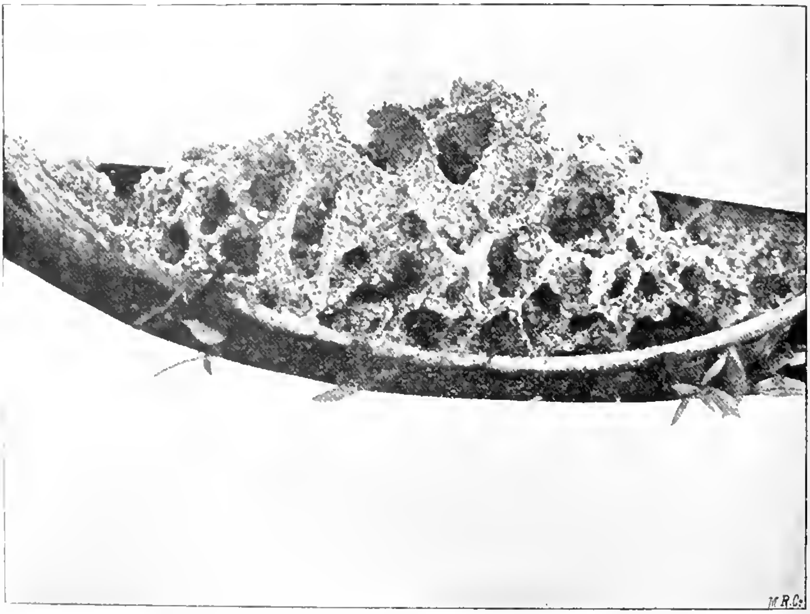

FIG. 73. A fungus-garden prepared on a plate in three days by hairy ants (Apterostigma IV mentioned in the text on p. 138) in confinement. Natural size. After Alf. Möller.

The imported pieces of leaves serve only to a small extent for coverin the nests. Most of them are cut up again by the ants and kneade soft by their feet and mandibles, so that but few cells remain unbruised

Thus prepared, the now shapeless little masses are worked up into a coarsely porous spongy mass which fills the interior of the nest and forms the *fungus-garden* (Fig. 73). The little masses, the initial green colour of which changes first to bluish-black and finally to yellowish-brown, are traversed in all directions and bound together by fine mycelial threads. On closer inspection, innumerable little white bodies, at the most ·5 mm. in diameter, may also be seen; they spring laterally from the mycelial threads and are termed by Möller 'kohlrabi-clumps' (Fig. 74). They consist of an agglomeration of short branches with node-ike or globular swollen ends and very rich protoplasmic contents. *The kohlrabi-clumps' are the most important if not the sole food of the ants, and represent a new structure, which has arisen as a result of artificial selection exercised by the ants.*

The 'kohlrabi-clumps' appear very early in the fresh masses and hen disappear, when these assume a brown colour. Alf. Möller has, by ingenious experiments, revealed he whole workings of the ants in heir fungus-gardens, and has shown how the tiniest female workers keep off all foreign organisms, so that without further trouble the little masses can be used for pure culures, and how the ants, by indusriously biting off the subaërial hreads, prevent the vegetative prouting which will be described further on. He has also directly bserved, in numerous cases, the ctual eating of the 'kohlrabi-lumps' and has proved that in their absence the ants die of starvation.

FIG. 74. 'Kohlrabi-clumps' of Rozites gongylophora, Moll., the fungus of the South Brazilian species of Atta. Magnified 150. After Alf. Möller.

The fungus, as a rule, remains in the purely vegetative condition that has just been described. Only exceptionally, and under unknown onditions, do large pileate sporophores of a purely agaric type develop from the mycelium and crown the top of the ants' nest. a feature that all the more striking because large pileate fungi are rare in tropical rain-forests. Such discoveries have made it possible for Alf. Möller to etermine exactly the systematic position of the fungus, and to describe as a new species of the genus Rozites, R. gongylophora, Möll.

The four species of Atta that occur near Blumenau cultivate the same species of fungus, which is never found outside the ants' nests. We have therefore here a highly developed case of reciprocal adaptation between nlike organisms.

The removal of the ants from the fungus-garden results, after a few days, in the appearance of a very rich subaërial mycelium, on which two kinds of conidia are produced. This luxuriant growth occasions not only the rapid exhaustion of the substratum, but also the emptying of the 'kohlrabi-clumps' or the cessation of their production.

Möller was able, in cultures in nutritive solutions, to induce the fungus to form 'kohlrabi-clumps,' which were identical with those in the fungus-gardens and were eaten just as greedily by the ants. These peculiar structures are therefore by no means ant-galls, but a product of cultivation comparable with kohlrabi. The phylogenetic starting-point of their evolution is to be sought in the tendency of the fungus to produce all kinds of swellings.

The parasol-ants are not the only species that cultivate fungi. Frau Brockes, one of the daughters of Fritz Müller, discovered the same custom in another genus of ant, Apterostigma, near Blumenau, and Alf. Möller has minutely investigated the fungus-gardens of the remarkably hairy little species of this genus, which are therefore termed *hairy ants*. They belong to four different species: Apterostigma Mölleri, Forel, A. pilosum Mayr, A. Wasmanni, Forel, and another species not yet described and here referred to as A. IV. They live in much smaller communities than do the species of Atta, and construct correspondingly smaller gardens for which purpose they chiefly employ wood-dust, produced by the activity of insect-larvae, and the excrements of the latter.

Finally, Möller also recognized the *hump-backed ants*—species of the genus Cyphomyrmex (C. auritus, Mayr, and C. strigatus, Mayr)—as fungus-cultivators. Their fungus-gardens resemble those of the hairy ants.

The fungi of the gardens of the hairy and the hump-backed ants diffe specifically from one another as well as from those of the species o Atta, but the different species of each genus of ant cultivate the same species of fungus. The fungus of Apterostigma and of Cyphomyrmex, like that of Atta, produces kohlrabi, but of a somewhat different structure, and after the ants are removed, also produces a luxuriant subaërial myceliun from which conidia are abstricted. Unfortunately the highest form o sporophore has not been observed, so that the systematic position o the fungi associated with the hairy and hump-backed ants is not ye precisely determined, but they undoubtedly belong to the Basidiomycetes and probably to the Agaricinae. The 'kohlrabi-clumps' of the different species of ants are highly instructive, as they represent structure that have remained at different stages of selective evolution. The specie of Atta have elaborated the most highly developed product (Fig. 74) Somewhat less developed are the 'kohlrabi-clumps' of Apterostigm Wasmanni, as the apices of the individual kohlrabi-hyphae assume no a globular, but a swollen clublike form, and are arranged in less definit clumps. Besides this, in opposition to those of the Atta-fungus they regularly develop in a nutritive solution into ordinary hyphae and thus show that they have lost less of their filamentous character. At a still lower stage, in spite of the better definition of their shape as a whole, we find the 'kohlrabi-clumps' of Cyphomyrmex strigatus (Fig. 75). The lowest stage of development, however, is shown in the fungus-gardens of Cyphomyrmex auritus, Apterostigma pilosum, A. Mölleri, and A. IV, where the swellings show no strict localization in their arrangement on the hyphae and no constancy in their dimensions.

A factor so destructive as the parasol-ants in tropical America, in particular near the Equator and north of it, cannot have persisted without nfluencing the character of the vegetation. The fate of introduced plants s very instructive from this point of view. Many plants are so sought after that their cultivation is quite impossible where parasol-ants are common; such are rose, orange, coffee, chicory, mango, cabbage; other plants are comparatively unmolested, such as Eucalyptus, the ramie plant Boehmeria), grasses, heliotrope, magnolia, bay, Cucurbitaceae, wormwood, radish, parsley, celery[1]. We must assume that a similar condition prevailed in regard to the vegetation of ropical America before the appearance of the parasol-ants. The vegeation consisted on the one hand of pecies that were very frequently ttacked, and on the other of those hat were seldom or not at all ttacked. The former, unless they belonged to the most rapidly growing and commonest species, were either completely annihilated, or persisted only in such examples as owed their individual immunity to some characteristic or other. This haracteristic was further selected in the struggle against the parasol-ants. The protective characteristics in many cases may be of a histological nature, as in very fibrous plants, such as grasses, palms, Bromeliaceae, which are included among the plants very rarely or not at all attacked. n other cases, it is probably due to substances that have a sharp taste nd smell, or are poisonous, or to very viscous latex rich in caoutchouc, which however is not always protective (Manihot). The number of romatic plants is relatively very great, as well among those that are ought after as among those that are almost always avoided, a fact

FIG. 75. 'Kohlrabi-clumps' of the fungus of a South Brazilian hump-backed ant, Cyphomyrmex strigatus. Magnified 270. After Alf. Möller.

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[1] Alf. Möller, op. cit. p. 83. These data refer to South Brazil only. The species of Atta near the Equator may have other preferences.

which appears to prove that certain ethereal oils attract the parasol-ants, whilst others repel them. Such phenomena give indications regarding the paths that natural selection must have followed in the struggle of the vegetation against the parasol-ants.

Whilst the protective contrivances belonging to the plant itself and causing the species to be more or less completely avoided by the leaf-cutters can at present form the subject of hypothesis alone, yet, in the case of some species, it has been proved that in order to keep their foes at bay, the plants enter into symbiotic relations with definite bellicose ants by whom they are wellnigh perfectly protected.

ii. *MYRMECOPHILY.*

Plants with adaptations for attracting ants are termed *myrmecophilous* As is proved by the occurrence of such contrivances in the tropical zones of the Old World, myrmecophily has also been evolved for the purpose of combating other enemies of vegetation, and chiefly, in fact, for the protection of flowers from insect-bites. On the other hand, in temperate zones, in accordance with the relative paucity in ants, definite allurement for these insects are weakly indicated and only in a few plants. Typica myrmecophily is one of the characteristic features of the tropical flora.

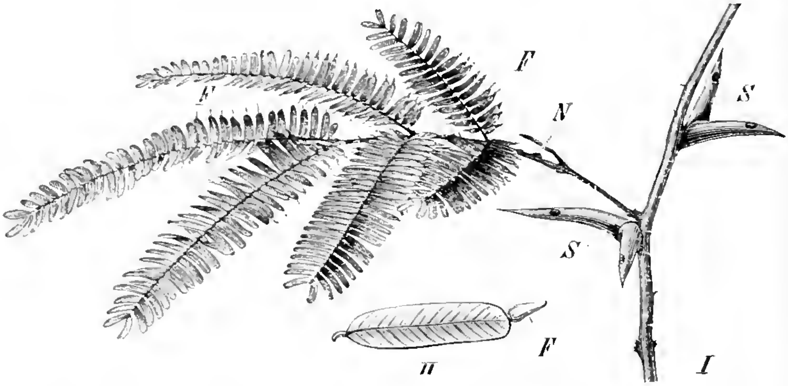

FIG. 76. Acacia sphaerocephala. *I* Part of stem with stipular thorns, *S*, and a leaf with Belt's corpuscles, *F*. On the petiole at *N* a nectary. Reduced. *II* Single leaflet, *F* Belt's corpuscles. Somewhat enlarged. From Strasburger's Text-book of Botany.

Belt must be considered as the actual discoverer of myrmecophily although Delpino, on the basis of much less convincing material, nearly simultaneously and quite independently published the same idea. I Nicaragua, and on the Amazon, Belt became acquainted with severa species of myrmecophytes, but he devoted his attention chiefly to Acaci cornigera, which is now one of the best-known examples of this clas of phenomena, as is also the very similar A. sphaerocephala (Fig. 76) which has been frequently the subject of subsequent investigations. Both these acacias, and many other species besides, possess large, hollow, and relatively thin-walled, stipular thorns that serve as dwelling-places for a definite species of fierce ant, which bores an entrance-hole into them near the tip. At the ends of the leaflets, but for the most part only in the upper half of the leaf, there are found small ovoid or pear-shaped structures, which are industriously collected and eaten by the ants. These edible objects, termed after their discoverer *Belt's corpuscles*, may, from a morphological point of view, fairly be regarded as transformed glands. They are however distinguished from all known glands by definite characters—larger size, longer duration, richness in proteids, easy severance when touched—all of which features may, with as much certainty as is possible in such cases, be regarded as adaptations to ants. In addition, hey have no secretory power, at least during the later stages of their development. A fact of special significance is that precisely similar bodies occur in the moraceous genus Cecropia and the acanthaceous genus Thunbergia, and are likewise associated with protective ants. The ike has never been observed in other plants. Moreover, a nectary situated at the base of the petiole affords a liquid rich in sugar.

Of all myrmecophytes, none have hitherto been so thoroughly investigated in all respects as some species of the genus Cecropia, especially he South Brazilian C. adenopus.

The species of Cecropia (trumpet trees, bois canot, pao de imbaúba) are among the most conspicuous trees in tropical America. They are widely distributed and common everywhere, in rain-forests as well as in he thin forest strips of the xerophilous districts, and in the young woods *capoeiras* of the Brazilians) which in rainy districts speedily cover abandoned plantations or restock ruined virgin forest. Their slender stems shoot p everywhere like candelabra, supported on short prop-roots, and ivide above into boughs that are simply or scarcely branched. Their arge palmately lobed leaves occur only at the ends of the branches.

A few active ants are always running along the branches and petioles f Cecropia adenopus. If however the tree be somewhat roughly shaken, hen from minute holes in the stem and twigs an army of ants rushes ut and savagely attacks the disturber. In Santa Catharina, it is always he same species of ant, Azteca instabilis, and the species apparently ccurs only on Cecropia. It is one of the most bellicose ants that know, and its sting is most irritating. In both these ways it surpasses ll the ants that I became acquainted with as inhabitants of other plants, nd even, in spite of the possibly exaggerated accounts of travellers, the nts of the 'living ants' nests' of the Malayan Archipelago, Myrmecodia nd Hydnophytum, which will be described further on.

The most formidable foes of the imbaúba-tree are the leaf-cutting ants, or rather they would be so if they were not kept at a distance by their relatives which form the defensive army. They show such a preference for the foliage of Cecropia, that, at Blumenau, Fritz Müller and I found every one of the uninhabited trees, which are rare, had its leaves bitten down to the midrib, whereas not a single tree with a protective army of ants showed a trace of such injury. Only during the lowest winter temperatures is an inhabited tree exposed to its enemies for the protective ants are much more sensitive to cold than are the parasol-ants[1]. Other animals, as it appears, are no kept off. Caterpillars occu on the tree, though withou doing much damage, and the sloth exhibits such preference for it, as to receive the same name (imbaúba) in Brazil. None of it enemies, however, can compare with the parasol-ant in destructiveness.

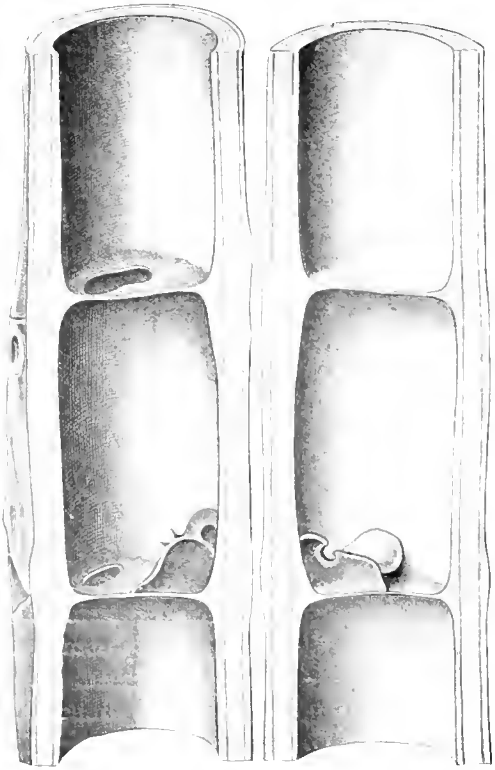

FIG. 77. Cecropia adenopus. Portion of a young stem split longitudinally. Central hollow with septa perforated by the ants, and structures made by them. Natural size.

A closer investigatio proves that the imbaúba-tre provides its guests with dwelling and food. The centre of the stem is traverse by a transversely divide cavity, which increases i calibre from below upward like a funnel, correspondin to the increasing thicknes of the growing apex, so tha the uppermost chambers i the stem are larger tha those represented in ou illustration (Fig. 77). Th cavity, and therefore th dwelling-place of the ants, in spite of its great utility, is not an adaptatio to the guests; it represents rather a feature that is common to man other plants, and may be explained on the mechanical principle c construction as being the method of producing the greatest resistanc to bending with the least expenditure of material. The dwelling existe before the symbiosis. It is otherwise with the entrances to it. Her

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[1] Alf. Möller, op. cit., p. 82.

an indubitable adaptation is exhibited. Above the insertion of every leaf there runs nearly up to the next node a shallow groove, the summit of which displays a roundish depression, both in non-myrmecophilous trees and in young internodes that are not yet inhabited (Fig. 78). As the external depression corresponds to an internal one, the wall at this place is very thin and is a mere diaphragm in a tube (Fig. 79). The diaphragm differs essentially in its histological structure from the adjoining parts of the wall, for it is devoid of the hard and tough elements, such as vascular bundles, collenchyma, lignified parenchyma, which form the main mass of the tissues in all other places. In the tissue of the wall underneath the groove the vascular bundles arise as secondary structures, and stop short just beneath the diaphragm. The diaphragm is destined to be the entrance; and the wall is bored through always at this spot.

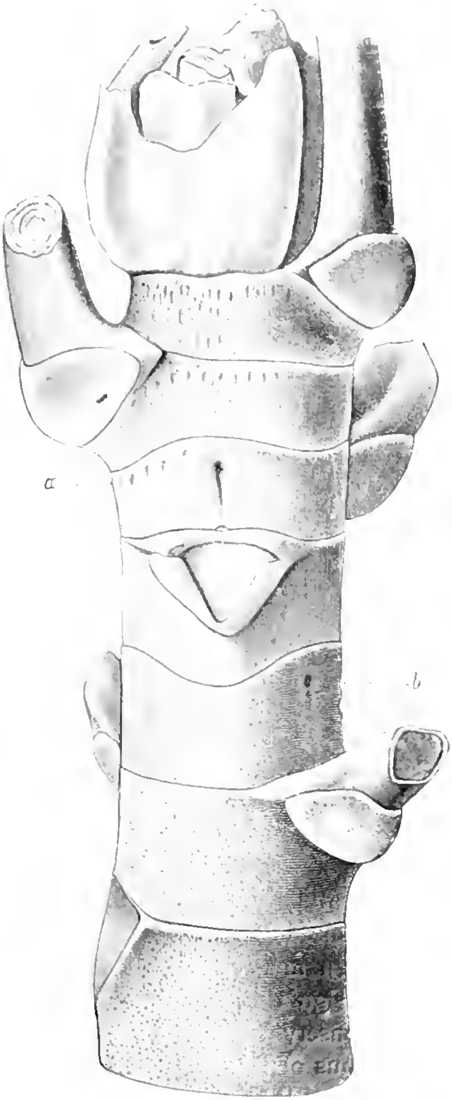

FIG. 78. Cecropia adenopus. Summit of a young stem. On one internode the place of entrance *a* is not yet bored through; on another internode the entrance *b* is bored through. Natural size.

Investigations into the history of the development show that at first the depression arises as a result of the pressure exerted by the little axillary bud, which s visible in the accompanying igure (Fig. 78) at the base of he internode. This pressure is exerted during the whole longiudinal growth of the internode and causes the formation of the groove. The tissues internal to he groove resemble those of the parts that are not exposed to pressure except the original little pit, which increases in circumference fter the pressure has ceased and at the same time is further modified.
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At the phylogenetic commencement of symbiosis, the ants bored an entrance through the groove, evidently because the wall was somewhat thinner there, and in particular, in accordance with a custom that is almost always followed and is connected with the domestic arrangements, they bored as much as possible in the upper part of their dwelling. All features that facilitate boring through this place must have been retained in the struggle for existence, and been further added to through selection[1]. They finally led to the differentiation of the thin weak diaphragm that has been described.

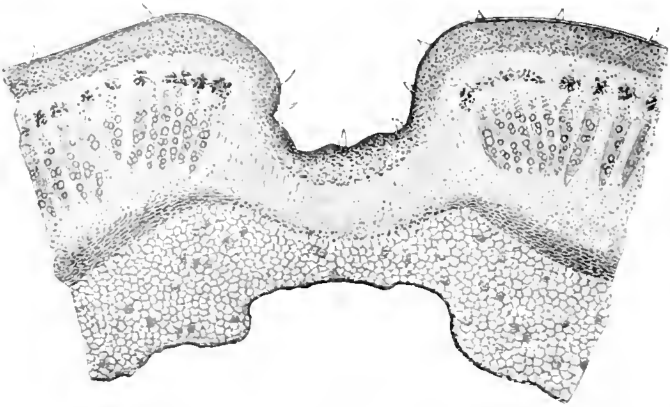

FIG. 79. Cecropia adenopus. Part of a transverse section of the wall of an internode, showing the diaphragm. Slightly enlarged.

The ants of the Cecropia devote themselves in their dwellings to th tending of Aphidae; they would seldom leave this work, and would rarely o never visit the foliage, were it not that the latter merited continued attention The base of the petiole is covered on its dorsal surface with a brow velvety coating upon which, in uninhabited trees, ovoid whitish bodies about 2 mm. long, lie quite loose (Fig. 80). The presence of such bodies which are named *Müller's corpuscles* after Fritz Müller their discovere is a sure sign that the tree is uninhabited, and they are always visibl in our conservatories. They are absolutely wanting on the surface the pulvinus of inhabited trees, because they are continually carried awa and eaten by the ants that are always looking for them, just as in Acaci cornigera. Müller's corpuscles, like those of Belt, consist of delicat parenchyma rich in proteids and oil.

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[1] I have observed on the mountains between the provinces Rio and Minas a species Cecropia which appears to have attained a lower stage of adaptation, since, among othe points, the entrance is absent in younger plants. The observations, however, were bu fragmentary.

Like the ant-fungi and the acacias referred to, Cecropia affords an xceptional case of the voluntary surrender by the plant of proteid bstances even in relatively rge quantity, for Müller's orpuscles are produced connuously and in profusion. If e cut through the brown elvety coating (Fig. 81), we e among the hairs numerous ensely crowded objects of the ind represented in the various ages of development. Having rown to their full size, these odies become loose at the base nd are pushed to the surface by ne pressure of the elastic hairs nat are crowded together side y side. Their developmental story, as well as the presence a stoma at the apex of each, ows that Müller's corpuscles, e those of Belt, are to be garded as metamorphosed ands; they do not however lfil the functions of glands en in their early stages. hilst normal leaf-glands, with this exception, cur only on young leaves and forthwith die, e glands of Cecropia converted into nutritive dies for ants are continually produced during e whole life of the leaf, and are continually ed when they are gorged with albuminoids.

FIG. 80. Cecropia adenopus. Base of the petiole with pulvinus and Müller's corpuscles. Natural size.

The assumption that the entrance-door and üller's corpuscles represent adaptations to ts was surprisingly confirmed by the disvery in the Corcovado, near Rio de Janeiro, a *species of Cecropia devoid not only of the ts but also of the entrance-door and of Müller's puscles* (Fig. 82). In this case also the young illary bud presses on the internode and thus ses the formation of an isodiametric deession, which subsequently, owing to the gitudinal growth, gives place to a groove. But the original depression

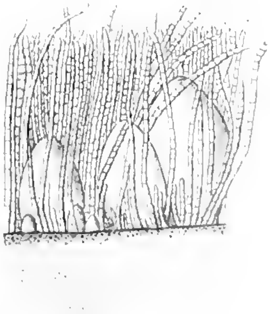

FIG. 81. Cecropia adenopus. Transverse section of part of the velvety coating at the base of the petiole, with Muller's corpuscles in various stages of development. Slightly magnified

differs neither externally, nor in the nature of the tissues lying with it, from the groove of which it forms the upper extremity. In spi of the absence of a protective army, the ant-free Cecropia proved be quite uninjured, apparently because the waxy coating of the ste prevented the leaf-cutting ants from climbing. It has indeed been prov experimentally that a waxy coating offers an insuperable obstacle[1].

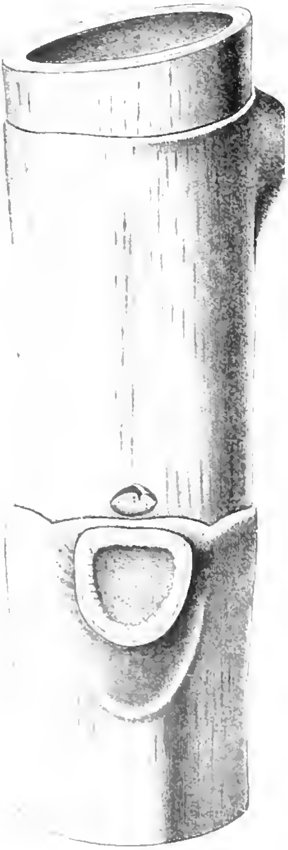

Fig. 82. Cecropia sp. of the Corcovado Mountains, near Rio de Janeiro. Part of the myrmecophilous stem. Natural size.

Cecropia adenopus, which probably mo of the other species of the genus resemb represents a higher stage of adaptation th Acacia cornigera and A. sphaerocephala, f it exhibits as adaptations not only the foo bodies, but also the spot that is prepar beforehand to be bored through. In the latt respect Clerodendron fistulosum, discovered Beccari in Borneo, resembles Cecropia. Oth species however have gone a step further, they have succeeded in forming an openi through the wall of the hollow interno The causes that lead to the formation of opening have not yet been explained; certain cases it may be the result of a tensi in others perhaps due to the death of t tissues of a circumscribed area. The openi is sometimes narrow, like a slit, so that has to be widened by the ants, as in Dur hirsuta, according to Schumann; sometim from the first it is more circular and poreli and thus perfectly fitted for its subsequent (Fig. 83, 1–3).

The spontaneous appearance of an open in the previously intact wall of hollow int nodes was first rendered probable by Bo in the case of Humboldtia laurifolia, th by Schumann in several species. I fi became fully convinced of its truth in e botanic garden at Buitenzorg, where I served quite free from ants specimens Humboldtia laurifolia and Triplaris americana, also Ficus inaequali hitherto unknown as a myrmecophyte, all with a well-differentia entrance-aperture at the upper end of most, or of all the internodes.

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[1] Schimper, op. cit. p. 66.

[2] Proof is still wanting that it is inhabited by ants in its native habitat. In Singapore botanic garden most of the specimens were inhabited.

Of the three last-mentioned cases, that of Triplaris americana, a olygonaceous plant belonging to equatorial South America, and of allied pecies of the same genus, is the simplest. Hollow axes are frequent n the family. The dwelling, here, as in Cecropia, is by no means an daptation to ants. On the other hand, the entrance-aperture may safely e described as such. Food-bodies, resembling those of Cecropia and

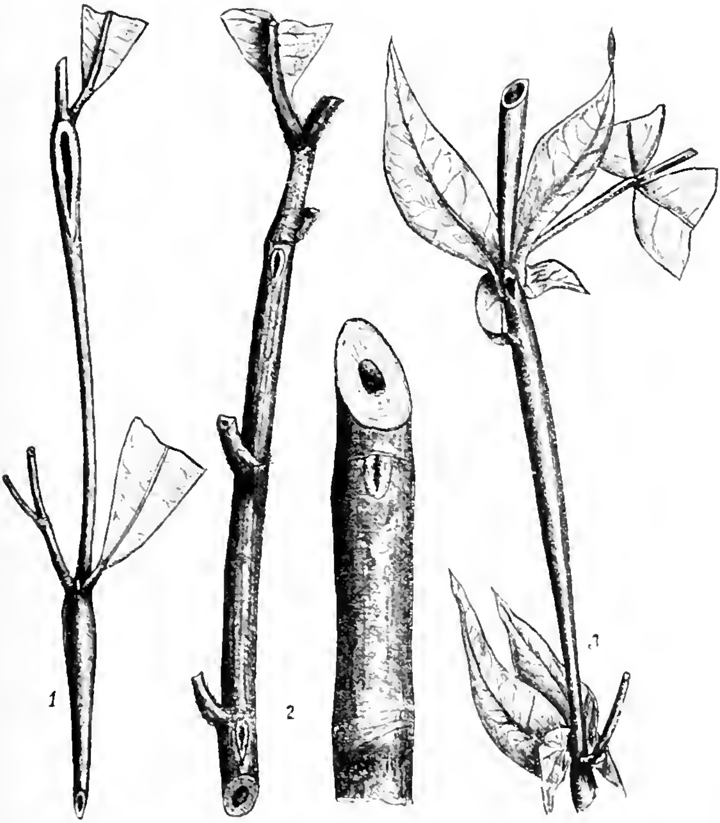

FIG. 83. Myrmecophytes. 1. Ficus inaequalis. From the botanic garden, Singapore. 2. On e left: Triplaris americana. Young internodes. From the Buitenzorg botanic garden. On the ght: T. caracasana. Old internode. Caracas. 3. Humboldtia laurifolia. From the Buitenzorg tanic garden. All natural size. Drawn by R. Anheisser.

cacia cornigera, are wanting, but extra-floral nectaries occur on the aves. Such extra-floral sugar-secreting glands, quite apart from the wers and without oecological connexion with pollination, occur very mmonly in plants inhabited by ants.

In Ficus inaequalis, with which may be included a number of plants thentically inhabited by ants, for example species of Duroia, not only e opening but apparently also the hollow chamber has arisen as an aptation, for the latter is present on some only of the internodes and occupies only the upper half of the internode in which it occur so that the principle of providing resistance to bending is no long applicable.

Whether Humboldtia laurifolia belongs to the last-mentioned type to that of Triplaris, I must leave undecided. In this case numerou bright red nectaries are present on the leaves and stipules.

Cordia nodosa (Fig. 84), of which I was able to observe numerou specimens growing wild at Pernambuco, belongs to still another typ Here the long inferior internode of the flowering shoot, which in i upper part forms a condensed tuft, bears, immediately below the leav and inflorescence, a lateral bladder into which a little pre-existing openin

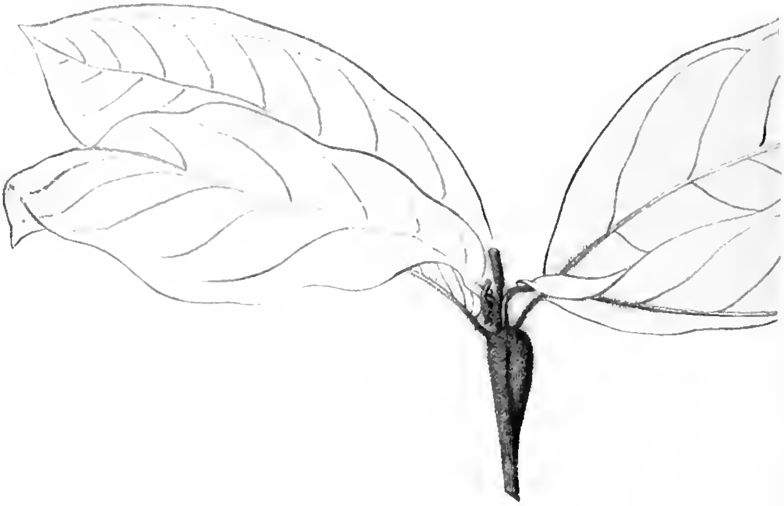

FIG. 84. Cordia nodosa. False whorl with inflorescence-axis and bladders. One-half natural size.

leads between the petioles. I found the bladder always occupied minute ants. Here the connexion between the dwelling-place of t ants and the flowers is very clearly exhibited, and the same featu is repeated in numerous other cases, for example in the laurace Pleurothyrium macranthum, where only the axes of the infloresce are hollow and inhabited by ants.

The famed myrmecophytes of the Malayan Archipelago, species Myrmecodia and Hydnophytum (Figs. 85 and 86), exhibit a type axial chamber quite different from the foregoing ones. Here it is longer a case of a single central chamber in a cylindrical woody interno but of numerous sponge-like communicating spaces in a succulent tub which since the plants in question are epiphytes, possibly in the fi place serve as a water-reservoir. The water is stored in the parenchy of the more or less thin partition-walls: the chambers themselves contain air and are inhabited by ants. Fairly numerous, but very small, openings allow for communication with the exterior. From them the ants rush out ready to attack, as soon as the tubers are touched. I have observed Myrmecodia echinata and Hydnophytum montanum growing wild in different parts of Java and have always found the tubers inhabited. The argest of the tubers. that I have observed, is shown reduced to one-third of its size in Fig. 86, having been drawn from a specimen preserved in alcohol.

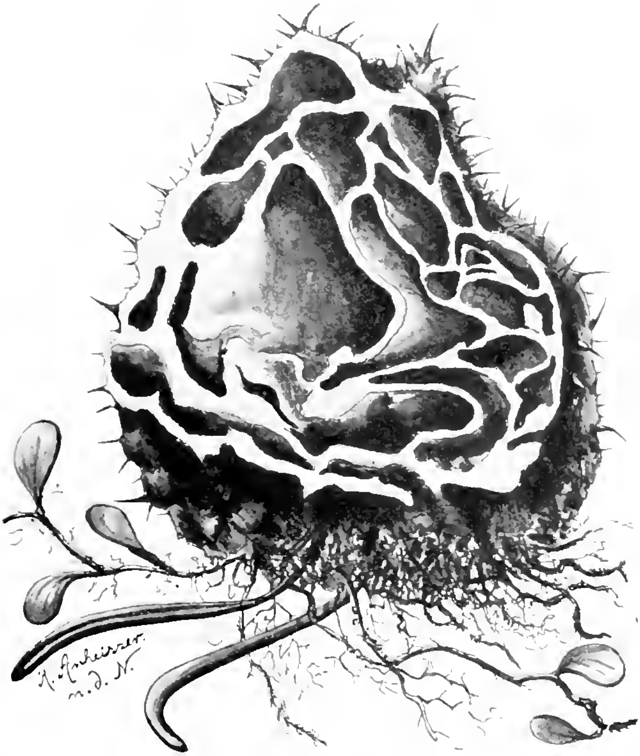

FIG. 85. Myrmecodia echinata. Tuber cut longitudinally. Below is an epiphytic fern. West Java. Natural size.

The structure and development of the tubers of Myrmecodia and Hydnophytum have been admirably described by Treub. He proved hat the structures, which were considered by Rumphius and other later bservers as a kind of ant-gall, are, with all their peculiarities, brought bout without any assistance from ants. As regards their function, Treub xpressed himself very cautiously; yet he did not think himself warranted n considering the tubers as adaptations to ants, but was rather inclined o connect the utility of the chambers with aeration. Most botanists who

FIG. 86. Hydnophytum montanum. Noesa Kambangan, South Java. One-third natural size

ave occupied themselves with myrmecophytes, and who have in some ases obtained certain proof of adaptations in them, will prefer to consider lyrmecodia and Hydnophytum as myrmecophytes. A proof of this iew has not yet, however, been obtained.

Phyllome-structures serving as dwelling-places for ants are even considerably more varied than axial parts that are used for the same purpose. hey are in some points extremely peculiar; yet, in all cases coming under his head, the myrmecophily is highly conjectural. Even in the certainly yrmecophilous acacias, only the nutritive corpuscles, and not the hollow tipular thorns, may be considered as indubitable adaptations.

7. Capura alata. Myrmecophyte. garden, Buitenzorg. Natural size.

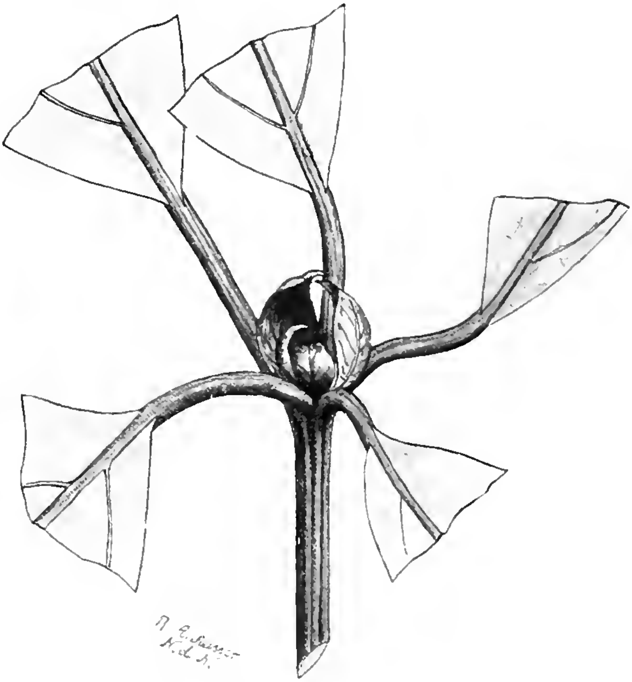

Fig. 88. Actinodaphne sp., from Salak. Botanic garden, Buitenzorg. Natural size.

In many plants the transformation of a leaf or a petiole into a ambered structure suitable for and actually used as an ant-dwelling ay be shown to be associated with other factors, for example in iphytic ferns, Asclepiadaceae and Bromeliaceae, in which the chambers rve for storing water or earth.

Figs. 87 and 88 are illustrations of plants that I studied in the otanic garden at Buitenzorg, in which myrmecophily might more readily be suspected. In Capura alata the large spoon-shaped stipule of each leaf are bent in such a manner as to enclose within then a chamber-like space, the marginal gap of which is closed as far as a entrance-aperture by a kind of web spun by the ants. I found th chambers nearly always inhabited by ants. Still more peculiar an requiring morphological investigation was the state of matters in a tree described as Actinodaphne sp. coming from Salak, in which each twi terminates in a roomy chamber lying above the minute terminal bu and formed by a whorl of small scale-leaves. The phyllomes describe here as scale-leaves are distinguished from the foliage-leaves by muc smaller size, absence of petiole, and different shape. I have alway found the chambers inhabited by ants, which appeared to belong t a species very abundant else where in the garden. It i no wonder that such suitabl structures should be inhabite by ants; it appears muc more remarkable that the hol low stems of Triplaris an Humboldtia, provided wit entrance-apertures, should b free from ants in the garde of Buitenzorg, at least so fa as my observations go.

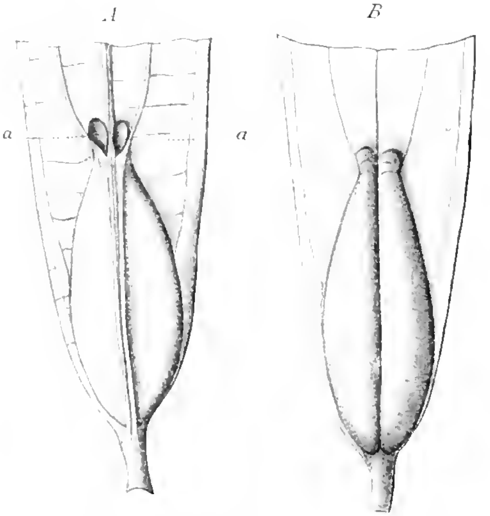

FIG. 89. Tococa lancifolia. Base of leaf with utricles. A seen from below, showing the entrance a. B seen from above. Natural size. After K. Schumann.

Still further deviations fro the normal leaf-structure occu among the tropical America Melastomaceae in the gener Tococa, Maieta, Calophys Myrmidone, and Microphys as well as, according to Schumann, in the rubiaceous Remijia physophora and Duroia saccifera, and th tropical African sterculiaceous Cola Marsupium [1]. Here at the base c the blade of the leaf, on both sides of the midrib and sometimes also o the petiole, are found two hollow outgrowths (Fig. 89), which in th Melastomaceae are situated on the under surface of the leaf and are t be regarded as modified domatia, whilst in Duroia they belong to th upper surface and morphologically represent new structures.

All the above-mentioned plants, and others besides that are inhabite by ants, are, as Schumann first pointed out, provided with an abundan brownish-red coat of hairs, which appears in some way to be connecte with the symbiosis.

[1] See Schumann, I, regarding all these plants.

Most plants provided with ant-dwellings at the same time supply food to their protectors, usually in the form of a sugary liquid in extra-floral nectaries. A very great number of plants, especially in the tropics[1], possess such nectaries without at the same time providing dwelling-places for the ants. Nevertheless some naturalists, especially Delpino, regard all such structures as allurements to protective ants, an opinion which is clearly untenable when we bear in mind the frequent occurrence of extra-floral nectaries and the rarity of observations on their efficiency in inducing ants to protect plants. It is however proved that protection is afforded in certain cases. Thus, when at Blumenau in Southern Brazil, I was able to observe how ants, which there very commonly visited Cassia neglecta in order to suck the sweet liquid excreted by nectaries at the base of the petiole, put to flight marauding leaf-cutting ants[2], though they did not interfere with a beetle that was usually present. In like manner R. von Wettstein proved experimentally in the case of Jurinea mollis, and Burck in several plants in the Buitenzorg botanic garden, that unwelcome visitors were kept away from the flowers by the ants. On the other hand, I have not been able to prove visits by ants to several species of plants provided with extra-floral nectaries.

The most probable view at present appears to be that extra-floral nectaries fulfil a still unknown function, which is independent of the ants, but is in some way connected with a warm climate, and that they have only secondarily become myrmecophilous organs, just like Belt's and Müller's corpuscles or the structures rich in albuminoids that Burck found on Thunbergia.

We may, in the first place, tentatively regard as allurements selectively adapted o ants and as extra-floral nectaries modified for this purpose, these structures hat are characterized by their size, striking colour, excretory activity, by their ongregation near the flowers, and especially by the great assiduity with which hey are visited by ants; but only the proof that ants afford an essential protection o the plant will give a firm basis to this hypothesis. On the other hand, it is o be hoped that success will be attained in discovering what was the original, nd in many cases is still the exclusive, significance of the nectaries. That this s not a case of any very essential function is proved by experiments made with plants of Cassia neglecta which I deprived of all their nectaries, without oing them any injury. The wounds healed quickly and excreted no sugar, so hat the function in question might be considered as being completely in abeyance. Unfortunately there was not time to ascertain whether the plants, thus deprived f their nectar and no longer visited by the protective ants, became victims to he leaf-cutters.

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[1] Complete references in Delpino.

[2] Schimper, op. cit., p. 68, Plate iii. fig. 9.

SELECT LITERATURE.

1. Geographical Distribution of the Arrangements for Pollination.

Belt, Th. I. The naturalist in Nicaragua. 1874. 2nd edition. London, 1888.

—— II. Bees and clover. Nature. 1876.

Briquet, J. Études de biologie florale. Bullet. du laborat. de bot. générale d l'univ. de Genève. Vol. I. 1896–1897.

Delpino, F. Ulteriori osservazioni sulla dicogamia nel regno vegetale. Atti d. Soc Italiana di Milano. Vol. XI–XIII. 1868.

Eaton, A. E. First report of the naturalist attached to the Transit of Venu expedition to Kerguelen's Island. Proceedings of the Royal Society Vol. XXIII. 1876.

Ekstram, O. Zur Kenntniss der Blüthenbestäubung auf Novaja Semlja Oefvers. Svensk. Vetensk. Acad. Förhandl. 1894.

Galpin, E. E. The fertilization of flowers by birds. Gardeners' Chronicle 3rd ser., Vol. IX. 1891.

Johow, Fr. Estudios sobre la flora de las islas de Juan Fernandez. Santiago d Chile. 1896. (Pollination. p. 255.)

Knuth, P. I. Blumen und Insekten auf den nordfriesischen Inseln. Kiel un Leipzig, 1894.

—— II. Neue Beobachtungen über fledermausblüthige Pflanzen. Botanische Centralblatt. Bd. LXXII. 1897.

Lindman, C. A. M. Blühen und Bestäubungseinrichtungen im skandinavische Hochgebirge. Ibid. Bd. XXX. 1887.

Loew, E. Blüthenbiologische Floristik des mittleren und nördlichen Europa sowi Grönlands. Stuttgart, 1894.

Ludwig, F. Zur Biologie der phanerogamischen Süsswasserflora. In O. Zacharia Die Thier- und Pflanzenwelt des Süsswassers. Leipzig, 1891. Bd. II.

MacLeod, J. Pyreneenbloemen en hare bevruchting door insecten; een bijdrage tot de bloemengeographie. Dodonaea. Bd. III. 1891.

Moseley, H. N. Further notes on the plants of Kerguelen, with some remark on the insects. Journ. Linn. Soc. Botany. Vol. XV. 1876.

Müller, Fr. I. Botanische Notizen aus einem Briefe Fritz Müller's. Mitgethei von Hildebrand. Botanische Zeitung. Bd. XXVIII. 1870.

—— II. Feijoa. Ein Baum, der Vögeln seine Blumenblätter als Lockspeise biete Kosmos I.

Müller, H. I. Ueber die Bestäubung der Primula farinosa. Verhandl. des bota Vereins der Provinz Brandenburg. Bd. XX. 1878.

—— II. Alpenblumen. Ihre Befruchtung durch Insekten und ihre Anpassunge an dieselben. Leipzig, 1881.

Ridley, H. N. On the method of fertilization in Bulbophyllum macranthum ar allied Orchids. Annals of Botany. Vol. IV. 1889–1891.

Riley, C. V. The Yucca moth and Yucca pollination. 3rd Ann. Rep. Missou Botanic Garden for 1891. St. Louis, 1892.

Scott-Elliot, G. F. I. Ornithophilous flowers in South Africa. Annals of Botan Vol. IV. 1889–1891.

—— II. Notes on the fertilization of South African and Madagascar floweri plants. Ibid. Vol. V. 1890–1891.

Thomson, G. M. Fertilization of New Zealand flowering plants. Transactions and Proceedings of the New Zealand Institute. Vol. VIII. 1880.

Verhoeff, C. Blumen und Insekten der Insel Norderney und ihre Wechselbeziehungen etc. Nova Act. Acad. Leop. Carol. Bd. LXI. 1893.

Wallace, A. R. I. On the peculiar relations of plants as exhibited in islands. Nature. 1876.

— II. Tropical Nature: and other essays. London, 1878. (Insular plants and species of insects. p. 281.)

— III. Island life. 2nd edition. London, 1892.

Warming, E. Om Grönlands Vegetation. Meddelelser om Grönland. Kjöbenhavn, 1888.

2. Plants and Ants.

eccari, O. Piante ospitatrici ossia piante formicarie della Malesia e della Papuasia. Malesia. Bd. II.

elt, Th. The naturalist in Nicaragua. London, 1874. 2nd edition. London, 1888.

urck, W. Beitr. z. Kenntniss d. myrmecoph. Pflanzen etc. Annales du jardin botanique de Buitenzorg. Vol. X. 1891.

arwin, Fr. On the glandular bodies of Acacia sphaerocephala and Cecropia peltata serving as food for ants, with an appendix on the nectar-glands of the common brake fern, Pteris aquilina. Jour. Linn. Soc. Botany. Vol. XV. 1876.

elpino, F. I. Rapporti tra insetti e tra nectarii estranuziali in alcune piante. Bullettino entomologico. Anno VI.

— II. Weitere Bemerkungen über myrmecophile Pflanzen. Huth's Monatl. Mittheil. aus dem Gesammtgeb. der Naturw. etc. Jahrg. V. 1887.

— III. Funzione mirmecofila nel regno vegetale. Prodromo d'una monografia delle piante formicarie. Parte prima. Bologna. 1886.

orbes, H. Wanderings of a naturalist in the Malay Archipelago.

oebel, K. Morphologische und biologische Studien. Annales du jardin botanique de Buitenzorg. Vol. VII. 1888.

uth, E. I. Ameisen als Pflanzenschutz. Verzeichniss der bisher bekannten myrmecophilen Pflanzen. Berlin, 1886.

— II. Myrmecophile und myrmecophobe Pflanzen. Berlin, 1887.

undström, A. N. Die Anpassungen der Pflanzen an die Thiere. Upsala. 1887.

öller, Alf. Die Pilzgärten einiger südbrasilianischer Ameisen. Botan. Mittheil. aus den Tropen. Heft VI. Jena, 1893.

üller, Fritz. Die Imbauba und ihre Beschützer. Kosmos. Bd. VIII. 1880.

umpf, G. E. Herbarium amboinense. Deel VI. Amstelodami, 1750.

chimper, A. F. W. Die Wechselbeziehungen zwischen Pflanzen und Ameisen im tropischen Amerika. Botan. Mittheil. aus den Tropen. Heft I. Jena, 1888.

chumann, K. I. Einige neue Ameisenpflanzen. Pringsheim's Jahrbücher. Bd. XIX. 1888.

— II. Einige weitere Ameisenpflanzen. Abhandl. des Botan. Vereins der Prov. Brandenburg. Bd. XXXI. 1889.

— III. Rubiaceae. In Engler and Prantl, Die natürlichen Pflanzenfamilien. IV. 4.

Schumann, K. IV. Ueber afrikanische Ameisenpflanzen. Berichte der deutscher botanischen Gesellschaft. Bd. IX. 1891.

Treub, M. I. Sur le Myrmecodia echinata Gaudich. Annales du jardin botanique de Buitenzorg. Vol. III. 1883.

—— II. Nouvelles recherches sur le Myrmecodia de Java. Ibid. Vol. VII. 1888

Wallace, A. R. Tropical Nature: and other essays. London, 1878.

Warburg, O. Ueber Ameisenpflanzen (Myrmecophyten). Biologisches Centralblatt. Bd. XII. 1892.

Wettstein, R. v. Sitzungsberichte der Wiener Akademie. Bd. XCVII, Abth. I 1888.

SECOND PART

FORMATIONS AND GUILDS

FORMATIONS AND GUILDS

CHAPTER I

THE FORMATIONS

1. **Climatic and Edaphic Factors.** General type of the vegetation determined by tmospheric precipitation. General type of the flora determined chiefly by heat. Details etermined by edaphic influences. The formations. Principal and subsidiary members. istinction between climatic and edaphic formations. 2. **The Climatic Formations.** . *Classification.* Characteristics of woodland and grassland. The struggle between hem. Invasion of the Malayan forest by the alang-steppe. Degradation of woodland nd grassland into desert. Characteristics of deserts. ii. *Woodland Climate.* Climatic onditions for the existence of trees. Hygrophilous and xerophilous trees. The imits of tree-growth. Brushwood. Characteristics of woodland climate. iii. *Grassland limate.* Climatic conditions for the existence of grasses. Characteristics of grassland limate. iv. *Meteorological Tables.* What they tell and what they should tell. . **The Edaphic Formations.** i. *Edaphic Influences in general.* ii. *Edaphic Formations ue to Telluric Water.* iii. *Open Edaphic Formations.* Rocks, gravel, sandy soil. . *Transition from Edaphic into Climatic Formations.* Krakatoa. The volcano unter. The Camargue. 4. **Life of the Plant-commune in the Formations.**

1. CLIMATIC AND EDAPHIC FACTORS.

If one looks down upon the flat virgin tract of country from a onsiderable height, say from the top of a mountain, or better still from balloon, the character of its vegetation as a rule appears uniform, either s *woodland*, *grassland*, or *desert*. It is true that even from a great istance some interruptions of the prevailing monotony may be distinguished. Where for instance a river traverses the grassy landscape, ts banks are frequently clad by belts of forests, or the dry desert hows spots and strips of luxuriant vegetation. These are indeed mere ccidents, having no influence on the general character of the landscape, hich, excepting where two districts meet, always belongs to one or ther of the three above-mentioned types.

Chains of mountains are frequently boundary walls between districts f dissimilar types of vegetation. Thus the forest district of North frica is separated by the Atlas Mountains from the Sahara desert, hat of North Venezuela by the Cordilleras from the grassland of the

Llanos, the forest of Brazil and the Argentine by the Andes from th desert of Peru, Bolivia, and North Chili. In other cases the transitio is more gradual. The eastern forest district of North America graduall passes westward into the grassland district of the prairies, and the latte towards the west gradually assumes the condition of a desert; a simila phenomenon is exhibited in the transition from the Russian forest distric to the South Russian steppes, and from the latter to the Caspian desert Whether the change be more sudden or more gradual, it always correspond to a change in climatic humidity.

The type of vegetation in the tropical and temperate zones is determine by the amount and distribution of the rainfall, by the humidity of th air, and by the movements of the atmosphere, which essentially affec vegetation only by their desiccating influence.

The type of the flora in so far as it depends on existing factors i dependent primarily on heat, especially if we consider, not the group of lower order (genera and species), but those of higher order (cohorts orders, and families). Only in polar areas is the temperature importan as a climatic cause of a type of vegetation—in the cold desert o tundra.

On nearer approach the uniform character of the vegetation of district appears much less distinct, for to the irregularities already visibl from a distance a number of fresh ones are added, such as small patche covered with reeds in the midst of a forest, scantily stocked gravel, an the like. Moreover, woodland, grassland, and desert display many fin shades of differences within their types; here the character is mor hygrophilous, there more xerophilous, with countless stages between th two extremes. Finally, the composition of the flora that could in mos cases not be discerned from a distance is subject to more or less sudde changes. This fine differentiation of the vegetation and flora withi a climatic district is chiefly determined by the soil. Only when ther is considerable unevenness of surface does the inequality of the insolatio operate as well; but the influence of this factor is always subordinat to the physical and chemical nature of the soil.

The differentiation of the earth's vegetation is thus controlled by thr factors—heat, atmospheric precipitation (including winds), soil. He determines the flora, climatic humidity the vegetation; the soil as a ru merely picks out and blends the material supplied by these two climat factors, and on its own account adds a few details.

The blending activity of the soil leads to a differentiation into sometim smaller and sometimes larger groups of uniform oecological and floristic

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[1] [The introduction of this adjective in the sense of relation to 'flora,' as 'faunisti is used in relation to 'fauna,' appears to be necessary because of the botanical restrictio of 'floral' to the flower and its parts.]

ype, the characteristics of which are exactly repeated on the same kinds of soil so long as the climate is unchanged, whereas the different kinds of soil bear different kinds of plants. *The communities of plants s determined by the qualities of the soil are termed formations.*

In each formation one species of plant, or a group of species, is haracteristic: plants that merely occur sporadically are unessential to he formation, and commoner subsidiary constituents can only give a ifferent facies to the formation. Thus, in Europe, we are acquainted vith the formation of the beech-forest, where Fagus sylvatica predominates, nd with at least two facies of dissimilar herbaceous vegetation[1]. If he composition of the vegetation should alter while the nature of the oil remains unchanged, this is a certain indication of transition into nother climate. A sudden change of formations while the quality of he soil remains unaltered is only found in mountain ranges in relation o the sudden change in climate.

Whilst every formation is in its floristic and oecological character product of climate and soil, yet the influence of the several climatic nd edaphic factors is not equal. The influence of the soil is always ubordinate to that of the climatic temperature, whereas under certain onditions that are indeed merely local it neutralizes that of the mospheric precipitation. Thus woods occur in many spots where the imate would give rise to grassland, or we may find the converse, and gorous forest thrives in patches under a desert climate with a very anty atmospheric precipitation. Definite properties of the soil may so bring forth a character of vegetation that belongs to none of the imatic types. These climatic types demand a favourable constitution the soil congenial to the vast majority of the plants. Extreme operties of the soil that are unfavourable to the life of most plants t vegetation free from the controlling influence of atmospheric pre- pitation. Consequently the vegetation of rocks, gravel, swamps, and her special spots, bears in the highest degree the oecological impress the substratum, and this impress for the most part remains identical ider very dissimilar conditions of climatic humidity, which on such ils plays only a subordinate part.

From what has preceded it appears that *two oecological groups of rmations* should be distinguished—the *climatic or district formations*, e character of whose vegetation is governed by atmospheric precipitations, d the *edaphic or local formations*, whose vegetation is chiefly determined the nature of the soil.

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[1] See p. 111.

2. THE CLIMATIC FORMATIONS.

i. *CLASSIFICATION.*

Climatic formations may be traced back to three chief types—*woodlan* *grassland*, and *desert*.

Woodland is constituted essentially of woody plants, and is terme *forest* if trees grow in a closed condition; *bushwood*, when shrubs are s abundant as to keep the crowns of the trees from touching one another *shrubwood*, where shrubs constitute the chief feature. Herbaceous plant are always present on woodlands, but as accessory components only they are completely dominated in their oecology by woody plants.

Grassland consists essentially of perennial grasses growing in tuft Other herbaceous plants, even if they should be just as numerous the grasses, are merely companions of the grasses, for the existence the formation depends in the first place on its grassy covering. Gras land, when hygrophilous or tropophilous, is termed *meadow*; when xer philous, *steppe*; and xerophilous grassland containing isolated trees *savannah*.

Woodland and grassland stand opposed to one another like two equal powerful but hostile nations, which in the course of time have repeated fought against one another for the dominion over the soil. The climat that now prevail have limited the domains of each of the opponen but merely slight changes of climate would suffice to revive the conte In districts which, in a sense to be explained further on, possess neith a decided woodland climate nor a decided grassland climate, the acti of mankind suffices to start the struggle. Thus at the present tim owing to the clearance of forests in Eastern Java and a few other localiti in the Malayan Archipelago, districts formerly occupied by woodla are being invaded by grass. Although I have personally witnessed th contest, yet I will give an account of it in the words of Junghuhn, t veteran authority on Malayan vegetation, for it is hardly possible equal his clearness.

When the soil remains uncultivated after clearing the forest, ' a rule the social and dense-growing alang-grass (Imperata Koenig Beauv.) first replaces the vanished forests, then areas extending for mil even indeed for whole days' journeys, are transformed into a unifor wilderness of dense grass three to five feet high, while on mounta slopes the same grass extends far beyond its original zone, and spreadi over everything it ranges up to altitudes of 6,000–7,000 feet, being almo insensible to differences of temperature.

Its silken-haired seeds, light as the tenderest down, are wafted aw in millions by the slightest breath of wind and greatly facilitate its general distribution, whilst its creeping and deeply penetrating roots increase the difficulty of eradication when once this grass, so tenacious of life, has established itself. I have reasons for believing that while the land was in its original condition the alang-grass was restricted to sundry sterile, arid, waterless tracts of the hot zone, and was chiefly confined to heavy, hard, easily dried clay soil, with an iron-pan, but that at the present time, wherever we meet this grass on a fertile light soil and on mountain-slopes at above 2,000 feet, this state of affairs is first brought about by the hand of man. . . . In Northern Sumatra, especially in the Batta country that has been devastated by war, grassy wastes have consequently come into existence which cover everything far and wide with a hideous uniformity and overrun plain, mountain, and valley with their whitish-green mantle[1].'

It is probable that, unless man should again intervene, the alang-teppe will, in the course of time, again give way to the forest, for limatic conditions are in every way more suited to forest than to grass-and. In a decided forest climate, for example along the Brazilian coast, orest quickly succeeds to devastated forest, although it is of a more xerophilous character than before, being the so-called 'capoeira.'

Desert, the third leading type of climatic formation, originates when, n account of too great drought or cold, climatic conditions are hostile to all vegetation; the types of both woodland and grassland then become tunted and their differences become obliterated, for the struggle between hem ceases. The soil is then monopolized by such woody or herbaceous lants as can still contend successfully against the inclemency of the limate. Transition forms between desert on the one hand, and wood-and or grassland on the other, are termed *semi-deserts*.

In the woodland and in the grassland such plants alone can thrive as re at their oecological optimum in respect to all external factors, other-ise they would perish in the struggle with stronger competitors. In eserts this is no longer a necessary condition, as the struggle between he plants ceases. Woodlands and grasslands are closed formations, at east in an oecological sense; more components cannot be admitted nto them and numerous seedlings are continually perishing in the general onflict. The desert, on the contrary, is oecologically an open formation. Most seeds do not germinate in it, and seedlings frequently succumb to he inclemency of the climate. Others prolong their miserable existence. Many plants die and their places are not reoccupied. There are always many vacant spaces to be filled in the desert[2].

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[1] Junghuhn, op. cit., Bd. I, p. 153.

[2] Very sparsely stocked *stations* in climatic districts suitable for woodland or grassland ust not be confounded with *climatic deserts*. See under Edaphic Formations, p. 176.

To consider grassland, as is frequently done, as the sign of a 'bad climate,' as an evidence of poverty in Nature, as a transition state between forest and desert, is at best comprehensible from a forester's point of view, but is neither scientifically nor practically justifiable. Indeed certain forms of woodland are climatically more accommodating in their demands than is grassland. Victory in the struggle between woodland and grassland belongs to the one of the two antagonists with which the given climatic conditions best correspond.

Accurate knowledge of the demands made on the one hand by woody plants, and on the other by grasses, in regard to atmospheric precipitation, movements of the air, and heat, will yield us the elements of whicl a *woodland climate* and a *grassland climate* are composed.

ii. *WOODLAND CLIMATE.*

Let us first consider the woody plant in its most complete development as a *tree*. In the tree the transpiring surface is at a greater distanc from the water-supply in the soil than it is in the shrub or herb; beside this, the strata of air surrounding that transpiring surface have propertie different to a certain extent from those nearer the soil; finally, at leas in many cases, the transpiring surface of the tree is larger when compare with the corresponding surface of the ground than it is in the shrub o herb.

On the other hand, the tree has at its disposal a vast root-systen which is capable of utilizing very deep-lying supplies of water, and upo these it often mainly relies, as its root-tips for the most part lie a considerable depth below the surface of the ground.

Our present knowledge of the physiology of trees is in the mai derived from the Central European flora, the trees of which all transpir freely although in an unequal degree, and are correspondingly highl water-demanding and hygrophilous during the vegetative season. Th most comprehensive and useful investigations regarding the transpiratio of the forest trees of Central Europe have been carried out by R. vo Höhnel [1], from whose works the following data are taken:—

The author experimented with seedling-trees 5-6 years old and 50-80 cm. hig which had been planted in ordinary garden-pots 16 cm. high and each containi $3\frac{1}{2}$-5 kilograms of earth. The pots were surrounded by wide air-tight sheet-zi cases, made so that not only was it possible to water the plants while the p was kept completely enclosed, but also that the soil did not come into a contact with the zinc. In this way all loss of water from the soil was exclud and a correct determination of the amount of transpiration secured. Tl experiment was also so arranged that the pots could not be exposed to tl

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[1] Von Höhnel, op. cit.

direct rays of the sun, and should therefore necessarily assume about the same temperature as the soil. Care was also taken that the seedling-trees experimented with, and which stood in the forest-nursery at Mariabrunner, should be under external conditions at least approximately similar to those of the different parts of the crowns of trees in the forest.

AVERAGE AMOUNT OF TRANSPIRATION FROM JUNE 1 TO END OF NOVEMBER (after Von Höhnel).

(The figures represent grams of water lost on 100 grams dry weight of foliage or needles.

Birch	67·987	Pedunculate and sessile oak	28·345
Lime	61·519	Turkey oak	25·333
Ash	56·689	Common maple	24·683
Hornbeam	56·251		
Beech	47·246	Spruce	5·847
Norway maple	46·287	Scots pine	5·802
Sycamore	43·577	Silver fir	4·402
Common elm	40·731	Black pine	3·207

Von Höhnel came to the conclusion regarding the amount of water used by hectare[1] of beech high-forest 115 years old, that 'according to various ssumptions it amounts to 3,587,000–5,380,000 kilograms of water during the egetative season. A beech wood, fifty to sixty years old, during the six months' egetative season transpired 2,330,900 kilograms per hectare, and a beech-pole ood, thirty to forty years old, transpired in the same period 680,000 kilograms.' Since the total rainfall, roughly speaking, during the whole year amounted to 000,000 kilograms, it corresponded excellently with the results of the transpiraon obtained in the experiment[2].

Besides the few trees that are hygrophilous during the vegetative season, nd alone occur in Central Europe, *there are also some that are markedly rophilous,* in fact some that will thrive on the driest desert-soil. It may rove to be one of the most interesting tasks for future botanical travellers investigate the conditions of life of these markedly xerophilous trees, r example those that appear in great variety in dry savannahs and in opical deserts.

The depth of their root-system renders it possible for trees to thrive in eas where long seasons of drought accompanied by great heat recur riodically, as in the Mediterranean countries, in Cisgangetic India, nd in the Soudan. The incorrectness of the opinion frequently held, at forest for its proper development requires atmospheric precipitations all seasons of the year, but especially during the vegetative season, satisfactorily shown by the occurrence of forest in regions with hot y seasons.

It is neither frequent atmospheric precipitation nor a rainy vegetative

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[1] 2·47 acres.

[2] Von Hohnel, op. cit., p. 290.

season that is of importance to tree-growth, but it is the continuous presence of a supply of water within reach of the extremities of the roots, and therefore at a considerable depth in the soil. It is immaterial during what season this supply is renewed. *There are forest districts with rain at all seasons of the year and others with dry seasons.* In districts with dry seasons *the rainy season may mainly or entirely coincide with the vegetative season,* as in the tropics or the interior of Argentina, or *the rainy season may coincide with a season that is relatively one of rest for vegetation,* as in extra-tropical districts with winter rain, including Mediterranean countries, the South Caspian district, Chili, California, South-west and South Australia.

The trees of a forest district with a dry vegetative season are dependent on water-supplies, collected during winter, and occurring at a considerable depth: they have corresponding characteristics. Their root-system penetrates deeply into the soil and is strongly developed, the stem and roots are frequently furnished with apparatus for storing water, the foliage is protected against rapid loss of water in hot dry air. In districts without a markedly dry season, or where this is at the same time a period of rest for tree-vegetation, the trees possess less perfect absorptive and protective contrivances. The foliage is delicate and transpires freely, the whole character is hygrophilous, but yet, in abnormall dry seasons, even hygrophilous trees, like all deep-rooted plants a opposed to shallow-rooted ones, show remarkable powers of resistance.

Thus during the rainless vegetative season of the year 1893, along th Rhine and in Western Switzerland, meadow grass grew to a quite inconsider able height only, and most perennial herbs in the meadows completely drie up before the end of June. Above the low straw-coloured sward of th meadows, lucerne, sainfoin, and other deeply rooted perennial herbs stoo out as fresh, sap-green, luxuriant bushes. The foliage of trees only in Jul became partially dry, and the fruit was as succulent as usual and grew t its ordinary size. Considerable supplies of water provided by the winte rain, therefore, still remained stored in the soil, though only accessible t deeply rooted plants. Yet here we are dealing with a vegetation tha is hygrophilous during the summer and under normal conditions is n exposed to drought associated with a high temperature.

Important observations regarding the significance of the amount rainfall and winter rain to the forest have been communicated b Woeikof:—

> 'I will not deny the influence of summer rain on forests, as on all other kin of vegetation, but atmospheric precipitations falling in the cold season, especiall when they occur in the form of snow, are far more important. Forests requi a continuous supply of water in the stratum containing their roots, in order to balance the continuous evaporation from the leaves. The colder the season

during which the precipitations occur, the finer these precipitations are and the more regularly distributed, so much the more water penetrates into the deeper strata of the soil, instead of running quickly over the ground and filling the rivers. Still better for vegetation is a covering of snow. Whether it fall early or late, the snow always melts in the spring, when vegetation requires most water. The permanent snow-covering of winter is the chief cause of the presence of forests in North Russia and Sweden, although the annual rainfall is much less there than in Western Europe. In the south, in the steppes the amount of snow that falls is much less, and even that which has fallen is blown away by the strong winds and collects in hollows, whilst the ridges remain free from snow[1].'

'A proof that woody plants exist without summer rain is afforded by the trees that are cultivated without artificial supplies of water in Southern Europe, where during summer frequently not a drop of rain falls for months, and yet even the vine bears plenty of fruit, and for this of course much water is needed. On the south coast of the Crimea, for instance, the vine-growers set not the slightest value on the summer rain; it has no influence on the abundance of the vintage, for it wets the soil too superficially. It is quite different with the rains during late autumn and winter, which are plentiful enough to render the soil thoroughly wet to the depth of a meter and to yield a supply for the whole of the succeeding summer.

'Not only vine-growers but all persons engaged in agriculture or horticulture know very well that frequent but light showers of rain do little or no good, and that it is better if in the course of a month there are two rainy days with a fortnight's interval between them, each giving 20 mm. of rainfall, than if the same amount were to fall in fourteen days at the rate of 3 mm. on each rainy day: since in the former case the soil is wetted to a greater depth, but in the latter case the rain-water remains almost entirely in the uppermost stratum of the soil, provided that drought prevailed before the rain fell[2].'

'A consideration of the country near the Volga and the Eastern Caucasus has convinced me of the close connexion between the cultivation of winter corn and forest growth. In districts with a cold winter (below 0° C.) a continuous snowy covering is necessary, so that the soil in the spring may be completely permeated with moisture; summer rain cannot compensate for the absence of snow because of the irregularity of its occurrence and the great amount of rain that falls at one time and forthwith runs off without benefiting the soil.

'In more southern districts regular winter rains are necessary in order to render the cultivation of winter fruits possible. If the rainfall is scanty, cereals will grow and yield a safe harvest, but forests cannot exist. This, for instance, we see on the peninsula of Apsheron. There winter wheat is everywhere sown; it yields unsatisfactory but safe harvests, for wheat requires moisture only in the uppermost stratum of the soil. If the atmospheric precipitations in autumn and winter are more plentiful, forest vegetation can also thrive. This, for instance, we see at Leukoran. Somewhat to the north of the town are some colonies of Russian sectaries, who sow winter wheat and barley exclusively.

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[1] Woeikof, I, p. 243.

[2] Id. II, Bd. II, p. 255.

The yield is excellent, but summer fruits cannot be cultivated; the soil dries up so completely even in May that it is impossible for the plants to flower. In this district there are forests with large, tall-stemmed trees. The supply of water that is collected in winter suffices to cover the evaporation during summer[1].'

The greater the amount of water in the soil, whether it is derived from rain or from percolating water telluric in origin, the greater in general is the height of the trees and the richer their foliage. However, the tallest known trees, such as the Sequoia of California and the Eucalyptus of Australia, are not inhabitants of a specially moist soil; here specific characters are largely involved. With a decreasing supply of water in the soil, the height of trees and the surface of their foliage generally diminish, yet many lofty trees are still found on dry soil, for example in tropical savannahs. The driest districts possess only stunted trees. *Tree-growth is entirely prevented only by such a degree of drought as excludes all kinds of plants with the exception of the lower cryptogams.*

The amount of water necessary for the well-being of hygrophilous trees obviously increases with the temperature. In the temperate zones, hygrophilous trees[2] thrive with a rainfall that in the tropics would satisfy only xerophilous trees. This matter is considered more in detail under the special climatic headings dealing with the individual zones. Here however it may be mentioned, that in the tropics—with the obvious exception of the banks of sheets of water—hygrophilous trees require an annual rainfall of at least 150 cm., whereas in the cool regions of the temperate zones 60 cm. are sufficient. The occurrence of lofty xerophilous trees depends less on the amount of rain than on specific characteristics.

Another important factor in relation to the growth is the *amount of aqueous vapour in the atmosphere*, in which of course it is not the absolute but the relative vapour tension that is of significance. In this respect trees are less favourably situated than plants of less height, *for their transpiring surfaces are situated in higher and therefore drier and more agitated strata of the atmosphere.* The larger hygrophilous trees, when in leaf, require an average relative humidity of about 80 %, descending to 60 % for a few hours only during the day. Less atmospheric humidity suffices for xerophilous trees, and some species, even when in leaf, appear able to endure without injury a relative humidity of 30 %, lasting for some time.

As has been explained in an earlier chapter[3], it is of the greatest importance in relation to *tree-growth whether the surrounding atmospheric strata are usually at rest or in motion*, as the wind causes a vast increase in transpiration. *Dry winds during frosty weather determine the polar limit of the growth of trees.* Before the final proof of the fact was

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[1] Woeikof, I, p. 243.

[2] Trees hygrophilous in the vegetative season.

[3] See p. 77.

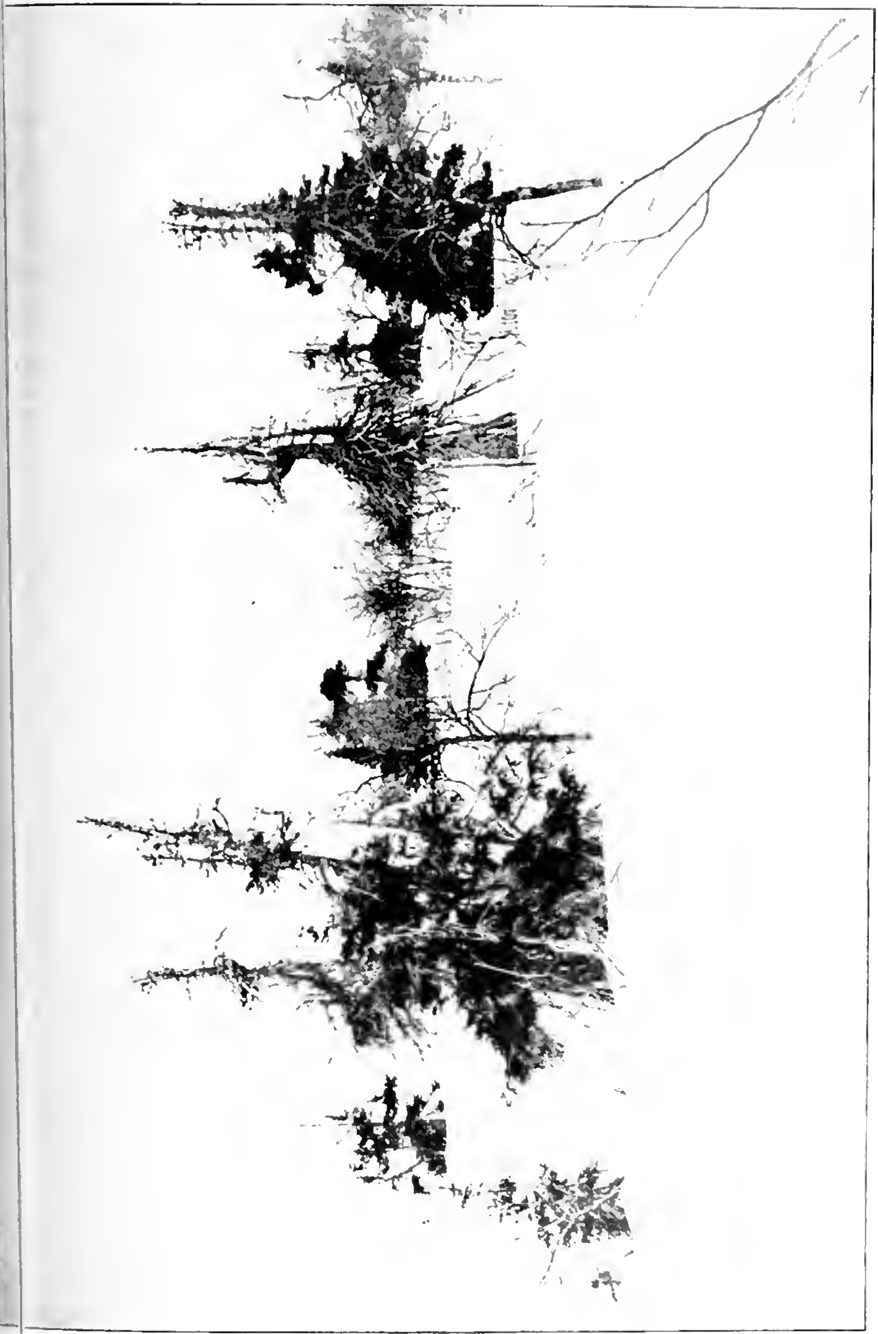

FIG. 90. Limit of the spruce-forest near Lymbes-Sijt, Russian Lapland. After Kihlman.

supplied by Kihlman, very hazy ideas prevailed in geographical botany as to the causes of the absence of trees within the arctic zone. At one time it was ascribed to the cold, then to the shortness of the vegetative season, then to a combination of both these factors, although no character founded on the physiology of trees could in any way support such an assumption. That severe and persistent winter cold is not incompatible with the growth of trees follows from the fact that the lowest degree of cold known anywhere occurs in the Siberian forest district[1].

The significance of the wind in relation to tree-growth was already recognized by Middendorff, though not on physiological grounds, as appears from the following extract from his work on Siberia[2]: 'I am ready to maintain that in the extreme north a favourably formed shelter against the wind is of much greater importance than the geographical latitude or altitude above sea-level. A shelter a few fathoms high favours tree-growth there much more than fifty thousand or a hundred thousand fathoms less of northern latitude.'

It is well known that the north polar tree-limit does not form a sharp line of demarcation between forest and treeless tundra. Tree-growth becomes gradually reduced before it entirely disappears, as was clearly pointed out by Middendorff and especially by Kihlman. Middendorff gives a rough description of the phenomenon without entering into its causes:—

FIG. 91. Juniperus communis. Tabular growth. At the limits of tree-growth. After Kihlman.

'If we follow the tree-limit over large tracts of country and observe all the different species of trees appearing on them round the North Pole, we see tha they all in like manner become stunted and degenerate into gnarled growths (Fig. 90): both broad-leaved species and conifers eventually become dwarfed into veterans, two feet or even one foot in height[3].'

The deformities that tree-growth experiences near its polar limit originate, as Kihlman shows, from desiccation in winter, the increase o which in the northerly direction finally checks all tree-growth:—

'On observing the development of the juniper, as it appears in the highe forest region or in the interior of the tundra (Fig. 91), it will be found that th tip of the main axis regularly dies as soon as it has attained a certain, somewha variable, height above the ground. The side branches however continue to grow obliquely upwards, or almost horizontally, until their tips also die at the fixe

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[1] See p. 40. [2] Middendorff, op. cit., p. 683. [3] Id. p. 675.

fatal level. As the juniper has absolutely no power of emitting suckers from its roots or even supplementary shoots from the base of the stem, there results a low tabular little tree, whose dense umbrella-shaped crown attains a diameter of 3-4 meters, and whose central cylindrical stem at an age of 300-400 years may have a diameter of more than thirty centimeters. The height of the whole plant is, on the average, about 1 meter, but may occasionally reach nearly 2 meters. . . . If the little stem, which is in great request as firewood, should remain standing long enough, there comes, sooner or later, a moment when the adherence of the roots to the soil can no longer resist the increasing pressure upon the crown by the wind: the little tree falls over and is obliquely held up by the half of its crown that is now turned downwards, whilst its upper half quickly dies off and disappears along the critical line.

'The line above which all twigs perish is defined by the average height of the snow-covering at the commencement of the thaw. . . . In April, 1889, I was able to satisfy myself that the living juniper branches reached close up to the surface of the melting snow, or that at the most they projected a few centimeters above it. I have convinced myself that the juniper in Russian Lapland can withstand the winter only if for several months it is completely covered with snow[1]. . . . The birch also assumes the form of tabular or closely cropped bushes, which are quite characteristic of the tundra landscape, n accordance with the wide distribution of this tree beyond the limit of forests[2].'

Finally, as an extreme case, Kihlman mentions the formation of mats, 'that merely reach the height of the surrounding felt of lichens or undershrubs, but which occasionally attain quite considerable dimensions in the horizontal plane. . . The shallow-rooted spruce assumes this form most successfully (Fig. 92); long the tundra belt near Orlova I saw mat-like spruces from one to five meters long, the thin sterile twigs of which had crept about in the felt of lichens nd evidently all sprang from one seedling plant. . . . In all these mats one nds that the *one-year-old shoots, in so far as they project above the level of the urrounding tufts of moss and lichens, are dried up and defoliated*[3].'

As will be shown in a later chapter[4], the conditions in regard to the movements of the air also determine the vertical limit of forest vegetation.

It appears to be advisable to group together *shrubs* and *dwarf-trees* as *rushwood.*

The existence of brushwood also is determined by the amount of water n the soil, and the season when the water is renewed is a matter of inifference. The amount of water necessary for the well-being of brushwood is less than that for tree-growth: when it increases, tree-growth ppears. Like forest, brushwood thrives better in damp than in dry ir, and better in calm than in agitated air; in both respects, however, is more accommodating than is tree-vegetation.

A good woodland climate is, then, composed of the following elements:—

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[1] Kihlman, op. cit., p. 71.

[2] Id. p. 73.

[3] Id. p. 68.

[4] In Part III, Sect. IV.

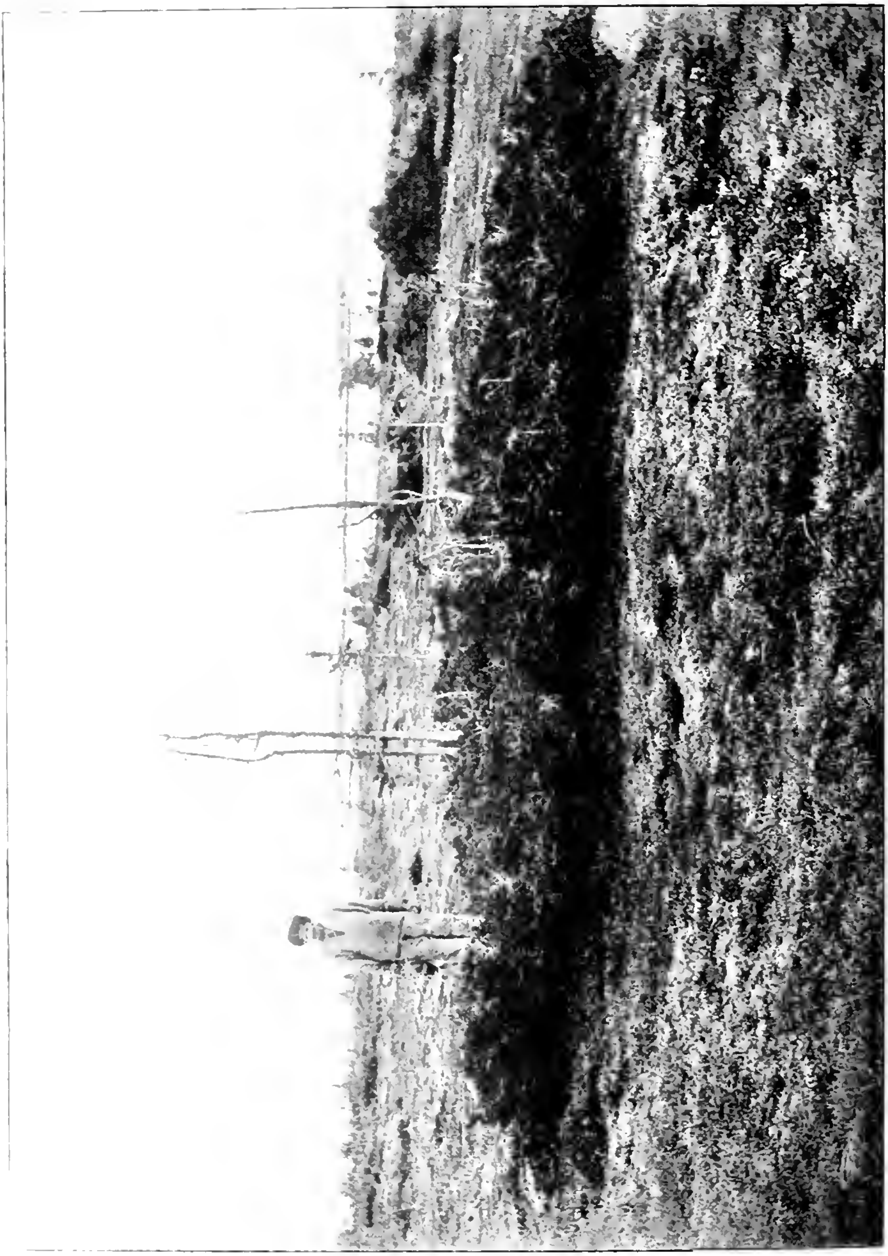

FIG. 92. Shrubby growth of spruce. From the polar limit of tree-growth. Near [illegible], Russian Lapland.

a warm vegetative season, a continuously moist subsoil, damp and calm air especially in winter.

Immaterial for woodland is:—whether the moisture in the soil is supplied by rain or by telluric water, whether the rain falls frequently or rarely, or whether the rain falls during the period of activity or of rest. To the optimum of the woodland climate corresponds the hygrophilous tree, and to the lower grades of woodland climate, in descending order, correspond the tropophilous tree, the xerophilous tree, and brushwood.

Hostile to woodland in the higher latitudes is a climate with dry winters, because, during the winter, trees cannot replace the water lost n transpiration.

iii. *GRASSLAND CLIMATE.*

The demands that grassland makes on climate are quite different from those of woodland. As already stated, the grassy covering is the controlling feature of grassland. Formations of perennial herbs partially or entirely devoid of grasses cannot successfully contend against woodland growth, and are found only in deserts, as in the so-called Artemesia-steppes, possibly in most cases mingled with brushwood.

Herbaceous grasses are in the main inhabitants of temperate lands. n the tropics, we find luxuriant grassland, rich in grass, chiefly on the high plateaux that are periodically cool, for example in the interior of Brazil and in Central Africa, and a scanty growth of grass only where he temperature during the vegetative season constantly exceeds 30° C. n the daytime. It cannot be decided at present why high temperatures o not suit most herbaceous grasses. During the season of rest, the ighest temperatures that occur naturally do not injure the parched carpet f grass.

When compared with woody plants and many perennial herbs, the rasses composing the covering of grassland are *shallow-rooted* plants, nd therefore suffer in prolonged drought during the vegetative season. t has been already mentioned what disastrous effects the dry vegetative eason of the year 1893 had on grasses in contrast to woody plants nd deeply rooted perennial herbs, and Woeikof has also cited similar observations. A climate in which the dry and hot seasons are ynchronous, like that of the countries bordering on the Mediterranean, consequently unfavourable to the growth of grass, and therefore also o grassland. Thus in August, 1886, near Lisbon I saw the grass and ost herbaceous perennials quite dried up, while deeply rooted thistles ere blossoming gaily and trees displayed their foliage unimpaired.

Moisture in the subsoil has little influence on the covering of grass; ly moisture in the superficial soil is important to it. As the latter soon lost owing to evaporation and filtration, frequent, even if weak, atmospheric precipitations are necessary. During the resting season grasses can endure great drought without injury.

Grasses do not rise so high above the surface of the ground as do trees and consequently occupy damper atmospheric strata. Very dry air, then, does them as little injury during the resting period as does the lack of rain. The lowest atmospheric strata are also the calmest so that grasses suffer less than woody plants from the drying action o the wind. Winds that prevail during the dry seasons or during th winter, and that are so injurious to trees, are devoid of significance i relation to grasses.

A good grassland climate is then composed of the following elements:— frequent, even if weak, atmospheric precipitations during the vegetativ season, so that the superficial soil is kept in a moist condition, an further a moderate degree of heat during the same period.

Almost immaterial for grassland are the following:—Moisture in th subsoil (except when the superficial soil has a great power of capillar conduction), dryness of the air especially during resting periods (dr season, winter), and winds.

Hostile to grassland in the higher latitudes is drought in the chi vegetative season of grasses (spring, early summer).

A woodland climate leads to victory on the part of the woodland, grassland climate to victory on the part of the grassland. In transition climates edaphic influences decide the victory. Strong deviations from woodland or grassland climate produce desert.

That the interior of continents, especially outside the tropics, affor poorer tree-vegetation than districts near the coast, is due in the fir place to the great dryness of the air that prevails there during certai seasons and especially in winter. Middendorff adduces evidence of t unfavourable influence of a continental climate:—

> 'At the same latitude, 58° N., in which at Yeniseisk I plunged into the fores of Siberia, at Sitka conifers that are so closely allied to the Siberian ones to be distinguished from them specifically only by specialists, attain a height 160 feet with 7–10 feet diameter. . . . From Yeniseisk going northwards, according eye-measurements taken in Livland, one could hardly ascribe to the forests age of more than a half-century, certainly not a century[1]. . . . Also beyond t limits of the frozen soil, under the most favourable conditions, in Southern Siber the species of trees growing there attain no considerable dimensions, never the that they or their representatives attain in Europe[2]. . . . At least 99% of apparently mature trees in the forest, even in the favourable localities of Southe Siberia, were not more than 1 foot to 1¼ feet in diameter. Three or four centur appear, even in Southern Siberia, to be the extreme age-limit to which the bet trees in the forest attain on the average. The average life of the trees of a Siberi

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[1] Middendorff, op. cit. p. 631.

[2] Id. p. 632.

timber-forest I must estimate much lower[1]. . . . If we glance over the results obtained in the above paragraphs, we cannot help expressing the opinion that *n extreme continental climate is unfavourable to tree-growth, which can only attain ts maximum development in a maritime climate*[2].'

The woodland-climate in its various gradations and the grassland-limate remain qualitatively the same in all the zones, but differ uantitatively from one another, so that their elements can be expressed umerically only for each zone treated separately. The meteorological ables on which the opinions here developed are based are therefore elegated to a later part of this book[3].

iv. *METEOROLOGICAL TABLES.*

The number of districts for which really useful and complete meteoroogical observations, extending over prolonged periods, are available, is ot yet considerable. Yet in reference to several regions, that are well haracterized both as regards their climate and vegetation, there are lready data which are sufficient in both these respects as a foundation for eneral conclusions. Meteorologists do not always take into consideration ll the factors that concern the climatic knowledge of vegetation; though his is partly the fault of geographical botanists, who formerly made ery modest demands on meteorology owing to their misapprehension s to the significance of many climatic elements.

A Table really fit for use from a phytogeographical standpoint should, in my pinion, contain the following headings:—

LOCALITY . . . .

Longitude . . .; Latitude . . .; Altitude . . .; Mean Barometric pressure (only at high ations) . . . .

	Temperature.		Rainfall.		Relative humidity.				
lonths.	Mean Min.	Mean Max.	Amount.	Days.	Mean Min.	Mean Max.	Sunshine. Hours.	Strength of wind.	Evaporation.
un. . .									
eb. .									
ar. .									
&c.									

ean annual extremes . . . .

The variations in the atmospheric pressure carefully noted by meteorologists e devoid of significance to vegetation. Of the data regarding temperature, ose of the daily minima and maxima are the most important, in fact quite fficient. Records of the hours of observation are hardly necessary, since the inima occur at night and the maxima during daytime. The former give us the mperatures at which the processes of growth chiefly occur, the maxima are pecially important as factors influencing transpiration. The mean diurnal

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[1] Middendorff, op. cit., p. 632.

[2] Id. p. 640.

[3] See Part. III.

temperature is worthless in geographical botany, unless at least the amplitude of the daily variation is also given. Mean annual extremes are important, not indeed for the study of formations, but sometimes for the range of species; the mean annual temperature is quite unimportant.

Data regarding the absolute rainfall are very useful, but not sufficient when taken alone. Much depends on the fact whether the rain falls in relatively rare but heavy showers, or in frequent and light ones. Of this we are informed under the headings 'Rainfall in Days' ('Rainfall in Hours' would also be useful, but this is hardly ever given) and 'Hours of Sunshine.' The last are also among the factors influencing transpiration.

Among the most important headings is 'Relative Humidity.' High atmospheric humidity promotes growth and depresses transpiration; low humidity acts in the opposite direction.

To winds great importance is attached owing to their desiccating action. The heading 'Evaporation' facilitates direct conclusions as to the strength of transpiration.

3. THE EDAPHIC FORMATIONS.

i. *EDAPHIC INFLUENCES IN GENERAL.*

The influence of differences in the physical and chemical nature of the soil is generally confined, as has been previously stated, to the finer differentiations within the type of vegetation and of flora which the climate determines. This edaphic differentiation is often extremely rich, as many species correspond so exactly to a constellation of external factors, that even slight changes in the latter remove the plants from their oecological optimum and consequently cause their downfall in the struggle with their competitors.

Suppose for instance that we consider a meadow having a somewhat uneven surface. Many of the predominant species especially among the grasses are present everywhere, so that such a meadow may be described as a single formation. Other species, on the contrary, appear confined to quite definite kinds of soil, so that the meadow presents a chequered appearance. This is especially the case where two or more allied species have to divide the soil between them. If, for instance, Primula officinalis and P. elatior are present, we can from a distance distinguish by means of the dissimilar tints of the flowers the drier spots occupied by the former, from the damper spots where the latter grows. We shall never find them growing side by side. In a similar way, Ranunculus bulbosus, R. acris, and R. repens frequently denote three grades of increasing humidity. On the Simplon, two species of dwarf Senecio, S. incanus and S. uniflorus, frequent the dry alpine meadows, often close together but never intermixed. I found the large-headed Senecio uniflorus only in places where the meadow-soil extended in a thin coating over stones

FIG. 93. Fringing-woodland along a river bank,
Department of Nebraska University.

nd rocks, whilst S. incanus exclusively occupied spots where the soil was deeper. The hybrid between the two species was confined to the place between these two habitats.

Such a grouping is determined much more rarely by chemical than by physical differences in the substratum, since the latter usually change much more rapidly and are more varied than the former.

Much more marked than in the cases of the above description are the effects of the soil in edaphic formations, where the type of vegetation s determined, not by the climate, but by the soil, so that it remains essentially the same in both woodland and grassland districts. Climate exercises merely a differentiating action in edaphic formations, just as does the soil in climatic formations.

The presence of plenty of water in the soil, due to the infiltration of continuous supplies of water, determines the existence of certain edaphic ormations, but it is the mechanical texture of the substratum that determines the existence of others. Chemical differences in the soil have at most merely a regulating or differentiating action. Only large quantities of easily soluble salts, especially common salt, or of free humous acids can efface the climatic character of vegetation and evoke, or instance, xerophytic formations in a hygrophytic climate.

ii. *EDAPHIC FORMATIONS DUE TO TELLURIC WATER.*

In the neighbourhood of water the soil remains constantly moist, down o a considerable depth; this is the case even in a grassland climate, where the rain merely wets the superficial soil. Accordingly, we find he banks of rivers and lakes stocked with woods as far as infiltration xtends. These are often mere bush-woods, but not unfrequently developed s luxuriant forests (*fringing forests*) not inferior to those of the best orest climate (Fig. 93). Such edaphic woodlands are evidently always istinguishable from climatic ones by their dependence on collections f water, whether this be superficially exposed to the air, or, as in *oases*, ubterranean.

Stagnant water determines the origin of those formations that are ermed *swamps*, which are again subdivided into several groups, of hich the peat *moors*, and the *mangroves* of tropical coasts, are the est characterized. Swamp-formations are but slightly affected by mospheric precipitations, and therefore exhibit essentially the same egetation both in a woodland climate and in a grassland climate; on he other hand, their two most striking forms, moor and mangrove, epend on the supply of heat, the latter for reasons not yet known, e former because the chemical processes on which the formation of eat depends come into play at a low temperature only.

iii. *OPEN EDAPHIC FORMATIONS.*

In many places the physical texture of the soil is such that it doe not permit the existence of closed formations. A feature that in desert is due to climate. in this case is due to the nature of the soil. Th soil is occupied by those plants that are able to establish themselve on it in spite of the unfavourable conditions. There are but few o such plants, however, and the formation remains open throughout, s that there is still space left for many plants, and accordingly there is n struggle between competitors. Whatever the climate may be, suc places possess the character neither of woodland nor of grassland, bu produce a confused mixture of woody and herbaceous plants that ar quite independent of one another.

To the open formations of the kind just described belong, in the firs place. those of *rock-plants.* Naked rock, after cooling down from molten condition, or after separation from a larger mass of roc remains bare of vegetation for a longer or shorter period. Sooner c later, sooner in a damp climate than in a dry one, plants appear on it surface, at first small Algae and lichens later on, and after these mo accommodating plants have produced a little humus, mosses and highe plants. The vegetation on the surface of rocks or stones may be terme that of *lithophytes.* Crevices in rocks, in which more finely graine components and more water accumulate than on the surface, produc a somewhat more copious vegetation, that of the *chasmophytes.* formation of plants on rock consists either of lithophytes only, especiall if the rock is free from cracks, or of lithophytes and chasmophytes.

Lithophytes are low, flat, spreading plants, the superficial developme of which is sometimes determined chiefly by the roots, sometimes by t shoots, which by the help of small roots—or in thallophytes by rhizoi —become attached to the hard substratum. Mosses and phanerogan frequently assume the form of cushions. Chasmophytes, as opposed lithophytes, are long straggling plants, since their substratum often li at the bottom of a crevice at a great distance from its mouth ar therefore from the light. Hence, many chasmophytes possess extreme long rhizomes and roots, yet such extreme forms are less frequent rocky crevices than among gravels, which owe their origin to the di integration of rocks under the influence of atmospheric agencies, and whi usually form large heaps at the foot of the masses of rock from whi they have fallen, or create the moraines along the course of glacie On these gravels lithophytes are much less frequent than chasmophyt and the chasmophytes exhibit the frequently extraordinary growth length to which reference has just been made.

Some of the fragments of rock come down to the water-cours where mutual attrition reduces them, partly to pebbles, partly to sand, and where the weathered felspars are ground into finely grained earthy clay. A change in the water-level leads to deposits in river-beds and along their banks of masses of pebble, sand, and clay, which are sometimes more, sometimes less, frequently, or only exceptionally, covered again by the water. Such deposits bear an open vegetation, which is in some cases more transitory, in others more lasting, and the species growing on them are for the most part characteristic of such habitats (Figs. 94-96).

FIG. 94. Stony tracts in the bed of Craigieburn river, near its opening into Lake Pearson, in the rest region of the Southern Island of New Zealand, 600 meters above the sea. Ozothamnus depressus, ook. f., and Epilobium melanocaulon, Hook. f. From a photograph by Cockayne.

The fragments of the rock finally reach the sea along the water-courses. f the sea-shores are flat, sand, clay, and small pebbles are thrown up y the action of stormy waves on the land to distances more or less bove the usual high tide-mark, and their deposits, if neither too much rned over by the wind nor carried back into the sea, within a few onths bear some vegetation. If this can maintain itself, these new eposits become gradually fixed and definitely united to the land.

Of the sea-shore deposits, sand is the most extensively developed, as e wind carries it further inland than clay and pebbles, and frequently heaps it up into *dunes* (Fig. 97). The formations of the sandy sea-shore and of dunes serve as excellent examples of the vegetation of *psammophytes*, which are specially well developed in such spots. These sandy strips of coast are usually subdivided into three zones—the *foreshore*, between the ordinary high tide-mark and low tide-mark, the flat *mid-shore*, above the ordinary high tide-mark, and the *dunes*, which are heaped up like hills between the shore and the mainland.

Dunes are not always present. The sandy coast frequently rises quite gradually, without any sharp separating line, into woodland or grassland, or the mainland rises abruptly beyond the flat shore, without assuming the character of dunes. Such is the case either when the stretch of coast is relatively calm or where the sand is either coarse-grained or largely mixed with pebbles and therefore heavier for transport by the wind.

FIG. 95. Grand Cañon of Colorado, Arizona. Stony river-bed. In the background are the desert that correspond to the climate. From a photograph.

The following description of the vegetation on the sandy sea-shore of Java can be taken generally as representative of the conditions of vegetation in such habitats:—

The southern coast of Java is in parts covered with tracts of dune quite similar to those which, for instance, are so extensive along th

North Sea. Behind the sandy shore, here rich in lime, there rises first a range of dunes poor in plants, behind which there are dunes that are better clad and which serve as a transition to the mainland. Only the flat shore and the dunes lying nearest the sea exhibit in their vegetation the characteristic influence of the habitat. Difficulty in fixing themselves to the loose substratum, difficulty in obtaining a supply of water, a struggle against the sea-wind, the use of the wind for the transport of fruits on the smooth sandy surface, all these may at once be inferred from the remarkable forms that occur.

FIG. 96. Nebraska. Sandy deposits with open mixed formation of plants in a river-bed. In the background, grassland formation (prairie) corresponding to the climate, and bare rocks. Photograph rom the Geological Department of Nebraska University.

Adaptations in relation to such conditions are combined in the clearest manner in Spinifex squarrosus, a rigid bluish grass, with large globular inflorescences and infructescences[1], which latter appear to be composed of long radially arranged needles, the very long bracts. Frequently Spinifex alone covers the outermost dunes bounding the Indian Ocean with numerous apparently independent tufts; a closer inspection hows that, in many cases, even widely separated tufts are united by tolons more or less imbedded in sand, varying in thickness from that

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[1] See Fig. 369 for an illustration of the quite similar infructescence of Spinifex irsutus.

of a quill to that of a finger, and producing roots and tufts of leaves at their nodes. The tufts, like our sand-grasses, owe their pallor to a coating of wax.

The advantages due to this mode of growth in such habitats are obvious. The creeping shoots, firmly anchored by numerous deeply penetrating roots, offer a much better resistance to the wind, and incur much less danger of being torn out of the loose shifting substratum than do erect plants. It is therefore no wonder that many other littoral plants adopt a mode of life similar to that of Spinifex, such as

FIG. 97. Sand-dunes near New Brighton on the east coast of the South Island of New Zealand, with Scirpus frondosus, Banks et Soland. From a photograph by Cockayne.

Remirea maritima, which is almost ubiquitous in the tropics, and th still commoner and more widely distributed Ipomoea Pes-caprae (I. biloba) the extremely long and distantly rooted creeping shoots of which cove and fix the sand with a narrow-meshed net, and also the species c Canavalia that physiognomically resemble Ipomoea Pes-caprae. In th north temperate zone, the sea marram (Ammophila arundinacea) fixes th loose sand of the dunes by means of its extremely long and richly subdivide rhizomes, and so do some other grasses, such as Elymus arenarius an Agropyron junceum. All these plants have the important faculty c again growing out of the sand, after having been covered by it.

In many other respects also, Spinifex squarrosus exhibits a close connexion between structure and mode of life, for example in its leaves, the waxy coating and structure of which express the difficulty in obtaining water on the high permeable and salty dunes. Its spherical infructescence, however, formed of stiff bristles and nearly as big as one's head, claims special attention. When it is ripe, it breaks off from its dry stalk and becomes the sport of the wind. Rolling and dancing, it is hurried along the smooth surface of the sand and allows its fruits to drop. The bristles are gradually worn away, and the infructescence, now become cumbersome, is buried in the sand with the rest of the fruits.

FIG. 98. Shore of Garden Island, Lake of the Woods, Minnesota. Salix fluviatilis predominant. Besides this, Capnoides micranthum, Chenopodium album, Polygonum ramosissimum, and other plants. From a photograph by MacMillan.

Spinifex squarrosus, as regards its mode of growth, belongs to a very widespread type. A peculiar type, on the other hand, is formed by the species of Pandanus on the sandy sea-shores, which become firmly anchored in the shifting sand by prop-roots that grow down from the branches (Fig. 122).

In many plants living on the sandy sea-shore, at all events particularly n those that occupy sheltered spots, such obvious adaptations do not occur. Yet compared with other plants they have always an extraordinarily deep and extensive root-system.

Sandy shore-formations, similar to those by the sea, are also found by many saline or fresh-water *inland lakes*; but there the dunes are usually less pronounced in character, owing to the reduced strength of the wind and the smaller amount of sand. The formations in question have been described in much detail and in a very instructive manner by Conway MacMillan, as they occur about the Lake of the Woods, a moderate-sized lake (about 1,500 square miles in area) situate between Minnesota and Canada. The banks are partly rocky, partly loamy, partly sandy, and partly covered with humus. Fig. 98 shows the sandy flat shore, with a vegetation consisting chiefly of willows. Fig. 99 shows low dunes grown over with various grasses and shrubs.

FIG. 99. Dunes on the Île aux Sables, Lake of the Woods, Minnesota. Populus tremuloides, Juniperus communis, and Prunus pumila in the foreground and to the left; Elymus canadensis and Artemisia in the background. On the top of the dune, stunted little trees of Celtis occidentalis and Cerasus pennsylvanica. From a photograph by MacMillan.

Obviously the sandy shore of fresh-water lakes differs from that of the seaside, owing to its poverty in salt, and confers a xerophilous character only on the vegetation of the higher dunes.

iv. *TRANSITION FROM EDAPHIC INTO CLIMATIC FORMATIONS.*

Between the bare hard rock and the finely grained soil that finally esults from it, for the possession of which there is a struggle between voodland and grassland, there is, according to what has been said bove, a series of open transitional formations, which possess the character either of woodland nor of grassland, and which assume nearly the same ppearance even in dissimilar climates, and owe their individuality chiefly o the mechanical texture of the soil. The transformation of these ransitional formations into the definite ones of woodland and grassland s continually proceeding under our eyes, but so slowly that we can bserve only a part of the process directly, and can form an estimate f their sequence only by comparing their condition at different ages. n spite of the highly interesting nature of the development of formations ery slight attention has hitherto been paid to it.

An excellent piece of work in this respect is Treub's description of he *vegetation at Krakatoa* three years after the well-known eruption, hich covered the whole island with a hot deposit of pumice and shes.

As has been already stated[1], the vegetation of Krakatoa at the time of reub's visit consisted chiefly of ferns (eleven species), whilst phanerogams ppeared only isolated and almost exclusively on the sea-shore. Ferns us form the earliest vegetation on volcanic islands—or rather only e earliest *macroscopic* vegetation. They are preceded by a microscopic egetation of *Cyanophyceae, which cover in a thin film the whole surface f ash and pumice, and prepare the soil for the development of ferns.*

By the advice of my honoured friend Treub, I visited the volcano Gunong untur in West Java, which, by the eruption of 1843, had been covered own to its base with large hot heaps of detritus[2]. Naturally I found e vegetation there in a far more developed stage than Treub did in rakatoa, yet it was still quite open and on the whole very poor. There ere absolutely no trees, but shrubby and herbaceous plants of very rious species were present (Fig. 100). As in Krakatoa, ferns were irly numerous both in species and individuals, without however forming e main mass of the vegetation. The most essential part was played plants that grew as epiphytes in the neighbouring woods, namely any orchids, as well as several ferns and the shrubby Rhododendron vanicum, which found suitable conditions here, such as a hard substratum, mp air, and rich illumination, and which could thus, undisturbed by mpetitors, take possession of the soil. It was also interesting to find merous specimens of a Nepenthes, the pitchers of which held such

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[1] Page 80.

[2] See Junghuhn. op. cit., Vol. II. p. 392

a quantity of water and insects that the occurrence of this luxurian and not remarkably xerophilous plant on such a soil did not appea wonderful.

As the result of their investigations on the sandy and loamy plain of th Camargue, which is 35,000 acres in extent and lies in the Rhone delt Flahault and Combres have described the gradual conversion of the bar soil within reach of storm-tides first into open, and later into close formations. They show that if a flat shoreland tract is withdrawn f

FIG. 100. Earliest vegetation on a new volcanic soil (pumice, ashes, &c.) in West Java. From a photograph.

a long time from the influence of the waves, the earliest vegetation produces is composed of tufts of Salicornia macrostachya growing wide apart (Fig. 101). A shoreland thus colonized is frequently flooded winter storms and again deprived of all vegetation; occasionally, howev the first settlers become able to maintain themselves and collect amo and on their bushy branches a quantity of sand, small indeed, b sufficient to render possible the appearance of some new plants, such Salicornia sarmentosa, Atriplex portulacoides, and Dactylis sarmento

Sand, and gradually humus, accumulates round these groups of plants, so that in time they form the centre of little sandy hillocks, termed touradons,' only about a decimeter high.

The touradons, thanks to the matting of the roots and stolons, already ossess considerable powers of resistance and can withstand even the inter floods. Every year they increase in breadth, so that after a few ears they attain a diameter of one to two meters and already support bout twenty species of halophytes, among others Inula crithmoides, species f Juncus, Statice, Plantago, and several grasses. Slowly, continually ruggling against the floods, the touradons gradually raise the soil, hilst the rain continually sweetens them and renders them suitable for e growth of non-halophytes.

IG. 101. From the Camargue. Horizontal sandy flats liable to be flooded by storm-tides, with the earliest vegetation of Salicornia macrostachya. After Flahault and Combres.

The dunes in the Camargue are also very instructive. In some parts the coast they form parallel ridges separated, valley-like, by the iginally flooded tract with its touradons. Their vegetation constantly creases inland. Evidently there was once a general upheaval of the ound; and dunes as well as touradons have remained as geological urvivals. The succession of the dunes exhibits all intermediate stages, om the commencement of vegetation on the outermost dunes to the closed formations of the innermost, where the psammophytic characte is only weakly exhibited.

The vegetation of the outermost dunes is scanty, but highly characteristic. There are found various grasses, sedges and rushes, besides a fe other plants with long creeping rhizomes, taking root at the nodes, fo example Juncus maritimus, Cynodon Dactylon, Scirpus Holoschoenus species of Agropyron, Ephedra distachya, Eryngium maritimum; als species of plants with extremely deep rhizomes and roots, for exampl Ammophila arundinacea, Echinophora spinosa, Clematis Flammula. Mos of the species have a halophilous as well as a psammophilous characte

FIG. 102. From the Camargue. Forest of Pinus Pinea with Juniperus phoenicea and oth plants as underwood. The depression in the centre is chiefly clad by psammophilous grasses. Aft Flahault and Combres.

On the oldest dunes, but also on flatter elevations ('radeaux') coev in origin, the edaphic influences are much reduced. Trees and tall shru appear, and most of the species there are the same as occur far fro the sea and on various kinds of soil. Yet the absence of several speci common elsewhere shows that the soil is relatively new. Fig. 1 presents a picture from the older dunes. The higher places are occupie by a pinewood the rich underwood of which is chiefly formed by Juniper phoenicea, but by other characteristic Mediterranean shrubs as well, suc as Rosmarinus officinalis, Phillyrea angustifolia, Cistus salvifolius. T lower sites bear chiefly psammophilous grasses.

4. LIFE OF THE PLANT-COMMUNE IN THE FORMATIONS.

The various plants composing a formation indubitably stand in the nost manifold relations to one another as well as to the animals—worms, nsects, birds—that inhabit the formation. The question regarding the nature and mode of action of these relations promises to yield most mportant conclusions bearing on the oecological explanation of the ormations, but has hitherto been but rarely approached, and then only n individual cases[1]. The floristic branch of geographical botany, on the other hand, has indirectly yielded valuable material by the compilation of lists of species that are constantly found growing together. Thus, according to Flahault, there are always found accompanying Quercus lex in France, thirteen other species of plants, amongst them Cistus nonspeliensis, Lavandula latifolia, Thymus vulgaris; whilst Fagus sylvatica s always accompanied by the following amongst other species: Vaccinium Myrtillus, Rubus Idaeus, Oxalis Acetosella, Mercurialis perennis. Höck has drawn up such lists for several German formations. Naturally they do not hold good for all regions nor for all kinds of soil, as to each agglomeraion of external factors there must correspond a definite grouping. This fact obviously does not take from the value of such compilations, t least if they are accompanied by accurate data regarding climate nd soil.

To the same category of questions belongs an inquiry into the cause of he social growth of some species and the invariably isolated appearance of others. It appears, however, superfluous to inquire more closely into he hypotheses that have been put forward in regard to these matters, or they have as yet no solid foundations, except in the case of a few tropical formations which will be discussed further on[2].

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[1] Schimper, op. cit.

[2] See upon this question de Candolle, op. cit.; Warming, op. cit. p. 106; especially randis, op. cit.

SELECT LITERATURE.

1. The Climatic Formations.

Fliche. Un reboisement. Annales agronomiques. 1888.

Henry, Ed. La végétation forestière en Lorraine pendant l'année 1893. Revu générale de botanique. Tome VII. 1895.

Junghuhn, F. W. Java, deszelfs gedaante, bekleeding en invendige structuu German Edition by Hasskarl. Bd. I und II. Leipzig, 1854.

Kihlman, A. O. Pflanzenbiologische Studien aus Russisch-Lappland. Acta So pro Fauna et Flora fennica. Bd. VI. 1890.

Koorders, S. H. I. Waarnemingen over spontane reboisatie op Java. Tey mannia. 1894.

—— II. Iets over spontane reboisatie van verlaten Koffietuinen op het M dangan-gebergte etc. Tijdschrift voor Nijverheid en Landbouw. De XLIX, Afl. V en VI. 1894.

—— III. Beobachtungen über spontane Neubewaldung auf Java. Forstlic Naturw. Zeitschr. 1895.

Middendorff, A. Th. von. Reise in dem äussersten Norden und Osten Sibirier während der Jahre 1843 und 1844. Bd. I, Theil I. St. Petersburg, 1856.

Woeikof, A. I. Beiträge zur Kenntniss der Wald- und Regenzonen d Kaukasus. Zeitschr. d. Gesellsch. für Meteorologie. Bd. VI. 1871.

—— II. Die Klimate der Erde. Jena, 1887.

See also of this book, Part III, Sect. I, Chap. III, and Sect. II, Chaps. III, VI, I

2. The Edaphic Formations.

Altenkirch, G. Studien über die Verdunstungserscheinungen in der trockene Geröllflora Sachsens. Engler's Jahrbücher. Bd. XVIII. 1896.

Buchenau, F. Ueber die Vegetationsverhältnisse des 'Helms' (Psamn arenaria) und der verwandten Dünengräser. Abhandl. d. naturw. Verei zu Bremen. Bd. X. 1889.

Drude, O. I. Ueber die Principien in der Unterscheidung von Pflanze formationen. Engler's Jahrbücher. Bd. XI. 1889.

—— II. Deutschlands Pflanzengeographie. Theil I. 1895.

Erikson, Joh. I. Studier öfver sandfloran i östra Skåne. Bihang till k. svensl vet.-akad. Handlingar. Bd. XXII, Afd. III. 1896. With German Résun (Xerophilous Structure of Sand Plants).

—— II. Ueber negativ-geotropische Wurzeln bei Sandpflanzen. Botanisches Ce tralblatt. Bd. LXI. 1895.

Flahault, Ch. Distribution des végétaux dans un coin du Languedoc. Mor pellier. 1893.

Flahault, Ch., et Combres, P. Sur la flore de la Camargue et des alluvions Rhône. Bulletin de la société botanique de France. Tome XLI. 1894.

Graebner, P. Studien über die norddeutsche Heide. Engler's Jahrbüche Bd. XX. 1895.

MacMillan, C. I. On the formation of circular muskeag in Tamarack swamp Bulletin of the Torrey Botanical Club. Vol. XXIII. 1896.

—— II. Observations on the distribution of plants along shore at Lake of t Woods. Minnesota Botanical Studies. Geolog. and nat. hist. survey Minnesota. Minneapolis, 1897.

Nägeli, C. I. Bedingungen des Vorkommens von Arten und Varietaten innerhalb ihres Verbreitungsbezirkes. Sitzungsberichte der Bayrischen Akademie. 1865.

— II. Verdrängung der Pflanzenformen durch ihre Mitbewerber. Ibid. 1872.

Schimper, A. F. W. Die indo-malayische Strandflora. Botan. Mittheil. aus den Tropen. Heft II. Jena, 1891.

Sendtner, O. Die Vegetationsverhältnisse Südbayerns. München, 1854.

Treub, M. Notice sur la nouvelle flore de Krakatau. Annales du jardin botanique de Buitenzorg. Vol. VII. 1888.

Warming, E. I. De psammofile Vegetationer i Danmark. Vidensk. Meddelelser naturh. Forening. Kjöbenhavn, 1890.

— II. Exkursionen til Fanö og Blaavand i Juli 1893. Botanisk Tidskrift. Band XIX. 1894-1895.

— III. Plantesamfund. Kjøbenhavn, 1895. German Edition. Berlin, 1896.

See also of this book, Part III, Sect. I, Chap. VI. and Sect. II, Chap. X.

3. The Life of the Plant-commune in the Formations.

randis, D. (Gesellig wachsende Holzgewächse.) Sitzungsber. d. Niederrh. Ges. für Natur- und Heilk. zu Bonn. 5. März 1894.

andolle, A. de. Géographie botanique raisonnée. Tome I. 1855. p. 460.

lahault, Ch. I. Projet de carte botanique, forestière et agricole de la France. Bulletin de la société botanique de France. Tome XLI. 1894.

— II. Au sujet de la carte botanique, forestiere et agricole de France etc. Annales de géographie. 1896.

öck, F. I. Pflanzen der Schwarzerlenbestände Norddeutschlands. Engler's Jahrbücher. Bd. XXII. 1897.

— II. Die Flora der Nadelwälder Norddeutschlands. Die Natur. 1892.

— III. Laubwaldflora Norddeutschlands. Forschungen zur deutschen Landes- und Volkskunde. Bd. IX. Stuttgart, 1896.

— IV. Begleitpflanzen der Buche. Die Natur. 1891. (Reference in Botanisches Centralblatt. Bd. XLIX. 1892.)

— V. Begleitpflanzen der Kiefer in Norddeutschland. Berichte der deutschen botanischen Gesellschaft. Bd. XI. 1893.

chimper, A. F. W. Die epiphytische Vegetation Amerikas. Botan. Mittheil. aus den Tropen. Heft I. Jena, 1888.

arming, E. Plantesamfund. Kjøbenhavn, 1895. German Edition. Berlin, 1896.

CHAPTER II

GUILDS

Introduction. 1. **Lianes.** Scramblers, Root-climbers, Twiners, Tendril-climbers Geographical distribution of lianes. 2. **Epiphytes.** Oecological conditions of life Transition from the terrestrial to the epiphytic mode of life. Contrivances for ensurin dispersal of seeds. Geographical distribution of epiphytes. 3. **Saprophytes.** Occurrence in families of plants. Connexion between structure and mode of life. Geographica distribution. Hemisaprophytes. 4. **Parasites.** Hemiparasites and holoparasite Resemblances to saprophytes. Organs of absorption: haustoria. Occurrence in familie of plants. Geographical distribution.

INTRODUCTION.

Dispersed among the plants that occupy the ground and are essentiall responsible for the building up of the formations, there are almost alway found other plants of quite different modes of life, which appear indiscriminately as accessory components of the most diverse formations withou ever grouping themselves into one of their own. In fact they are unable t do so, for they depend on other plants for their existence. Each of thes groups of plants has, in accordance with its mode of life, characteristic trait which may undergo many modifications with any change in the environmen but which always remain unchanged in their leading features. Such oecological groups are termed *guilds*[1]. They are four in number—*lianc epiphytes, saprophytes, parasites.*

The transition between the plants that produce formations and the plant that form guilds is supplied by the lithophytes described in the precedin chapter, which range themselves into formations of their own, but also occu as subsidiary components on scattered rocks and stones in the midst o other formations. Lithophytes in particular show intimate relations wit epiphytes, and many plants thrive as well on the surface of rocks as on th bark of trees.

1. LIANES[2].

Whilst formerly only climbing woody plants were termed lianes, H Schenck includes under this term all plants that take root in the groun and, being furnished with long stems having long internodes, make use o other plants as supports in order to raise their foliage and flowers from th

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[1] Schimper, op. cit., p. 8.

[2] H. Schenck, I and II.

round and bring them into a favourable situation as regards light. They clude woody plants with evergreen leaves as well as deciduous climbing rubs, also forms with herbaceous stems that exist for one vegetative ason only, or are perennial in their subterranean organs[1]. That lianes imb upon and around other plants is due only to the fact that, in nature, e plant kingdom alone provides objects having the necessary form as pports; it is the form alone that is of importance and not the chemical ture of the support, for, as cultivated plants show, the support may be mposed of the most miscellaneous materials. Certain forms of lianes do cur naturally as rock-climbers, but the number of these is relatively small.

Lianes may be arranged in four groups, according to their mode of mbing; they are, *scramblers, root-climbers, twiners, tendril-climbers.*

Scramblers.

The majority of scramblers are shrubs distinguishable in the simplest c ses, from other shrubs only by their long straggling branches, which s pport themselves on other branches without fastening in any active nner. The climbing of these plants is often assisted by prickles or t orns, without our being able to regard the latter as adaptations to a c mbing mode of life, for example in roses and brambles. Whilst the r jority of scramblers represent the lowest degree of liane, there are a ong them forms with very complete, even if passive, contrivances, for e ample the palm-lianes of the tropical forests. These will be described h eafter.

Root-climbers.

These form a small group, the representatives of which grow upwards means of subaërial roots fixed to the support. Such fixing roots are s ort and thin as in ivy, or they may attain the thickness of a quill with a ength of 2–3 decimeters and wind like hoops round cylindrical supports. S ch vigorous development of fixing-roots is exhibited only by tropical f ms like Vanilla and many Araceae, such as Monstera and Philodendron.

Twiners.

In twining plants the axes grow spirally around slender supports in virtue o their unilateral transverse geotropism, which later on passes over into n gative geotropism. To this group belong a number of well-known h baceous climbers, such as hop, kidney-bean, bindweed, also many woody li es, for example, honeysuckle, the widely cultivated Wistaria chinensis, a l species of Aristolochia.

Tendril-climbers.

This group is richest in forms. Climbing is rendered possible amongst t m by the possession of irritable organs, which, when in contact with

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[1] H. Schenck, I, p. 2.

a support, curl round it. Morphologically the tendrils are either leaves c axes. Oecologically they are very varied, so that, following H. Schencl we may arrange tendri climbers, in the wide sense, into six group according to their mode of climbing :—

In *leaf-climbers* a par petiole or blade, of th otherwise unmodified le is endowed with the necessary irritability. Fo instance, Clematis V talba is a petiole-climbe Fumaria officinalis in i varieties Wirtgenii an vulgaris a leaf-blac climber ; Flagellaria i dica, a monocotyledo ous plant common in tl tropics of the Old Worl is a leaf-tip climber.

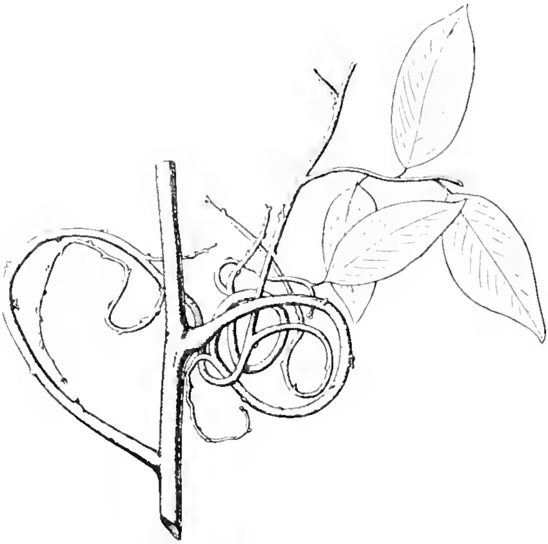

FIG. 103. Securidaca Sellowiana, Klotzsch. Lateral shoot acting as a tendril. Two-thirds of natural size. After H. Schenck.

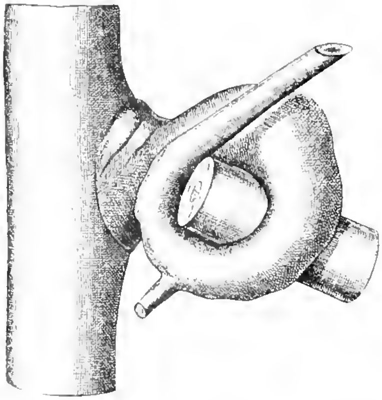

FIG. 104. Dalbergia variabilis, Vog. Old and considerably thickened twining branch. Two-thirds of natural size. After H. Schenck.

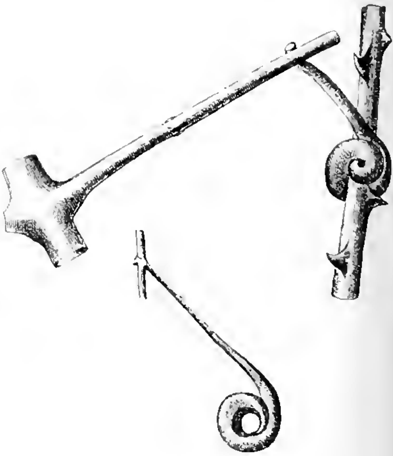

FIG. 105. Strychnos triplinervia, Mart. Sor what old lignified and thickened climb hooks.

In *leaf-tendril climbers*, the leaf, or a part of it, is differentiated as filamentous organ functioning as a tendril only. We see this in the p and other Vicieae, Cucurbitaceae, and many other plants.

The group of *branch-climbers*[1], like that of leaf-climbers, represents phylogenetically a low degree of liane. The climbing branches in the least adapted cases differ from ordinary branches by their irritability only, and are provided with lateral shoots and leaves (Figs. 103, 104). Branch-climbers are confined to he tropics and the adjoining reions. Examples occur among he Polygalaceae, Papilionaceae, Iimosaceae, Connaraceae, and ther families.

The two following groups re also tropical and their reresentatives are not generally nown.

The climbing organs of *hook'imbers*[2] are metamorphosed iorns or flower-stalks, which, fter embracing the support, ecome considerably thickened. xamples are found in many nonaceae, Loganiaceae, Diterocarpaceae, Rubiaceae, and sewhere (Fig. 105).

The *watch-spring climbers*[3] ave thin, spirally coiled, bare imbing organs, which, owing the stimulus of contact, ecome thicker and harder. hey are found in several hamnaceae and Sapindaceae igs. 106, 107).

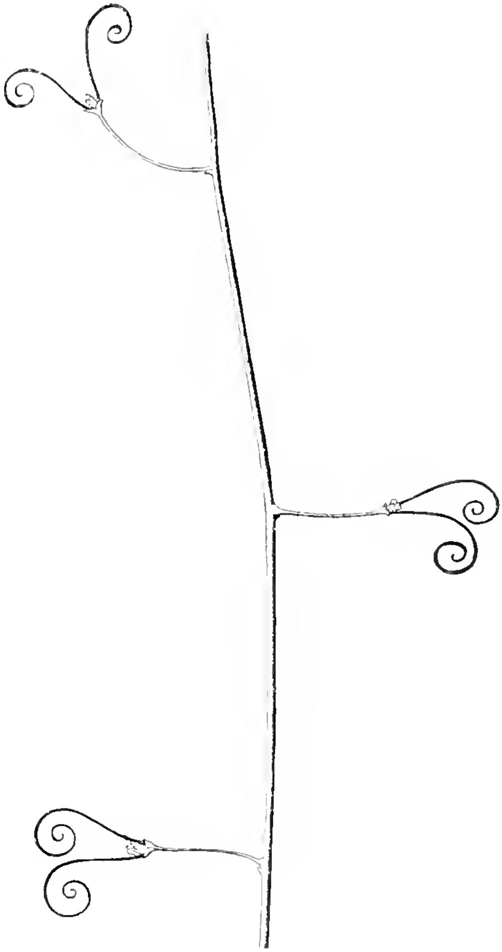

FIG. 106. Bauhinia sp. at Blumenau. Twig with watch-spring tendrils. Two-thirds of natural size. After H. Schenck.

The most comprehensive oup of plants endowed with ial climbing organs is that of *m-tendril climbers*, the climbg organs of which often closely ree in their external features, well as in physiological characters, with leaf-tendril climbers; but their ial nature is often betrayed externally not only by their position but also the presence of rudimentary leaves, as in the vine. The group includes any species, for example in the families of the Vitaceae and Passifloraceae.

[1] This and the following groups were first separated and described by Fritz Müller.

[2] Investigated by Treub.

[3] Investigated first by H. Schenck.

The stem of a liane is always constructed upon the same oecological principle; its wood is not compact and unbroken as in the stem of a tree, but fissured in various ways or even subdivided into isolated strands. Hence various anomalies result, such as those represented in Figs. 108–110. A more detailed account cannot be given here[1].

Lianes are further characterized by the great length and width of their conducting tubes, wood-vessels as well as sieve-tubes, by means of whic the conveyance along the frequently extremely long stem of non-elaborat sap and of proteids respectively is facilitated.

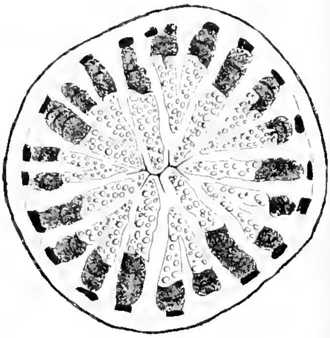

FIG. 108. Anisosperma Passiflora, Manso. Transverse section of stem. Magnified 3·2 times.

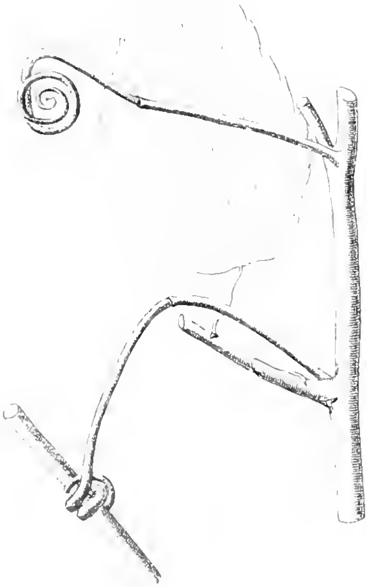

FIG. 107. Gouania urticaefolia, Reiss. Watch-spring tendrils. Two-thirds of natural size. After H. Schenck.

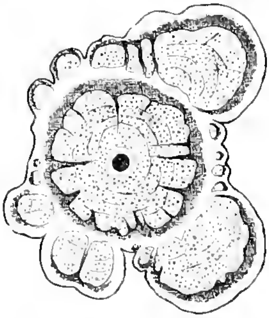

FIG. 109. Transverse section of stem of Dalechampia ficifolia, Lamk. Natural size. After H. Schenck.

Geographical Distribution of Lianes.

Lianes thrive in nearly all climates; they are absent only in the polar ar and in the alpine regions of high mountains, where certain climatic facto

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[1] They have been described in detail and beautifully figured by H. Schenck, A short account of them is given in Strasburger's Text-book of Botany, Eng. e London, 1888, p. 137.

re unfavourable to the production of long axes[1]. The guild therefore nhabits an enormous area, although it is very unequally distributed. In y far the majority of cases, lianes are inhabitants of the tropics and of few neighbouring lands with tropical climate, such as outhern Brazil and South lorida. According to an stimate, which H. Schenck onsiders as probably too low, bout ten-elevenths or over inety per cent. of the lianes re tropical. Even in the ropics the distribution of anes is very unequal; most f the long woody forms nly appear in damp rainrests and monsoon-forests[2], hilst dry woodlands and vannahs produce hardly any but thin-stemmed and chiefly herbaceous rms.

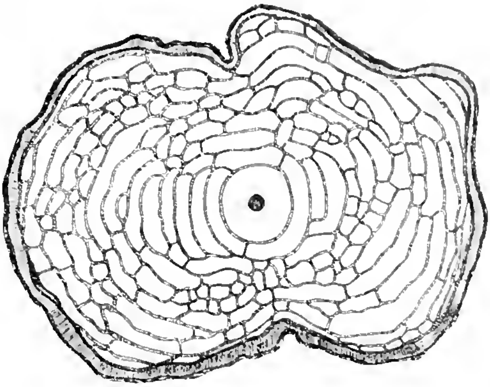

FIG. 110. Transverse section of stem of Securidaca lanceolata, St.-Hil. Natural size. After H. Schenck.

Outside the tropics, lianes occur chiefly in temperate rain-forests in outhern Japan, New Zealand, Southern Chili, more rarely and in less ariety in very damp summer-forests[3] in Central Japan, Atlantic and entral North America, without showing anything like such variety as the tropics.

2. EPIPHYTES[4].

Epiphytes are plants that germinate on other plants and grow without btaining nutriment at the cost of the substance of their host. In this hey differ from true parasites, with which they are often confounded.

Their mode of life makes the acquisition of the necessary nourishment matter of difficulty, but starvation is not the chief danger to which hey are exposed. Epiphytes, attached as they are to the surface of other lants, are more exposed to the danger of drought, and they are conequently confined to regions where long persistent drought is unknown, xcept when they have the faculty of existing in a desiccated condition, power which is possessed by many mosses and lichens, but which appears o be altogether wanting in ferns and phanerogams, in spite of the ability f a few species to withstand very considerable loss of water. The epiphytic uild therefore exhibits, according to the nature of the climate, an inquality in systematic composition and in diversity and luxuriance of growth.

Districts where a drying up of the plants owing to scarcity of water is

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[1] See Part III, Sects. III and IV.

[2] See Part III, Sect. II.

[3] See Part III, Sect. I, Chap. III.

[4] Schimper, op. cit.

impossible are confined to the tropics. The rain-forests of the tropics ar always moist. This is much less true of rain-forests of the warme temperate zones and not at all true of the summer-forests of highe latitudes, for the cold of winter there constitutes a period of physiologica drought, which, even with the heaviest atmospheric precipitation, is mor opposed to the supply of water than great dryness when united with hea Under heat and dryness transpiration is indeed much greater, but th absorption of water is not hindered and the nightly dew is of dire advantage to the superficial roots of the epiphytes, whereas under temperat conditions there is no supply of water to be set against its loss by epiphyte for the frozen or at any rate very cold exposed roots transpire, but absor nothing.

Corresponding to these conditions of life, the vast majority of epiphyt belong to tropical rain-forests. Only there do they luxuriantly cov stems, branches, and frequently even the leaves of trees, and often ther selves attain the dimensions of trees. In districts with markedly d seasons, and on the isolated trees of savannahs, epiphytes are eith completely wanting, or rare and represented by relatively few forms. Su forms as are found are emigrants from the rain-forests, and their presence always a sign that the dry season is not long, or, as in the monsoon-fores is accompanied by copious dew.

The origin of the guild of epiphytes in tropical forests may have co about in the following way. Many terrestrial plants living in the forest a able to settle and grow on rough fissured stems, in the forks of boughs, a on other spots where humus collects. This happens in the tropics in t case of many Solanaceae, Melastomaceae, and ferns. From such acciden epiphytes true epiphytes were derived, since many of these plants ow their existence to this faculty, which secured for them a safe retreat outsi the seat of conflict. The competition on the trees was limited to f species, because the faculty of existing as an epiphyte demands cert definite and by no means common characters. Obviously, for instan only such plants germinate on trees as are provided with seeds capable f dispersal not only in a horizontal, but also in a vertical direction, and t latter demands adaptations to arboreal animals and to the wind. Moreov the seeds must be very small, so that they can enter narrow crevices, a in the case of dispersal by the wind they must be extremely light, beca vertical wind-currents are weak in the forest. The seeds of epiphy actually fulfil all these conditions; they are always small, and eit surrounded by succulent envelopes, as in Aroideae, many Bromelia Rubiaceae, Melastomaceae, Ficus, Cactaceae, and Gesneraceae, or they extremely light, even like powder, as for instance the spores of ferns, seeds of orchids, or they are provided, in spite of their very small dimensi with a most suitable parachute, as in Rhododendron, many Bromelia

Asclepiadaceae, Gesneraceae, and Rubiaceae. Moreover, from the first all plants that produce many lateral roots and require relatively little water gain an advantage. Hence the number of species that could emigrate to rees was relatively small, and victory over competitors was dependent on conditions other than those prevailing on the ground.

In those species which no longer grew on the ground and therefore could persist as epiphytes only, those characters were naturally selected that were specially suited for existence on trees; they have been adapted to this. Especially was every characteristic that enabled an epiphyte to advance upwards towards the light preserved and further developed. In the first place, in this relation protective means against the loss of water are in question, for every step on the way from the base to the summit of a tree brings with it not only more light but also greater dryness. Epiphytes growing at the base of trees in a rain-forest are hygrophilous, those that occur on the highest branches are xerophilous. The whole matter gives the impression of a gradual ascent from the deep shade into the sunlight, from the damp cool air of the interior of the forest to the dry heat of the top of the forest.

Xerophilous sun-loving epiphytes of the summits of trees, although they represent the descendants of hygrophilous shade-bearing plants, are able to desert the rain-forest. Thanks to their changed characters they are able to inhabit quite open country. Thus they emigrated from the rain-forests, and colonized regions with markedly dry seasons, especially monsoon-forests. savannahs, and savannah-forests. A limit was set to their success only where the drought lasted several months without being nterrupted regularly by heavy falls of dew; yet there they were able to settle permanently on the banks of rivers and lakes. The winter cold more completely arrested the emigration of tropical epiphytes. Only few species endowed with specially strong powers of resisting drought and cold, such as Tillandsia usneoides and Polypodium incanum in North America, were able to advance into districts with cold winters.

The tropical rain-forests have been by far the most important sources of origin of the epiphytic guild, and their productions have penetrated far into the warm temperate zones of North America, Argentina, Japan, and Australia. We also find, however, in the temperate zones two limited autochthonous sources of origin of higher epiphytes, namely, in the comparatively inextensive temperate rain-forests of Southern Chili and of New Zealand. Here real temperate higher epiphytes have sprung from temperate phanerogams and ferns.

Outside this region, as autochthonous epiphytes, we find only small Algae, lichens, and mosses, that is to say. plants that, owing to their faculty of existing for months in a dry condition, can resist even the desiccating effects of prolonged winter cold. But even they are found richly developed

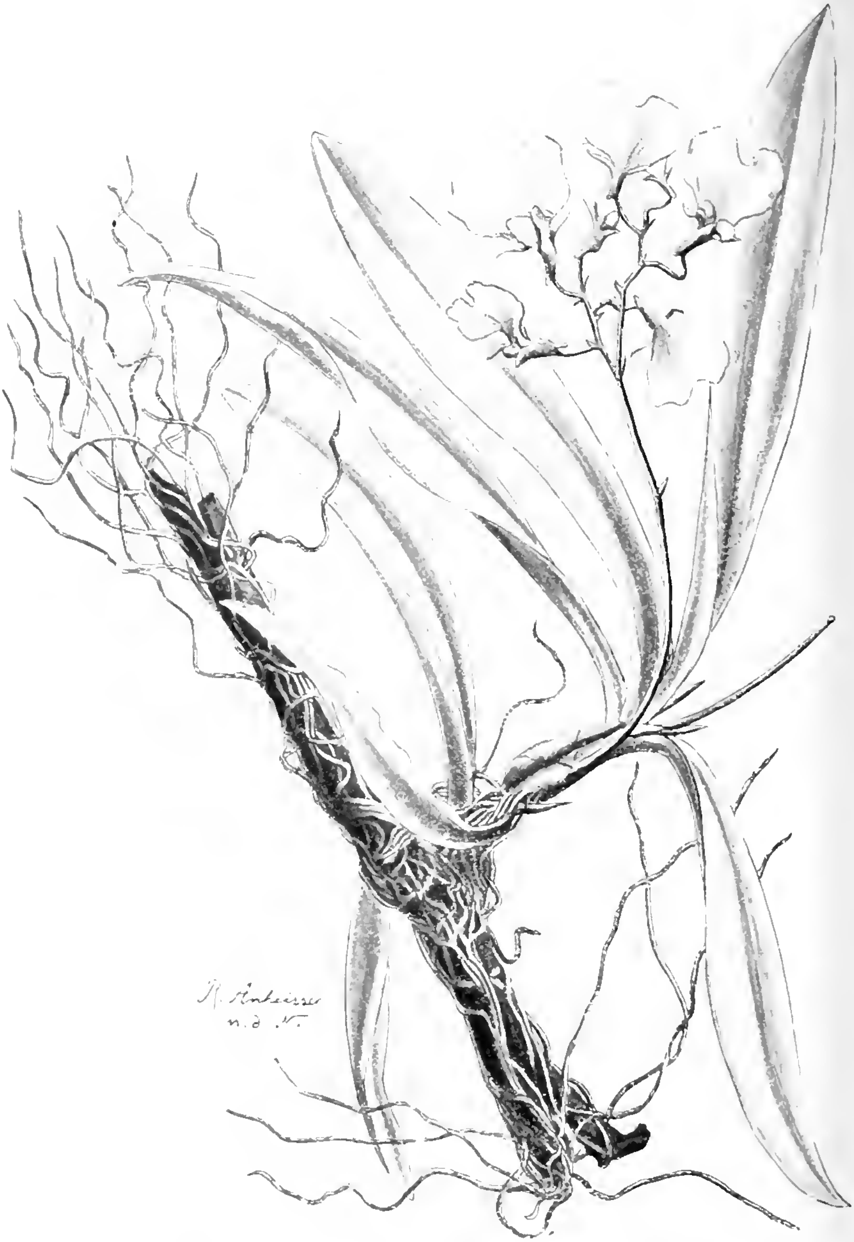

FIG. 111. Ionopsis sp. An epiphytic orchid on an orange branch. Blumenau, Southern Brazil. Natural size.

only in damp districts, especially in a cloudy climate, or near stretches of water. As in the tropics, so also in temperate regions, terrestrial plants may be found growing accidentally in the hollows of old trees; they occur however only in places where considerable masses of soil facilitate the development of true subterranean roots, and they cannot in any way be considered as epiphytes.

The varied contrivances by means of which higher epiphytes have become adapted to their mode of life are so closely connected with the conditions of existence in rain-forests and are so characteristic of the latter, that they and the forests should be discussed together. It may now merely be stated that they chiefly belong to the ferns and orchids (Fig. 111), and in America specially to the Bromeliaceae.

3. SAPROPHYTES.

Saprophytes constitute a group of plants that dispense with chlorophyll and are therefore dependent on organic nutriment. They obtain this nutriment from dead vegetable and animal substances, and in a more or less decomposed condition according to the particular species.

The vast majority of saprophytes belong to the Bacteria, Myxomycetes, and Fungi; the remainder are phanerogams. There are no other classes of plants represented among them. In accordance with their mode of nutrition, all saprophytes, except perhaps bacteria, must be derived from green assimilating plants. Among phanerogams, numerous transitions still exist between purely inorganic and purely organic methods of nutrition. The first stage is denoted by the appearance of the mycorhiza, by means of which phanerogams and ferns were first enabled to utilize the organic constituents of humus. Increasing dependence on the fungus of the mycorhiza, whose rôle has been transformed from that of a mere supplier of nitrogen to that of a universal provider, has led through numerous intermediate stages to the purely saprophytic mode of life. The saprophytic habit has conferred on the plants which possess it the power of occupying stations where, on account of insufficient illumination, green plants can exist feebly or not at all. Like halophytes and epiphytes, saprophytes are also fugitives from the struggle for existence.

Despite the wide distribution of mycorhiza only a relatively small number of phanerogams, belonging to a few families, have adopted the purely saprophytic mode of life. The majority of these are monocotyledons and chiefly orchids, but the small family of Burmanniaceae is chiefly saprophytic, and that of Triuridaceae exclusively so. Among dicotyledonous plants only Gentianaceae and Monotropeae possess saprophytic species.

The change in the mode of nutrition causes a change in the structure and oecology of the plant. Chlorophyll having become useless is suppressed or transformed into other brown, yellow, or brick-red pigments apparently allied to chlorophyll, and these give to saprophytes a vivid colour whose oecological significance, if existent, is not yet known. Simultaneously with the chlorophyll, the organs that are functionally connected with it are reduced, in particular the leaf-surface, which in saprophytes is still present only in the form of a small scale, the stomata, which have quite disappeared in some species, the tracheal passages, whose place is taken by a few narrow vessels and tracheids. The subterranean system, in accordance with the reduced transpiration, is less developed than in green plants, and in many cases assumes a coralloid appearance. Mycorhiza is well developed in saprophytes. So far as we can apprehend, their flowers do not essentially differ from those of their non-saprophytic allies; their colour frequently agrees with that of their vegetative organs. The peculiarities of their seeds have not yet been oecologically explained. They are very numerous, of minute size, and possess an undifferentiated feebly developed embryo.

Saprophytes, unlike lianes, and especially unlike epiphytes, are not confined to certain definite climates, but, at least in their systematically lower forms, appear in all climates, whilst the higher forms prefer damper climates and chiefly inhabit shady places. Their larger forms appear principally in forests, in which saprophytes constitute an essential, if only occasionally a noticeable part of the vegetation. The most conspicuous and commonest saprophytes in Europe are pileate fungi; phanerogamic saprophytes are much rarer. But a close investigation shows us at once that humus is completely permeated by fine mycelial hyphae, and that all dead stems branches, and leaves nourish a rich thallophytic flora of saprophytes.

The more the chlorophyll-apparatus is reduced in amount in *hemisaprophytes* the more do they approach in general structure true saprophytes Coralliorrhiza innata and Limodorum abortivum, two humicolous orchid poor in chlorophyll, very much resemble holosaprophytes, owing to thei leaves being reduced to scales, the first also by its coral-like rootless rhizom and the second by its violet colour. This violet colour is seen in a stil higher degree in Lecanorchis javanica, an orchid poor in chlorophyll, whic I observed in Java. The gentianaceous Obolaria virginica I may conside as belonging to a lower step in the transition to a saprophytic mode o life. I frequently found this pretty little plant on the deep humus of ver shady forests near Baltimore, and was struck with the fact that, differin from other shade-plants, it possessed a succulent stem and very smal leaves.

4. PARASITES.

Parasites derive their nutriment partially or entirely from other livin organisms, either plants or animals. They share with saprophytes th property of obtaining their carbon partially or entirely from organic compounds, and they assimilate the carbon-dioxide of the air in correspondingl small quantities, or not at all. The latter circumstance has caused similar results in both cases as regards members serving for the elaboration of carbon-dioxide. Like hemisaprophytes, *hemiparasites*, which obtain only a portion of their necessary carbon in an organic form, more or less resemble autotrophic plants as regards the amount of chlorophyll they contain and as regards the form of their leaves; whereas *holoparasites*, which live entirely at the cost of the organic substance of their host, like holosaprophytes are devoid of chlorophyll and, if phanerogams, develop scales in the place of foliage-leaves. All possible stages connect the two chief groups of parasites.

The absence or reduction of the organs serving in other cases for the assimilation of carbon dioxide endows holosaprophytes and holoparasites with a great resemblance to one another as regards habit. Parasitism, however, in certain cases has had a still deeper modifying influence on the vegetable organism than has saprophytism. Thus there are parasitic phanerogams, like Rafflesiaceae and Pilostyles, that are reduced to mere roots and flowers, others, such as Balanophoraceae and Lennoaceae, with a general fungoid form that no longer recalls the appearance of flowering plants. Such extreme forms are so modified by their parasitic mode of life, even in the formation of flower and fruit, that, although they are the descendants of autotrophic plants, their systematic position can no longer be determined with certainty.

It is easy to understand why the organs of absorption, the roots in phanerogams, should be the most deeply modified by a parasitic mode of life. It is only in this regard that an essential difference is exhibited between, on the one hand, saprophytes which absorb their organic nutriment from dead matter by means of the mycorhiza, and, on the other hand, parasites which take theirs from living organisms by means of haustoria. The *haustoria* of parasites are in many cases minute outgrowths of otherwise normal roots, for example in numerous terrestrial hemiparasites belonging to the genera Euphrasia, Rhinanthus, and other Scrophulariaceae, as well as to the genera Thesium and Santalum in the Santalaceae. The haustoria attach themselves closely to the host and drive into it processes which are the true organs of absorption.

In other cases, a larger portion of the root-system, or the whole of it, is enclosed within the host. In still other cases, the roots die early and the haustoria are developed on the stem, being apparently homologous with adventitious roots. This is found in Cuscuta and Cassytha (Fig. 112).

The mode of life of phanerogamic parasites is very varied. Some are terrestrial, either erect herbs rooted to their host in the ground like Euphrasia and Thesium among hemiparasites, Orobanche and Lathraea among holoparasites; or woody plants, as Santalum album. Others are rootless lianes, such as the species of the convolvulaceous genus Cuscuta and the lauraceous genus Cassytha—both leafless twiners with haustoria on their stems and more (Cuscuta) or less (Cassytha) poor in chlorophyll. Others again have the habitat of true epiphytes; such are the mistletoe (Viscum album), Loranthus europaeus and numerous other Loranthaceae, also several Santalaceae of extra-tropical South America. These epiphytic forms are all hemiparasites except Loranthus aphyllus[1] Many are at the same time climbers. Finally a separate oecological position may be assigned to those forms that, except for their organs of reproduction, are buried within their host.

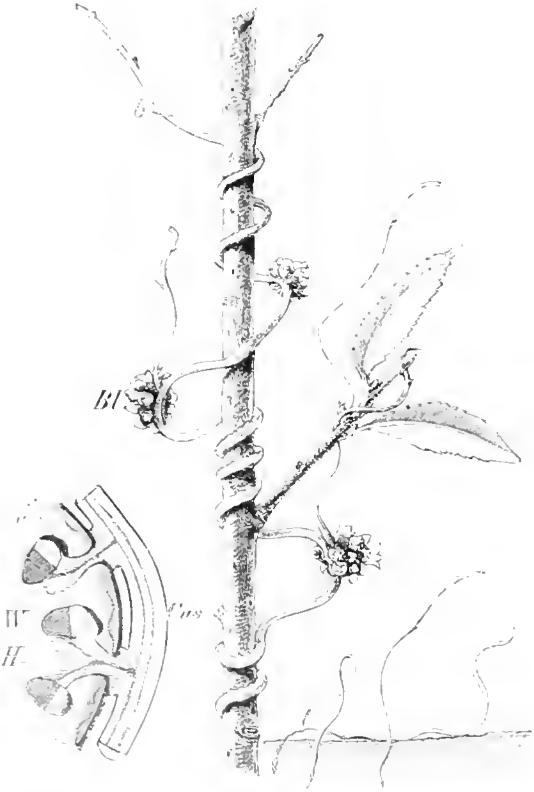

FIG. 112. Cuscuta europaea. In the centre a willow twig round which the parasite is twining. *l* reduced leaves. *Bl* flowers. On the left, connexion of the parasite *Cus* with its host *W*. *H* haustoria. *v. c. s* vascular bundle of the host. On the right, seedlings; *t* base of seedling dying off. From Strasburger's Text-book of Botany.

In the case of fungi, still greater differences in their mode of life exist; for one reason, because they, unlike phanerogams, are not confined to vegetable substrata but also attack animals, and also because many species assume different forms on different hosts.

Like saprophytes, parasites belong to a relatively small number of systematic groups, and are most numerous among fungi and bacteria. Algae include only a few holoparasites compared with the more numerous hemiparasites in the group. Holoparasites and holosaprophytes alike are wanting among mosses, pteridophytes, and gymnosperms. The analogy between the two oecological groups of holoparasites and holosaprophytes does not extend to angiosperms. Although there is a parasite (Melampyrum pratense) that apparently can also exist saprophytically (L. Koch yet the two modes of organic nutrition among angiosperms are systemati

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[1] According to Johow.

ally sharply divided. The majority of holosaprophytes belong to onocotyledons, which include no parasites, and the families in which arasites occur include no saprophytes. Not only the Balanophoraceae, Rafflesiaceae, Orobanchaceae, and Lennoaceae, which are exclusively oloparasites, and the Loranthaceae and Santalaceae, which consist chiefly f hemiparasites, but also the Convolvulaceae (Cuscuta), Scrophulariaceae Melampyrum, Euphrasia, Rhinanthus), and Lauraceae (Cassytha), in which nly some genera are parasitic, include no saprophytes. There are not ven any hemisaprophytes in the last-mentioned three families.

Parasites are not confined to definite climatic conditions and are herefore found in all zones and districts. Hence geographically they re only of slight interest, and have been referred to here only because hey frequently contribute some details to the oecological characters of ormations.

SELECT LITERATURE.

1. Lianes.

The numerous treatises on lianes deal for the most part only with their anatomical characters or physiological properties. They have been carefully catalogued by H. Schenck. The following works are oecologically interesting in relation to phyto-geography:

Müller, F. I. Notes on some of the climbing plants near Desterro in South Brazil. Journ. Linn. Soc. Botany. Vol. IX. 1867.

—— II. Zweigklimmer. Kosmos. Bd. VI. 1887.

Schenck, H. I. Beiträge zur Biologie und Anatomie der Lianen, im Besonderen der in Brasilien einheimischen Arten. Theil I. Beiträge zur Biologie der Lianen. Botan. Mittheil. aus den Tropen. Heft IV. Jena, 1897.

—— II. Beiträge, etc. Theil II. Beiträge zur Anatomie der Lianen. Ibid. Heft V. Jena, 1893.

Treub, M. I. Sur une nouvelle catégorie de plantes grimpantes. Annales du Jardin Botanique de Buitenzorg. Vol. III. 1882.

—— II. Observations sur les plantes grimpantes du Jardin Botanique de Buitenzorg. Ibid. Vol. IV. 1883.

Westermaier, M., und Ambronn, H. Beziehungen zwischen Lebensweise und Structur der Schling- und Kletterpflanzen. Flora. Jahrg. LXIV. 1881.

2. Epiphytes.

What refers to epiphytes is based on the following work:

Schimper, A. F. W. Die epiphytische Vegetation Amerikas. Botan. Mittheil. aus den Tropen. Heft I. Jena, 1888.

The literature in Chap. IV of Sect. I, Part III, may be consulted as regards epiphytes of the tropics, and for epiphytes of the temperate zones that of Chap. IV of Sect. II, Part III.

3. Saprophytes.

The literature regarding saprophytes is generally remote from the questions discussed in this book. Johow has published good general works, especially regarding the oecological and phytogeographical problems; in his papers the historica literature is also given. For fungi, de Bary's great work is the most important See also Part III, Sect. I, Chap. IV.

Bary, A. de. Comparative Morphology and Biology of the Fungi, Mycetozoa, an Bacteria. English Edition. Oxford, 1887.

Johow, F. I. Die chlorophyllfreien Humusbewohner West-Indiens. Pringsheim' Jahrbücher. Bd. XVI. 1885.

—— II. Die chlorophyllfreien Humuspflanzen nach ihren biologischen und anatomisch-entwickelungsgeschichtlichen Verhältnissen. Ibid. Bd. XX. 1889.

4. Parasites.

Similar remarks to those about saprophytes hold good regarding the literature o parasites. Johow's work is chiefly from an oecological and geographical point o view and gives a catalogue of the literature. Regarding morphology, &c., in th first place, Engler and Prantl's Die natürlichen Pflanzenfamilien should be utilize In the following list only a few fundamental works are mentioned.

Brown, R. An account of a new genus of plants, named Rafflesia. Trans. Lin Soc. Vol. XIII. 1820.

Hartig, R. Zur Kenntniss von Loranthus europaeus und Viscum album. Zeitsch f. Forst- und Jagdwesen. Bd. VIII. 1873.

Johow, F. Die phanerogamen Schmarotzerpflanzen. Verhandl. d. deutsche wissensch. Vereins zu Santiago. 1890.

Koch, L. I. Die Klee- und Flachsseide. Heidelberg, 1880.

—— II. Ueber die direkte Ausnutzung vegetabilischer Reste durch bestimmt chlorophyllhaltige Pflanzen. Berichte der deutschen botanischen Gesellschaft. Bd. III. 1885.

—— III. Die Entwicklungsgeschichte der Orobanchen. Heidelberg, 1887.

Martius, Th. Ueber die Vegetation der echten und unechten Parasiten, zunächst i Brasilien. Münchener Gel. Anzeigen. 1842.

Solms-Laubach, H. Graf zu. Ueber den Bau und die Entwickelung der Ernährungsorgane parasitischer Phanerogamen. Pringsheim's Jahrbücher. Bd. V 1867–1868.

THIRD PART

ZONES AND REGIONS

ZONES AND REGIONS

INTRODUCTION

THE summer and winter isotherms subdivide the earth's vegetation
to more or less parallel *zones* of different systematic character. Certain
ders and families of plants are dependent on constantly high tempera-
ures, such as prevail in the tropics alone, and perish at the freezing-
oint of water or even at some degrees above it (Macrotherms); whereas
r the development of other plants other temperatures, alternately high
low, are required (Mesotherms). The plants of the second category also
hibit differences in their susceptibility to temperatures below zero,
nd these differences call forth corresponding ones in the characters of
e flora as the latitude increases. Finally, polar zones are inhabited
plants that can support without injury, not only very low winter
mperatures, but also frosty weather during the vegetative season, and
e able to complete their cycle of development in a short time
licrotherms).

A reduction in the temperature, similar to that from the Equator to
ie Poles, occurs in a vertical direction up mountains that exceed the
nit of perpetual snow. But here the isothermal zones are much
arrower, so that, for instance, Kilimanjaro, 6,000 meters high, possesses
its base an equatorial climate, but at its summit one that may be
rmed polar as regards the temperature of the air.

The resemblance between the change in climate in passing from the
quator to the Poles, and from the base of mountains to their summit,
limited to the temperature of the air; the vertically increasing rare-
ction of the air bestows on other climatic factors very characteristic
atures, which are not at all comparable with those in the lowlands.
is accordingly inadvisable to apply the term zones to the climatic
lts of mountains, though this has frequently been done in recent times;
nce by this means a partial analogy receives an exaggerated and con-
sed expression; we should rather retain the term of *regions* used by
rlier geographical botanists, and by Grisebach among others.

Zones of temperature are by no means identical floristically and
cologically all round the earth; indeed they show themselves to be

subject to a more or less rapid change, attributable, as regards the flor partly to historical causes and partly to the inequality in the climati humidity, but as regards vegetation, to the climatic humidity exclusivel According to the nature of the atmospheric precipitations, either th woodland, grassland, or desert type predominates, and, excluding th local effects of soil, the type of vegetation changes its character onl on passing to a climate with a different degree of humidity. Tracts land bounded by such climates may be termed *districts*[1]. The variou districts of vegetation, in contrast to the floristic zones, exhibit ver irregular distribution and very unequal areas.

High mountains differ, as regards temperature and humidity, climaticall from the lowlands. Their regions defined by temperature are at the sam time those defined by atmospheric precipitations.

Owing to the great differences between the conditions of vegetati in mountains and lowlands, and to the manifold oecological relations the mountain vegetation everywhere, it appears advisable to separate t treatment of high regions from that of zones and districts and to devo a distinct section of the book to the vegetation on mountains. T sections on zones therefore, except in cases where the exclusion of l mountains or of the lower regions of mountains would be unnatural, a devoted to the lowlands.

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[1] See p. 160 and ff.

SECTION I. THE TROPICAL ZONES

CHAPTER I

GENERAL CHARACTERS OF THE TROPICAL CLIMATE AND ITS EFFECTS ON VEGETATION AND FLORA

1. **General Characters of the Tropical Climate.** i. *Atmospheric Precipitations.* Rain. Relative humidity. Clouds. ii. *Heat.* Temperature of the air. Heating by direct insolation. iii. *Light and the Ultra-violet Rays.* Intensity of the chemical rays of light. 2. **Some General Effects of the Tropical Climate on Plant-life.** i. *Processes that are chiefly influenced by Heat.* Cardinal points. Cases of rapid and slow growth. Transpiration in sun and shade. ii. *Physiological Action of Tropical Light on Plants.* Protective measures against intense light. Decomposition of chlorophyll. Position of foliage-leaves. Photic ration of shade-plants. iii. *Physiological Action of Atmospheric Precipitations on Plants.* The controlling influence on the character of the vegetation and the periodic processes. Ombrophily and ombrophoby. 3. **The Floristic Character of the Tropical Zone.** Survey of the megathermic group of forms.

1. GENERAL CHARACTERS OF THE TROPICAL CLIMATE.

i. *ATMOSPHERIC PRECIPITATIONS.*

THE *amount* of the annual rainfall in the tropics varies between 5 meters and more at some mountain-stations and a few centimeters in desert districts. It is on the average greatest in the equatorial zone, that is to say between 5° N. and 5° S., and it diminishes more rapidly in a northerly than in a southerly direction. The desert districts within the tropics belong with few exceptions to the border zones and merely represent the tropical continuations of the extensive subtropical deserts.

At least as important to plant-life as the amount of precipitation is its *seasonal distribution.* The year in the greater part of the tropical zone consists of a dry season. usually coinciding with the winter months, and a rainy season in the summer months. Some equatorial districts, for example Guiana, possess two unequally long rainy seasons, and some others, for example Singapore, have no distinct rainy season in the year. The difference between rainy and dry seasons is more decided inland, especially in plains, than along the coasts and on mountains, where its influence on plant-life is frequently no longer appreciable. The coincidence of the rainy and dry seasons with certain months in the year is not a matter of physiological importance to the vegetation, except in some border districts of limited area, since the differences between the temperatures in winter and summer are usually very small.

The relative humidity of the air usually corresponds to the amount of rainfall, and is naturally greater in the rainy than in the dry season. Again, districts on the coast, islands, and mountainous countries are characterized by a high degree of relative humidity, by which we understand a mean annual relative humidity of not less than 80 %. The relative humidity rises at night and in the early morning hours up to saturation, but falls during the day, in sunny weather, low enough at 65–70 % to exert considerable desiccating effects on vegetation. In districts with marked dry seasons, the relative atmospheric humidity during these descends on the average to 55–65 %, and much lower in desert districts. Many districts with dry seasons have during the nights in these seasons a heavy formation of *dew*, which is important to the vegetation.

In many districts during the rainy season constant *clouds* prevail, so that, according to Hann, a heavy, dark cloudy sky persists for months. This, however, is by no means the case everywhere, and does not agree with my own experience of tropical rainy seasons in Trinidad and Java, during which most days included several sunny hours; although completely rainy days were not wanting, yet, on the other hand, bright days were not less frequent. In Buitenzorg during the rainy season the sky is usually quite bright before midday, and the bursts of rain, which cause the high annual rainfall of about 4½ meters, for the most part fall only during some hours after midday, though with a violence unknown in Central Europe. The dry season in many districts is characterized by a continuously cloudless sky, whereas in some the dry season exhibits a cloudiness hardly or not at all less marked than does the rainy season.

The following table, taken from Hann and compiled by J. Murray and S. Arrhenius, represents the mean distribution of the atmospheric precipitations in the tropical zone and in the neighbouring belts of the temperate zones[1] :—

TABLE OF MEAN DISTRIBUTION OF ATMOSPHERIC PRECIPITATION IN TROPICS AND ADJACENT BELTS (after Hann).

Latitude.	N. 45°	N. 35°	N. 25°	N. 15°	N. 5°	S. 5°	S. 15°	S. 25°	S. 35°	S. 45°
Rainfall in centimeters.	57	55	68	95	197	189	123	65	70	106
Cloudiness per cent.	54	46	40	43	55	59	52	45	49	61
Relative humidity per cent.	74	70	71	76	79	81	78	77	79	81

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[1] Hann, op. cit., Bd. II, p. 37.

ii. *HEAT.*

The mean annual *atmospheric temperature* varies between 20° and 28°, nd is very steady when compared with that of higher latitudes; even the fferences between the annual highest and lowest temperatures in the uatorial district do not much exceed that of the diurnal variation of mperature, and on the average are from 10°–13° C., but often much less, en 5°.

'The difference of temperatures between the hottest and coldest month near the quator lies between 1° and 5° C., and does not exceed these figures, not even in e interior of continents—at Lado in Central Africa, 5° N., it is 4·8° C.; at Iquitos, ° S., it is 2·4° C.; at Equatorville on the Congo it is 1·2° C. But even towards the nits of the tropics, and in the extremest climates met with within the tropics, the nual variation of temperature hardly exceeds 13°. At Calcutta it is 10·3°; at Hong ong, 13·4°; at Vera Cruz, 6·5°; at Havana, 5·8°; at St. Louis in Senegal, 9·0°; at Rio Janeiro, 6·5°; at Kuka in Bornu, 12·1°; at Khartum, 12·9° C. The annual variation temperature is therefore at many places less than the diurnal variation, the limits which we may perhaps assume to be 5° and 13°, for example at Equatorville, 8°; in tavia, 6·5°, and during August, 7·7°; at Chinchosho in Loango, annual variation, °, but in July, 7·3°; at Kuka in the dry season, 11·4°; at Lado, difference 2h.–7h., nual variation 7·7°, in the dry season 11·1°; at Bakel in West Africa, 12·4° C.[1]'

Only at a few points, quite close to the limits of the zone, for example in Southern China, is zero or even a somewhat lower temperature actually reached now and then. The average maxima usually vary between 30° and 35° C. and remain below the extremes observed in extra-tropical districts.

Meteorological reports unfortunately only exceptionally give data regarding temperatures due to direct *insolation*, although this at least equals atmospheric temperature in its importance to organic life[2]. Corresponding to the position of the sun at the zenith or at a short distance from it, the intensity of insolation during a definite period, for example in an hour, is greater in the tropics than in higher latitudes, and must exert a correspondingly greater heating effect. In fact, Pechuel-Lösche at Chinchosho found the soil heated very often to 75°, frequently to 80°, and once even to 82° C. Haberlandt, on the other hand, at Buitenzorg during the wet season observed with a solar radiation-thermometer temperatures merely like those usual at Gratz, namely 55°–56·7° C. at noon. The relatively slight effect of insolation in this case is apparently a consequence of the large quantity of water-vapour in the air. In continental districts much higher temperatures prevail, at least during the dry season. The cooling of vegetation by nocturnal radiation is certainly considerable during the dry

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[1] Hann, op. cit., Bd. II, p. 12.

[2] Considering the danger of sunstroke in Cisgangetic India and other tropical continental districts.

season in tropical continental districts, and must be of considerable importance in relation to geographical botany; it is well known that i Bengal thin sheets of water freeze during the night in the dry season In districts on the coast, in the forest, and on the hills the cooling induce at night-time by radiation is much less, thanks to the large amount o water-vapour in the air, although physiologically it is by no means insignificant.

The following table gives a summary of mean temperatures in paralle belts of the tropical zone:—

MEAN TEMPERATURE IN PARALLEL BELTS OF THE TROPICAL ZONE[1] (after Spitaler).

	North.						South.				
Latitude	25°	20°	15°	10°	5°	0°	5°	10°	15°	20°	25°
January	18·4	21·7	23·9	25·7	26·2	26·2	26·1	25·9	25·7	25·2	24·7
July	28·0	28·1	27·9	26·7	26·1	25·5	24·9	24·0	22·6	20·5	18·1
Year	23·7	25·7	26·3	26·4	26·1	25·9	25·5	25·0	24·2	22·7	20·9

iii. *LIGHT AND THE ULTRA-VIOLET RAYS.*

The intensity of the rays of light, like that of the heat-rays, is naturall greater within than beyond the tropics, and the tropical daylight brighter than that of the temperate or polar zones. This feature ma be directly observed in the clearer reflection from the surface of wat and also from that of foliage when wet with rain, and it is very noticeab in photographs taken in the tropics. True as this is of the luminous ray it is equally true of the chemically effective ultra-violet part of tl spectrum.

In the tropical districts of America and of the Asiatic islands that I know, tl intensity of light is however not so strong as in East Africa, regarding the conditio of light of which P. Reichard writes as follows: 'In the natural features around u the dazzling brightness of the air is most striking. The more vertical tropical su produces a much brighter light than in Europe. At first the eyes can barely endu the glare, so that one is obliged to wear blue spectacles and to draw one's h down over one's eyes[2].'

There are no direct comparative observations regarding the intensi of luminous radiation for different latitudes, but some observations ha been made regarding the chemical rays. Thus simultaneous observ tions at Kew and at Para in Brazil on three April days of the year 18 showed an intensity of chemical action nearly twenty times greater at Pa than at Kew; even in August it was 3·3 times greater at Para.

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[1] Hann, op. cit., Bd. II, p. 17.

[2] Deutsche Rundschau, Oct. 1894. Quoted by Hann, op. cit., Bd. II, p. 40.

2. SOME GENERAL EFFECTS OF THE TROPICAL CLIMATE ON PLANT-LIFE.

i. *PROCESSES THAT ARE CHIEFLY INFLUENCED BY HEAT.*

It appears from the foregoing that the tropical climate differs from that of higher latitudes chiefly in its uniform and high temperature, and in the greater activity of the rays of heat and of light. The atmospheric precipitations exhibit neither in intensity, nor in their sequence in time, any essential difference as compared with the temperate zone, where at certain stations as great a rainfall occurs as at the rainiest points in the tropics, and where extensive districts exhibit a similar alternation of dry and rainy seasons. That, notwithstanding this, precipitations have still greater influence on the oecology of tropical plants than on temperate ones and evoke in them a series of characteristic peculiarities, is partly caused by the combination of greater heat with greater humidity, and partly by the fluctuation of the humidity in contrast with the steadiness of the heat.

Owing to the great uniformity and considerable height of the temperature in the tropics, much smaller differences in the harmonic optima, and consequently a much greater uniformity in the curve of temperature showing the oecological optimum [1], are to be expected, than in higher latitudes. More precise data on this matter are not at present available, since the physiological cardinal points as well as the oecologically most favourable degrees of temperature have as yet been determined only for temperate plants, in which, corresponding to the natural conditions, they lie far apart. We can therefore say no more upon this subject, for it is inadmissible to draw conclusions regarding the cardinal points of vegetation in the tropics merely from the extreme temperatures of the air, since the nocturnal cooling due to radiation, which in the dry season considerably exceeds that of the air, as well as the strong heating by direct insolation, must play an all-important part in many physiological processes.

Growth.

Among the physiological processes with a high optimum of temperature, growth, at any rate after the period of germination, takes a prominent place. It would be instructive to institute comparisons between plants of one and the same species in the tropics and in temperate zones, under external conditions otherwise as similar as possible. Up to the present only very few observations regarding the rate of growth of tropical plants are available, and from these only one conclusion can be

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[1] See p. 44.

drawn, namely, that certain tropical plants exceed all known temperate plants in rapidity of growth.

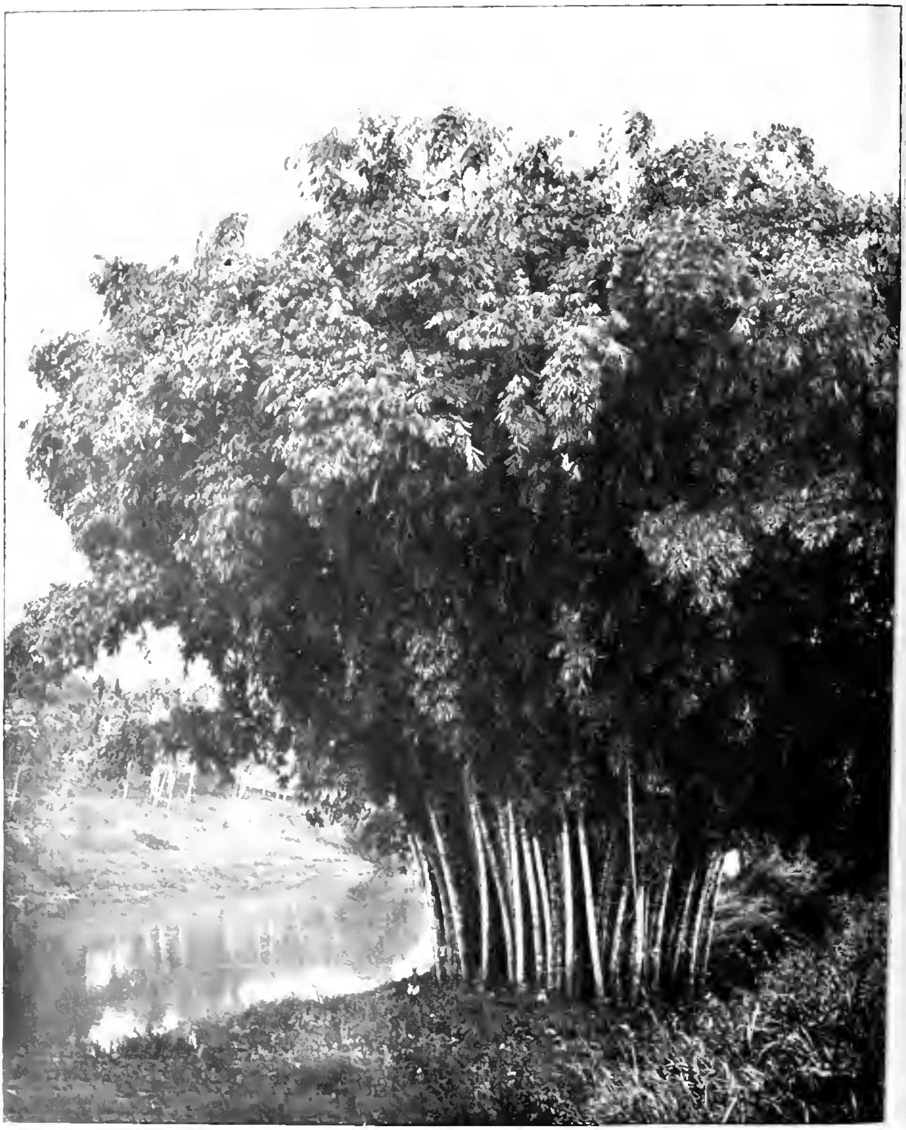

FIG. 113. Dendrocalamus giganteus in the botanic garden at Peradeniya in Ceylon.
From a photograph.

in bamboos must be numbered among the representatives of th kingdom that grow most rapidly. Wallich mentions tha Bambusa arundinacea increased in length about 7 meter

35 centimeters in 31 days. But more precise observations regarding his point have only quite recently been made by Kraus on a species of Dendrocalamus (Fig. 113) in the botanic garden at Buitenzorg. The ollowing tables give some of his results :—

GROWTH IN LENGTH OF DENDROCALAMUS AT BUITENZORG DURING FIVE DAYS.

		Length in cm.	Growth by day and night.	Forenoon and afternoon.
December 4	6 a.m.	164	Day, 10·5 cm.	Forenoon, 7·5 cm.
	12 „	171·5		Afternoon, 3·0 cm.
	6 p.m.	174·5	Night, 16 cm.	
December 5	6 a.m.	190·5	Day, 5 cm.	Forenoon, 1·5 cm.
	12 „	192		Afternoon, 3 cm.
	6 p.m.	195	Night, 15 cm.	
December 6	6 a.m.	210	Day, 8 cm.	Forenoon, 5 cm.
	12 „	215		Afternoon, 3 cm.
	6 p.m.	218	Night, 16 cm.	
December 7	6 a.m.	234·0	Day, 8·5 cm.	Forenoon, 4·5 cm.
	12 „	238·5		Afternoon, 4 cm.
	6 p.m.	242·5	Night, 12·5 cm.	
December 8	6 a.m.	255	Day, 12 cm.	Forenoon, 6 cm.
	12 „	261		Afternoon, 6 cm.
	6 p.m.	267		

GROWTH IN LENGTH PER HOUR DURING DAY AND NIGHT OF DENDROCALAMUS AT BUITENZORG.

Amount in millimeters.

Shoot II.

	Dec. 4.	Dec. 5.	Dec. 6.	Dec. 7.	Dec. 8.	Dec. 9.
Day . .	15·4	6·6	8·4	2·9	9·2	6·3
Night . .	12·4	13·0	16·6	12·1	17·5	13·8

Shoot III.

	Dec. 4.	Dec. 5.	Dec. 6.	Dec. 7.	Dec. 8.	Dec. 9.
Day . .	8·8	3·8	6·6	7·1	10·0	10·4
Night . .	13·3	12·5	13·3	10·2	11·0	10·4

The increment per hour was therefore on the average 7·7 millimeters by day and 3 millimeters by night.

The average daily increment during two months' observations was—

Culm No. 1,	in 58 days,	22·9 cm. per diem.
,, ,, 2,	,, 60 ,,	19·0 ,, ,,
,, ,, 3.	,, 60 ,,	19·9 ,, ,,

The greatest increment in twenty-four hours was—

Culm No. 1,	57 cm.	on 22nd December.
,, ,, 2,	42 ,,	,, 3rd January.
,, ,, 3,	45 ,,	,, 4th ,,

Very quick-growing plants are not at all rare in the tropics, at any rate in rainy districts. I have made some measurements, at the Buitenzorg botanic garden, on young shoots and leaves of woody plants which appeared to be growing very rapidly:—

On the 15th November I measured a still folded leaf of Amherstia nobilis and found, rachis 6 cm., a leaflet 2·9 cm. On the 24th Nov. the same rachis and leafle measured 31 cm. and 19·5 cm., showing an increased length of 5- and 7-fold respectively in 9 days, or a daily increment of 4·1 cm. and 1·8 cm. respectively. Of a somewhat older leaf of the same shoot the corresponding measurements on the 15th Nov were 10·8 cm. and 3·5 cm., on the 24th Nov. 36 cm. and 19·7 cm. In Brownea sp. the length of a bud just opening on the 15th Nov. was 8 cm.; on the 20th Nov. the young shoot, the leaves of which had not yet unrolled, was 18·5 cm. long; on the 24th Nov. with the leaves opened quite flat, the measurement was 29 cm. to the extrem leaf-tip. The total length had therefore increased more than 3½-fold in 9 days, in fac by 21 cm., and this gives a daily increment of 2·6 cm. Other measurements of th developing young shoots of Urostigma glabellum will be given subsequently i connexion with the leaf-fall of trees.

Haberlandt mentions several instances of rapid growth in Java:—

'In 1874, at Willem III's school in Batavia, a plant of Eucalyptus alba, indigenou in Timor, was planted: after three years' growth it was already a tree, 15 meters i height. In a plantation at Tjikömöh, near Buitenzorg, two-year-old mahogany plant are 4½ meters high, and three-year-old plants of Swietenia macrophylla 5-6 meter high. Albizzia moluccana—that admired shade-tree, the delicate pinnate foliage o which does not give one any impression of abundant vigour and activity—grows wit fabulous rapidity. Fine yearling plants actually attain a height of 5-6 meters, six year-old plants are already 25 meters high, with stems measuring 20-25 centimeter in diameter at the height of a man[1].'

In Honolulu Maxwell[2] undertook some investigations on the growth o banana leaves. The averages of his results he tabulates as follows:—

[1] Haberlandt, op. cit., p. 115.

[2] Maxwell, op. cit., p. 1.

TABLE OF AVERAGES OF GROWTH OF BANANA LEAF (after Maxwell).

Number of leaf.	Length of leaf.	Breadth of leaf.	Surface of leaf.	Mean growth in length in day period.	Mean growth in length in night period.	Mean growth in length day and night.	Mean growth in surface day and night.	Mean temperature.
	Inch.	Inch.	Sq. inch.	Inch.	Inch.	Inch.	Sq. inch.	Fahr.
I.	29½	14	413	—	—	4¼	59	72·5°
II.	35½	14	497	—	—	4½	62	72°
III.	43	15	645	3	1⅓	4⅓	64·5	70°
IV.	47½	17	803	2⅗	1⅕	3⅕	66·9	71·7°

The 'length of leaf' given is the total length of the mature leaf, less its length at the time of first measurement. Day period: 7.30 a.m. to 5.30 p.m. Night period: 5.30 p.m. to 7.30 a.m. Date: 26th January to 9th March.

Very rapid longitudinal growth appears to characterize the frequently enormously long absorbing roots of certain lianes and epiphytes. Went found a total increment of 44 millimeters in 48 hours in those of Philodendron melanochrysum.

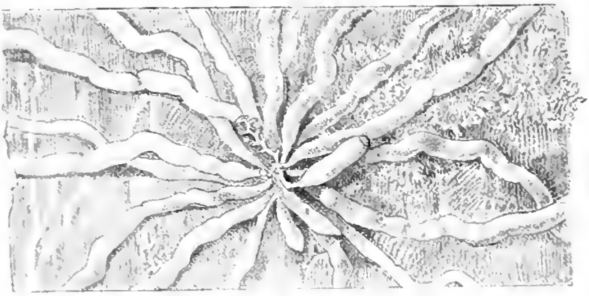

FIG. 114. Taeniophyllum Zollingeri, Rchb. f. Natural size. After Wiesner.

The above high values for the growth in length of stems, leaves, and roots must by no means be converted into a generalization that growth in length in the tropics considerably exceeds that in temperate zones. These statistics relate exclusively to plants in which growth is conspicuously rapid, and which for that reason induced closer investigation. That extremely slow-growing plants are not wanting, even in rainy tropical districts, has been shown by Wiesner in the case of Taeniophyllum Zollingeri, a leafless epiphytic orchid (Fig. 114), consisting almost exclusively of green aërial roots.

The figures observed in reference to the growth of several plants of Taeniophyllum, in their native habitats, are given in the following table, which also includes data regarding the photic ration which is an important factor.

GROWTH IN LENGTH OF ROOTS OF TAENIOPHYLLUM ZOLLINGERI (after Wiesner).

Growth.	Growth.	Photic ration.
In 29 days, 2·37 mm.	In 24 hours, 0·0817 mm.	$\frac{1}{21}$
,, 29 ,, 3·47 ,,	,, 0·1172 ,,	$\frac{1}{18}$
,, 30 ,, 8·55 ,,	,, 0·2830 ,,	$\frac{1}{8}$
,, 31 ,, 6·80 ,,	,, 0·2266 ,,	$\frac{1}{5}$
,, 31 ,, 2·50 ,,	,, 0·0806 ,,	$\frac{1}{4}$

Compared with the greatest diurnal increment of a bamboo-culm as given by G. Kraus the greatest increment of Taeniophyllum is as 570: 0·283 mm. or 2013 : 1. Hence the culm of bamboo observed by Kraus grew in round numbers 2,000 times more rapidly than the aërial roots of Taeniophyllum Zollingeri.

Transpiration.

The great physiological importance of the heating of plants by insolation and the part played in this matter by transpiration are very easily observed, and have quite recently formed the subject of closer investigation. *The action of insolation is stronger when the air contains much water-vapour* than when it contains little, because dryness of the air causes the stomata to close. The effect of insolation is consequently most strikingly observe in moist districts.

Every visitor to the botanic garden at Buitenzorg knows that man plants, during the later hours of the generally sunny forenoon, usuall exhibit clear signs of incipient wilting; this continues to increase rapidl until the occurrence of the afternoon shower of rain, by which time man leaves hang down quite in a drooping condition, although they are no unprovided with protective contrivances against transpiration[1]. Durin my visit to Buitenzorg in the midst of the rainy season, fourteen rainles sultry days passed in succession, and the vegetation presented a parche appearance such as would hardly have arisen in Europe after a perio three times that length; the crops were endangered and the populatio sought by appropriate weeping-ceremonies to invoke the favour of th Rain-god. The air remained very moist throughout this dry period, and in a less sunny climate, the rich nightly formation of dew would not hav been so ineffective.

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[1] See p. 18.

Wiesner has numerically determined the effects of direct sunlight on the transpiration of rice plants at Buitenzorg [1] :—

EFFECT OF DIRECT INSOLATION ON TRANSPIRATION.

RICE PLANT A.

Hours of experiment, a.m.	Temperature.	Relative humidity.	Illumination *.	Transpiration per hour.
6.50— 7.50	22·0—22·5°	95—96	diffuse	0·81 gram.
7.50— 9.17	22·5—23·8°	89—95	70 minutes diffuse 17 minutes S_0—S_2	2·32 grams.
7.20—10.10	25·0—25·2°	82—94	S_0—S_2	7·45 „
10.11—10.19	25·2—28·5	73—72	S_3—S_1	10·57 „

* S_0 sun completely hidden ; S_1 sun visible in the sky, only as a bright vision ; S_2 sun visible as a bright disk ; S_3 sun covered only by a light haze or a delicate veil of cloud ; S_4 sun completely exposed.

RICE PLANT B.

Hours of experiment.	Temperature.	Relative humidity.	Illumination.	Transpiration per hour.
8.43— 9.00	26·2°	82	sun	15·35 grams.
9 — 9.15	27°	70	diffuse	0·09 „
9.18— 9.34	27·2°	?	sun	8·91 „
9.39—10.10	27°	74	diffuse	2·85 „

A series of observations on a sunny morning with a young (red) and n old (green) leaf of Amherstia nobilis—the specimens stood with their talks in water—gave the following amount of transpiration in grams er 100 grams of living weight :—

FFECT OF DIRECT INSOLATION ON TRANSPIRATION OF AMHERSTIA NOBILIS.

Amount of transpiration in grams per 100 grams of living weight.

	Red leaf.	Green leaf.
Under covered veranda	1·22	1·00
Free exposure, S_0	1·88	2·56
„ S_2	2·40	5·33
„ S_4	3·11	8·44

The following observations of Wiesner show how great transpiration can be at uitenzorg. He placed several herbaceous plants (Coleus, Adiantum, Jatropha, limosa pudica) in pots, and imbedded them in the ground in a part of the garden lly exposed to the rain. For several days the plants received rain daily—sometimes ery heavy rain. 'On December 29 there was absolutely no rain ; the forenoon was unny, and at noon the sun was quite uncovered. On this day all the specimens ey were not watered on the day in question—died of desiccation.'

Giltay made comparative observations on the amount of transpiration of Helianthus berosus at Buitenzorg and at Wageningen in Holland. They showed that the

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[1] Recorded by Burgerstein, op. cit.

daily loss of water was the same in both cases, namely on the average 0·6 gram per hour, but even in this case transpiration during the hot midday hours appears to have been much stronger in Buitenzorg than in Holland.

Experiments made by G. Haberlandt at Buitenzorg in January, which is the middle of the rainy season, and at Gratz during the hot days of August, showed that transpiration in the *shade* in a moist tropical climate is much weaker than in Central Europe:—

The humidity of the air fluctuated at the time when Haberlandt made his experiments (December, January), between 70–97 %. 'The minimum (70–80 %) occurred at about midday, but frequently not till 1 p.m. Then the humidity increased rapidly as the rain began, and even by 3 or 4 p.m. attained 90–95 %. Omitting slight fluctuations, which seldom exceeded 5 %, the curve in its typical course remained from the evening till about 7 a.m. at 93–97 %, and then gradually sank again till noon[1].' The temperature during the period of observation showed a diurnal variation of 6–8° C.

'The diurnal curve of temperature, as a rule, showed the following course:—Between 6 and 7 a.m. the temperature was lowest. The minimum varied, omitting extreme cases, between 21 and 23° C. During the forenoon the temperature at first rose rapidly, then somewhat more slowly up to 29–30·5° C. This maximum was rarely attained by midday, usually not till between 1 and 2 p.m. Then the temperature fell to 23–25°, sometimes more rapidly, at others more slowly, according to the cloudiness, or amount and duration of the rainfall in the afternoon.'

AMOUNT OF TRANSPIRATION OF LEAVES IN BUITENZORG AND IN GRATZ (after G. Haberlandt[2]).

(In grams per diem and over one square decimeter of surface.)

I. Buitenzorg.

Conocephalus ovatus	0·29
Musa Ensete	0·45
Gonocaryum pyriforme	0·45
Daemonorops oblongus	0·47
Xanthophyllum vitellinum	0·58
Carica Papaya	0·62
Pterocarpus saxatilis	0·71
Cocos nucifera	0·89
Grammatophyllum speciosum	0·89
Bactris speciosa	1·00
Theobroma Cacao	1·06
Albizzia moluccana	1·19
Ficus elastica	1·52
Sanchezia nobilis	1·56
Loranthus pentandrus	1·86
Phoenix sp.	2·60
Acalypha tricolor	3·25

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[1] Haberlandt, I, p. 6.

[2] II, p. 807.

II. GRATZ.

Aesculus Hippocastanum	1·37
Syringa vulgaris	2·03
Acer Pseudoplatanus	2·03
Corylus Avellana	3·33
Cornus sanguinea	4·09
Pyrus communis	5·97

III. AFTER N. J. C. MÜLLER.

Poplar	2·42
Oak	2·89
Beech	3·50
Birch	3·65
Willow	4·22
Hornbeam	4·36
Alder	7·96

ii. *PHYSIOLOGICAL ACTION OF TROPICAL LIGHT ON PLANTS.*

From our knowledge of the effects of light on growth and transpiration, we may safely assume that the light of the tropics, in accordance with its greater intensity, influences these processes still more strongly than does the weaker light of higher latitudes. In fact the growth in length of a bamboo is quite strikingly less during the hours of the day than during those of the night; the growth in length of the aerial roots of Taeniophyllum Zollingeri stops altogether in daylight of relatively very moderate intensity, even in a very weak light; and the comparatively strong transpiration, which causes the flaccid drooping of the foliage of many tropical plants during the brightest hours of daylight, may be considered partly as an effect, even if indirect, of the rays of light.

The share that light takes in the above-mentioned functions has not yet been numerically determined. However a glimpse into the different specific actions of light has been afforded, in particular by Wiesner's observations at Buitenzorg.

The *lie in relation to light* of the leaves of tropical plants, according to Wiesner's observations, differs in general from that of the leaves of temperate plants. since they do not, like them, universally strive to attain a position perpendicular to the strongest *diffuse light*, but exhibit this disposition only in the inner. poorly lighted part of the crown; at the periphery of the tree. however, they give up this disposition in the face of rays of high incidence, and the lie of the leaves is there determined by *direct* sunlight.

Owing to this lie of the leaves when they are exposed to the direct rays of the sun, not only are strong heating and consequent excessive transpiration prevented. but at the same time the *destruction of the chlorophyll by intense light* is obviated. Several characteristics of tropical foliage appear to have been acquired with the special object of saving the chlorophyll, or at any rate they subserve that end; among them are movements of the leaflets of pinnate leaves, strong reflection of light by the foliar surfaces, prolonged retention of a non-turgid condition and the consequent flaccid drooping of young leaves, foldings, tomentum, and so forth[1]. In spite of all such protective devices, the destruction of chlorophyll by the intense tropical light is a very conspicuous and widespread phenomenon. Thus the leaves of Pisonia alba, which is frequently grown as an ornamental tree, are vertical and sap-green when young; later on they arrange themselves at right angles to the direction of the most intense daylight, and suffer such a complete destruction of their chlorophyll as to become almost pure white[2]. In sunny situations within the tropics yellowish discolorations of the foliage are very common.

The greater intensity of tropical light also renders possible a *mor luxuriant development of the shade-flora* than in higher latitudes. A the same time, the property plants possess of demanding less light a higher temperatures also operates in the same direction. Wiesner ha actually seen tropical plants thriving under such a feeble illuminatio as with us would entirely exclude all green vegetation. It would b extremely useful to investigate more closely the vegetation in the shad of a virgin forest from Wiesner's points of view and in accordance wit his methods.

Thus, Wiesner found a Javanese grass, Orthopogon Wiesneri, Schiffner, growin in patches in the shade of Myristica moschata with $L = \frac{1}{100}$ (I maximum=0·016) but not anywhere in the shade of the densest palm-thickets, where $L = \frac{1}{12}$ (I maximum=0·011, I mean=0·003). Of all herbaceous non-epiphytic Dicotyledone Wiesner found Geophila reniformis, Don., penetrating most deeply into the shad It continues to blossom with $L = \frac{1}{61}$ (I maximum=0·026; I mean=0·011). Witho flowering, it bears almost as great a deprivation of light as Orthopogon Wiesneri.

The intensity of insolation in the tropics is so great that many cultivated plant including coffee and cocoa, at least when young, require shade. For this purpos trees with a thin crown are used, especially those with pinnate leaves, for instan Albizzia moluccana, Miq., also Cedrela serrulata, Miq., Cedrela odorata, Lin Pithecolobium Saman, Benth., in Java. In tropical America species of Erythri are usually employed for the same purpose. Probably, it is less a question of kee ing off the luminous and chemical rays than the heat-rays, which would cause t great heating and consequently too great transpiration.

Wiesner made some measurements of the intensity of light under the shading trees in the experimental garden at Tjikömöh near Buitenzorg, and he found:—

Albizzia moluccana, Miq.	$\frac{1}{2·81}$
Cedrela serrulata, Miq.	$\frac{1}{5·5}$
Cedrela odorata, Linn.	$\frac{1}{5·7}$
Pithecolobium Saman, Benth.	$\frac{1}{4·2}$

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[1] Wiesner, Johow, Haberlandt.

[2] Wiesner.

[3] See p. 55.

iii. *PHYSIOLOGICAL ACTION OF ATMOSPHERIC PRECIPITATIONS ON PLANTS.*

The differences in the oecology of tropical plants are in the first place ssociated with differences in the atmospheric precipitations. These lone, usually without any, even indirect, co-operation on the part of the mperature, cause the domination of woodland or of grassland, the ygrophilous, tropophilous, or xerophilous character of the vegetation, nd the periodic phenomena. Accordingly, the differences in the climatic umidity also determine the range of species within the tropics.

A separate chapter is devoted to the various types of tropical woodnd and grassland arising from differences in the atmospheric precipitaons, and to the climatic conditions determining their presence, and also o the periodic phenomena.

Reference may here be made to Wiesner's investigations regarding *the ombrophily nd ombrophoby of tropical vegetation*, for they are as yet too incomplete to be rviceable in characterizing the several climatic districts. According to Wiesner, e great majority of plants in the moist hot western parts of Java possess markedly nbrophilous foliage, and this condition may probably extend to the vegetation in constantly moist tropical climate. On the other hand, in those parts of the torrid ne where long rainless periods regularly prevail, the condition of affairs may be anged in favour of ombrophobous species. Investigations on this subject have not en conducted, but the frequency in such districts of succulent species and other ants with unwettable coatings favours this opinion.

Nevertheless, many decidedly ombrophobous plants thrive in a constantly moist mate; thus Wiesner rightly draws attention to the fine growth of various species Opuntia and Cereus in the botanic garden at Buitenzorg. These plants are, however, confined to very open sunny situations, where strongly ombrophilous plants ould suffer from too great transpiration. On the other hand, the feeble growth West Java and other very moist tropical districts of many plants from a drier mate is to be attributed to ombrophoby. This has been proved by Wiesner rticularly in regard to roses, which nearly always assume a very stunted form tropical gardens. Their foliage is weakly developed and caducous, their corollas e small and irregular. The different kinds of roses are, however, unequally nbrophobous, and consequently display different degrees of deficiency, or may solutely refuse to grow.

To the indigenous ombrophobous plants of constantly humid districts there belong particular those with delicate pinnate leaves, which by their movements more less effectively evade the violence of the rain, such as Mimosaceae, species of calis, and the like. But such forms are scantily represented in Java, especially the forest; their abundance is characteristic of the vegetation of drier climates.

In accordance with its ombrophily, the foliage in a constantly humid climate is as ule easily wettable; besides, as Wiesner shows, foliage that is wetted with difficulty comes easily wettable when exposed to continuous humidity, and the reverse is e case. Young leaves are as a rule unwettable and ombrophobous; later they become wettable and ombrophilous, but in advanced age reassume the characters their youth. Hence after heavy rainfall they readily die and fall to the ground, sinc in contrast to the young leaves, they are not protected against the rain by their lie.

Many trees in periodically dry districts shed their leaves even during the rain season; one may see in this an effect associated with the increased ombrophoby age. On the other hand, I have met with the statement here and there in boo of travel that certain trees or even entire forests become leafless at the height of t rainy season. It is on the whole very probable that in many cases in nature, n drought but great humidity may be the cause of the periodic leaf-fall. It is desirab that in continuation of Wiesner's researches the cause of leaf-fall in the tropics m be more closely investigated.

3. THE FLORISTIC CHARACTER OF THE TROPICAL ZON

With the exception of some border districts, usually of limited ar where the winter temperature regularly descends to freezing-point, t zones enclosed by the tropics possess a pronounced megathermic flo which in places, for instance in Southern Florida and Southern Bra extends somewhat beyond the tropics. Yet in these latter extensio the megathermic flora is already perceptibly impoverished, because t annual curve of temperature no longer corresponds to the oecologi optimum of many species. In particular, the temperature necessary the ripening of fruit is frequently not maintained.

The following summary gives the general characteristics of the me- thermic floras, as it enumerates in systematic order the families t t occur in tropical lowlands, and briefly sketches the part they play s regards number of species and of individuals. Aquatic plants are omitt, because a separate chapter is devoted to them[1].

Thallophyta.

Though *Algae* as terrestrial plants are of merely subordinate importa e in the tropics, yet their significance, at least in rainy districts, is alw s greater than in other latitudes. Many species live as epiphytes, chi y on leaves. The *Fungi* of the tropics have not yet been satisfacto y investigated. Yet it seems to be already ascertained that the la er orders known to exist in Europe are all represented. In other resp ts deep-seated differences are not wanting, and many groups that in Cen al Europe are very prominent, especially among the Hymenomycetes, re feebly represented in the torrid zones.

The following remarks of Alfred Möller regarding the fungal vegeta on of the forests near the coast of South Brâzil hold good for all trop al forests that I know:—

> 'On wet autumn days we find in our German forests far more fungi that strik he [illegible] observer who is not specially looking for them, and that exercise cons er-

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[1] See Sect. V.

ible influence on the facies of the forest, than we ever do in the virgin forests of Brazil. There, nothing is to be found comparable with the gaily coloured clumps of the numerous Hymenomycetes of our forest soil. The first impression which a fresh-comer wandering in a Brazilian forest must receive, is that apparently very few ungi occur there. As a matter of fact this is in reality not the case: the fungal flora s extremely rich, but the minute forms especially appear in great abundance, and hese are seen only when one looks carefully for them, while the larger forms for the most part only occur here and there [1].'

Among *Lichenes*, the Ascolichenes, at any rate as far as number and size of individuals go, play a much smaller part than with us. Large tufted orms, such as Usneae, are seen only on high mountains and therefore outside the megathermic climate. Cora Pavonia, which alone forms the lass of Hymenolichenes, is exclusively tropical, and appears to be cosmopolitan within the tropics. It is found in its various forms of growth, but chiefly in its proper Cora-form, in abundance on moist soil and on the bark of trees.

Bryophyta.

Among Bryophyta, and especially among *Musci*, megatherms are rare, nd are represented for the most part by small inconspicuous species which occur scantily in cool damp situations, and are quite unimportant in their effect on the general facies of the vegetation. Much more richly do they appear in the cool regions of tropical mountains [2].

Pteridophyta.

Ferns in the tropics develop an extraordinary wealth of form, and vary in heir dimensions from small moss-like plants to trees. Most of them are ygrophilous and shade-lovers, so that only humid forests show a great ichness in ferns. Besides, the majority of them are not decidedly megahermic, but prefer a climate that is mild, even if it be as uniform as possible, so that the greatest development of ferns in numbers, especially f their arborescent forms, is exhibited less in the lowlands than in cooler mountain landscapes.

Three orders of ferns are exclusively tropical, the Gleicheniaceae, Schizaeaceae, and Marattiaceae.

The *Gleicheniaceae* are repeatedly branched in a dichotomous manner; hey present a very unique appearance, and in contrast with most of their ropical allies, these ferns occupy open sunny situations, and usually are in large numbers together. This last statement is specially true of the lmost cosmopolitan Gleichenia linearis (Fig. 116), which is common verywhere.

The *Schizaeaceae* (for example Aneimia, a xerophilous genus chiefly in

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[1] Alf. Möller, op. cit., p. 154.

[2] See Sect. IV.

the interior of Brazil, and Lygodium, species of which are twiners in rain-forests) and the *Marattiaceae* (for example Angiopteris evecta, a giganti

FIG. 115. Pandanus sechellarum, Balf. f. Seychelles. From a photograph by A. Brauer.

[illegible] ous form with a round subaërial stem as large as a man's head, [illegible] Asia) are never the chief members of any formations.

Mainly, but not exclusively, tropical are the *Cyatheaceae*, to which almost all tree-ferns belong (species of Cyathea, Dicksonia, Alsophila), and the *Hymenophyllaceae*, small, frequently moss-like herbs with transparent foliage, which cover stems of trees and rocks in moist, shady forests, just as mosses do with us.

The great mass of tropical ferns belongs to the order *Polypodiaceae*, which is also so strongly represented in Europe, and to a considerable extent by the same genera, namely Polypodium, Aspidium, Asplenium, Pteris, and so on. Only a few rare Polypodiaceae are tree-like.

FIG. 116. Forest landscape in the Seychelles. In the foreground, Gleichenia linearis; in the ackground, palms (probably Roscheria melanochaetes, H. Wendl.), Pandanus, and other plants. rom a photograph by A. Brauer.

The *Lycopodiaceae* are much less prominent than the ferns, but neverthe-ess of greater significance than in temperate floras. Species of Selaginella ften form the chief covering of the forest soil; Lycopodium cernuum is xtremely common in well-lighted spots; other species of Lycopodium as vell as of Psilotum are occasionally common epiphytes.

The *Equisetaceae* are not more strongly represented than in the emperate zones.

Gymnospermae.

Gymnosperms are of quite subordinate significance in the megathermic flora. *Coniferae* are almost entirely absent: they are found between the tropics wellnigh only on high mountain chains, outside the tropical climate. *Cycadeae* (Fig. 117) are a highly characteristic feature of the tropical flora but are subordinate as regards the number of species and individuals. The species of Gnetum which completely agree with Dicotyledones in thei vegetative organs are also a subordinate and at the same time inconspicuo element in the flora.

Fig. 117. Dioon edule. Mexico. Cerro Colorada, south-east from Jalapa. From a photograp by Stahl.

Monocotyledones.

Monocotyledones supply the most characteristic features of the tropic flora. In the first place, this is true of the *Palmae*, which however ov their predominance, in tropical landscapes chiefly at any rate, to cultivatio The latter statement is especially true of the coconut palm, Cocos nucifer the groves of which, fringing most tropical coasts, have only exceptionally originated without human aid (Figs. 118 and 226). In the cultivated lands of the tropics one will always find the royal palm, Oreodoxa regia, the finest of its race, which comes from the Antilles and Southern Florida (Fig. 119). The avenues of Oreodoxa regia in Rio de Janeiro and in Ceylon are renowned. [Among the commonest of cultivated palms may also be reckoned Arenga saccharifera, important not for beauty but only as an economic tree. In Eastern Asia, especially in the Malay peninsula, one can easily recognize from a distance the presence of human settlements by the occurrence of the betel-nut palm, Areca Catechu (Fig. 123). The slender but tall stem, straight as an arrow, bears a small crown of emerald-green leaves. Finally, we find the peculiar Caryota urens chiefly as an ornamental tree, the bipinnate leaves of which bear triangular leaflets, and to some extent remind one of Adiantum. A great number of other palms are also cultivated as economic or ornamental trees, but yet without being so generally distributed; for instance numerous fan palms, the sago palms, Metroxylon Rumphii, Mart., and M. laeve, Mart., the ivory-nut palm Phytelephas macrocarpa, and so on.

FIG. 118. Cocos nucifera. On the sea-shore in Seychelles. From a photograph by A. Brauer.

In natural landscapes the species of palm vary greatly according to the different districts, frequently in such a way that one of the tree-forms predominates over the others (see Figs. 116 and 121). Besides tree-palms, lianes like Calamus and Desmoncus are rarely absent from the forest, as well as short-stemmed species, like the species of Geonoma, or acaulous forms. Palms also grow scattered over savannahs, for example species of Hyphaene and Copernicia tectorum (Fig. 200). Real formations, *palm-woods*, appear chiefly on swampy or frequently inundated ground; they are formed by Mauritia setigera in Trinidad, by other species of Mauritia in the north of South America, by Phoenix sylvestris in Cisgangetic India (Fig. 120), by Nipa fruticans in the Eastern Asiatic mangroves (Figs. 226 and 227).

FIG. 119. Oreodoxa regia. Young specimen in the tropical rain-forest of Southern Florida. From Garden and Forest.

Next to the palms, the tree-like *Gramineae*, especially species of Bambusa and Dendrocalamus (Fig. 113), belong to the most characteristic forms of tropical landscapes; but, like palms, they are not altogether wanting in subtropical zones, and in Japan reach the cool temperate zones. Bamboos

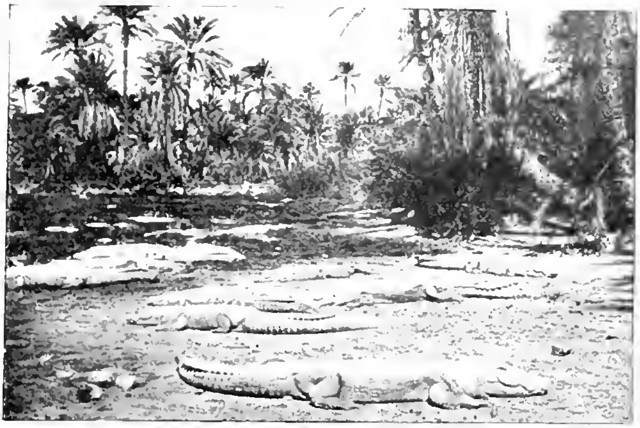

FIG. 120. Phoenix sylvestris. Forming a grove on swampy ground near Bombay. From a photograph by Deichmuller.

FIG. 121. Lodoicea Seychellarum. Growing wild on the island of Praslin, Seychelles. From a photograph by A. Brauer.

ve their appearance in vast numbers over the greater part of the tropical ne—Africa is poor in them—chiefly to cultivation. They are, however.

also frequently found wild. The largest forms grow in forests scattered among other trees, or they constitute independent forests (Fig. 207); smaller forms are common as underwood.

Very unique and occasionally very common forms of the megathermic flora are the species of *Pandanus* (Figs. 115, 116, 122, 212, 214), which however rarely occur in great numbers together. They are confined to the Old World. They occur chiefly by the seaside, but also in forests; only rarely do they form pure woods.

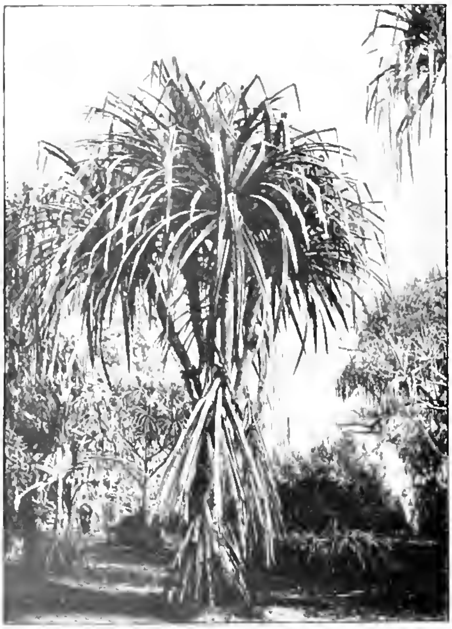

FIG. 122. Pandanus sp. Botanic garden at Buitenzorg. From a photograph by G. Karsten.

The *Araceae*, owing to their occurrence in great numbers and to the great diversity in their species, take a prominent place in tropical forest scenes. Among them are found lianes like species of Philodendron, Monstera, Pothos; epiphytes like species of Anthurium and Philodendron, and many terrestrial herbs which are often social. To the aroids belong some of the most remarkable productions of the tropics, for example the gigantic Amorphophallus Titanum in Sumatra. Araceae are also important constituents of the swamp-flora, as the species of Colocasia and Alocasia.

The *Scitamineae*, in the form of perennial herbs as tall as a man, are common and prominen constituents of the forest flora Bananas, Musa paradisiaca an M. sapientum (Fig. 49), are no only among the commonest and most conspicuous cultivated plants, bu also, in Asia, are frequent in the forest. Heliconieae are in particula characteristic of the tropical forests of America, as various Zingiberacea are of those of Asia. Madagascar possesses the only tree-form of the orde in the traveller's tree, Ravenala madagascariensis, which is grown in al tropical cultivated lands as an ornamental tree (Fig. 123).

Finally, amongst prominent monocotyledonous families forming constituents of the flora, mention should be made of the *Orchidaceae*, whic in particular, as epiphytes, develop an astonishing diversity of forms, an also of the *Bromeliaceae* in tropical America, which are likewise chiefl epiphytic. The grasslike *Eriocaulaceae* are, especially in species of th genus Paepalanthus, essential constituents of the South American grassland districts; and the *Commelinaceae*, belonging like the Eriocaulaceae to the Enantioblastae, are very widely distributed particularly as species of Commelina.

Several monocotyledonous families that are most prominent in temperate zones, such as Cyperaceae, Juncaceae, Liliaceae, Amaryllidaceae, are for the ost part of merely subordinate importance, except for some not exclusively ropical genera like Smilax, Agave, Fourcroya.

FIG. 123. To the left, Areca Catechu; to the right, Ravenala madagascariensis. From the botanic garden at Singapore. From a photograph by Kükenthal.

Dicotyledones [1].

Dicotyledones preponderate considerably over Monocotyledones in the ora of the tropics, and the number of their purely tropical families is much

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[The grouping of the families is that adopted in Strasburger's Text-book of Botany.]

greater. Their characteristics are however much less striking, so that a picture of vegetation essentially composed of Dicotyledones alone, frequently has a great resemblance to one in the temperate zones. When marked peculiarities such as those of branching, abnormal disposition of the leaves towards the horizon, plank-buttresses, subaërial roots, epiphytic growth, and so forth, do present themselves, they are not as a rule the characters of families, but oecological adaptive features recurring in the most different cycles of affinity.

The distribution of *Amentaceae* within the tropics is comparable with that of Coniferae, as they form a considerable contingent of the flora in the higher mountain regions outside the megathermic climate, whilst they are unimportant in the lowlands. They are not completely absent; there are, for instance, some megathermic oaks in Mexico, and, according to my own observations, in the forests near Singapore.

The *Urticineae* are extremely important in the tropical zones. The Moraceae in the first place, with the genus Ficus with its numerous arboreous and shrubby species, also with the genus Artocarpus, to which belong some of the commonest cultivated tropical trees, Artocarpus incisa, the bread-fruit tree, A. integrifolia, the jack-fruit tree; the Urticaceae with numerous genera of usually shrubby or herbaceous species.

Among the *Polygoninae*, the Piperaceae are exclusively megathermic. They are represented in the rain-forests chiefly by many shrubby and herbaceous terrestrial plants, as well as by root-climbing lianes and epiphytes. The Polygonaceae are limited to a few species, chiefly arboreous.

The families that in Central Europe chiefly represent the *Centrospermae* namely Caryophyllaceae and Chenopodiaceae, are almost exclusively mesothermic and of no importance within the tropics. On the other hand Amarantaceae are very numerous as inconspicuous herbs and more rarely as woody plants. The Phytolaccaceae and Nyctaginaceae are mainly tropical American.

The most important family of the north temperate zone among the *Polycarpicae*, that of the Ranunculaceae, is mesothermic and microthermic and therefore scarcely represented within the tropics except on high mountains. The Magnoliaceae also are less frequent than in the north temperate zone. The most important family of the group within the tropics is that of Lauraceae, to which numerous forest trees, also shrubs and the common herbaceous liane-parasite Cassytha, belong. The purely tropical families of the Anonaceae, Myristicaceae, Monimiaceae, and, in contrast with the allied mesothermic Berberidaceae, the family of the Menispermaceae, include many woody plants.

The tropical *Rhoeadinae* are almost restricted to the Cappärideae. Th few Cruciferae are mostly mountain forms.

Among the *Cistiflorae* are many purely megathermic families of wood plants, richly represented within the tropics, such as Clusiaceae, Dilleniaceae, Ochnaceae, Dipterocarpaceae, Bixaceae, also the Ternstroemiaceae, which includes some mesotherms, and the Marcgraviaceae, consisting of tropical American lianes and epiphytes. The tropical Violaceae are mainly woody plants and some are even trees. Among herbaceous families the Nepenthaceae are prominent in the eastern tropics

Of the *Columniferae*, the purely megathermic Bombacaceae are conspicuous for their large dimensions, especially the great thickness of their stems and the magnificence of their flowers. The allied Malvaceae, the Tiliaceae, and the purely tropical Sterculiaceae, both as woody and herbaceous species, are important constituents of the tropical flora.

The *Gruinales* are of less significance. The Oxalidaceae, Tropaeolaceae, and the Balsaminaceae, the last of which are very common in the East Indies, are chiefly represented by herbaceous plants ; the Geraniaceae are almost absent.

The *Terebinthinae* are, in particular, of considerable significance as contributing to the woody plants forming the floras of the drier districts. The families included here are exclusively megathermic, like Meliaceae, Simarubaceae, Burseraceae, or only partially so, as Rutaceae, Anacardiaceae, Zygophyllaceae.

Among the *Aesculinae* the Sapindaceae are mainly megathermic, the Malpighiaceae exclusively so, and frequently occur as lianes. The Erythroxylaceae and the American Vochysiaceae are also megathermic, but less rich in species; the Polygalaceae are represented, but not the Aceraceae.

The *Frangulinae* in the families of the Celastraceae, Hippocrateaceae (almost purely megathermic), Aquifoliaceae, Vitaceae (notably Cissus), and Rhamnaceae supply a great number of woody plants, especially lianes.

The *Tricoccae* are mainly megathermic in their most important family the Euphorbiaceae, and afford the tropical flora a great number of arborescent, shrubby, and herbaceous species, in particular belonging to the large genus Croton.

The largest family of the *Umbelliflorae*, namely the Umbelliferae, is almost exclusively mesothermic, so that within the tropics it is represented in the mountains, but only by a very few species in the lowlands. The Cornaceae also occur solely in the highlands, whilst the Araliaceae include representatives in the lowlands as well.

Of the *Saxifraginae*, the Crassulaceae, Saxifragaceae, Hamamelidaceae, and Platanaceae are pre-eminently mesothermic and of only slight importance within the tropics. The Podostemaceae are tropical aquatic plants.

The American family Cactaceae, the sole constituent of the *Opuntinae*, has numerous representatives in the dry districts of tropical America, and some common epiphytes and lianes in the rain-forests also belong to it.

The *Passiflorinae* are almost exclusively megathermic, and are represented in the first place by the Passifloraceae, Begoniaceae, and Flacourtiaceae, also by the Loasaceae (America), Samydaceae, Turneraceae, Caricaceae, some of the species of which are common and prominent.

The *Myrtiflorae* consist exclusively of megathermic species in the Melastomaceae, Combretaceae, and Rhizophoraceae, of which those of the first family play a prominent part, especially in America, as fine blossoming shrubs and herbs, whilst to the last two the majority of shrubs and trees of the mangroves[1] belong. Neither the Oenotheraceae nor the Lythraceae are absent.

Of the *Rosiflorae*, the Chrysobalaneae are exclusively megathermic, whilst the other groups of Rosaceae consist almost exclusively of mesothermic plants and therefore within the tropics occur only on mountains.

The three families of the *Leguminosae*, the Mimosaceae, Caesalpiniaceae and Papilionaceae, belong to the most important groups of forms of the tropical flora. They include trees, shrubs, and herbs, that frequently climb and are equally important in humid and dry districts, in woodland and in grassland; many are remarkable for their fine flowers.

The different families grouped together tentatively as *Hysterophyta* are pre-eminently megathermic, and include many of the most unique products of the tropical flora, especially among the Aristolochiaceae, Rafflesiaceae and Balanophoraceae.

The *Ericinae* are with few exceptions mesothermic, and therefore quite unimportant in the true tropical flora. They however show numerous species in the mountain flora—Vaccineae, Rhododendron.

Among the *Primulinae* the Myrsinaceae are exclusively tropical, whereas the Plumbaginaceae include only a small number of megathermic species and the few Primulaceae are alpine plants.

The families of the *Diospyrinae*—Ebenaceae, Diospyraceae, Sapotaceae—consist almost exclusively of tropical woody plants. Several of th Sapotaceae are commonly cultivated.

Among the *Contortae*, the Loganiaceae, Apocynaceae, and Asclepiadaceae are represented in many species of the most diverse forms o growth, whilst the Oleaceae and Gentianaceae, as mesothermic families occur only as mountain plants.

The *Tubiflorae* possess many megathermic species among the Convolvulaceae, and in the Boraginaceae the tribe of the Cordieae, characterize by stone-fruits, is purely tropical.

The most important tropical family of the *Personatae* is that of Solanacea to which very numerous herbs and shrubs and some small trees belong The pre-eminently megathermic families Bignoniaceae, Gesneraceae, an Acanthaceae have numerous representatives, and the Lentibulariacea

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[1] See Chap. VI of this section.

are chiefly represented by species of Utricularia. The Scrophulariaceae, however, are only feebly represented.

Among the *Labiatiflorae*, the Verbenaceae, to which arboreous as well as shrubby and herbaceous species belong, have a greater importance than the relatively less represented Labiatae.

The megathermic *Campanulinae* are limited to the Lobeliaceae, Goodeniaceae, and Cucurbitaceae; the Campanulaceae are mesothermic, and therefore only appear as mountain plants in the tropics.

The Rubiaceae, the largest of the three families of the *Rubiinae*, owing to their great number of species and the important part which many of their representatives play by their frequent occurrence, belong to the most important natural orders in tropical vegetation. The Caprifoliaceae, on the other hand, are extremely scarce in the tropical lowlands, and the Valerianaceae are hardly represented at all.

The Compositae are about equally important in the tropical and temperate zones; only a few Liguliflorae are megathermic, but numerous Tubuliflorae, sometimes special groups of them, are megathermic. Most tropical Compositae are herbs, but lianes and small trees also occur among them. The Dipsaceae, which with the Compositae and the small family of Calycereae form the cohort *Aggregatae*, are chiefly mesothermic, and in the tropics are nearly all mountain plants.

SELECT LITERATURE.

1. Climate.

The general climatic data are chiefly from Hann, Handbuch der Klimatologie. 2 Aufl. Stuttgart, 1897.

Burgerstein, Alf. Ueber die Transpirationsgrösse von Pflanzen feuchter Tropengebiete. Berichte der deutschen botanischen Gesellschaft. Bd. XV. 1897.

Giltay, E. Vergleichende Studien über die Stärke der Assimilation in den Tropen und im mitteleuropäischen Klima. Pringsheim's Jahrbücher. Bd. XXV. 1897.

Haberlandt, G. I. Ueber die Grösse der Transpiration im feuchten Tropenklima. Pringsheim's Jahrbücher. Bd. XXXII. 1897.

— II. Anatomisch-physiologische Untersuchungen über das tropische Laubblatt. Sitzungsberichte der Wiener Akademie. Bd. CI, Abth. I. 1892.

Johow, Fr. Ueber die Beziehungen einiger Eigenschaften der Laubblätter zu den Standortsverhältnissen. Pringsheim's Jahrbücher. Bd. XV. 1884.

Kraus, G. Das Längenwachsthum der Bambusrohre. Annales du jardin botanique de Buitenzorg. Vol. XII. 1894.

Maxwell, W. The rate of growth of banana-leaves. Botanisches Centralblatt. Bd. LXVII. 1896.

Stahl, E. Einige Versuche über Transpiration und Assimilation. Botanische Zeitung. Bd. LII. 1894.

Wallace, A. R. Tropical Nature: and other Essays. London, 1878.

Wiesner, J. I. Ueber den vorherrschend ombrophilen Charakter des Laubes der Tropengewächse. Sitzungsberichte der Wiener Akademie. Bd. CIII, Abth. I. 1894.

—— II. Photometrische Untersuchungen auf pflanzenphysiologischem Gebiete. Erste Abhandlung. Orientirende Versuche über den Einfluss der sogenannten chemischen Lichtintensität auf den Gestaltungsprocess der Pflanzenorgane. Ibid. Bd. CII. 1893.

—— III. Beobachtungen über die fixe Lichtlage der Blätter tropischer Gewächse. Ibid. Bd. CIII. Abth. I. 1894.

—— IV. Untersuchungen über den Lichtgenuss der Pflanzen mit Rücksicht auf die Vegetation von Wien, Cairo und Buitenzorg (Java). Ibid. Bd. CIV, Abth. I. 1895.

—— V. Beiträge zur Kenntniss des tropischen Regens. Ibid. Bd. CIV, Abth. I. 1895.

2. Floras.

Data regarding the occurrence and absence of families in the tropics are chiefly borrowed from Engler and Prantl, Die natürlichen Pflanzenfamilien.

The two following works were also utilized:—

Christ, H. Die Farnkräuter der Erde. Jena, 1897.

Moller, A. Ueber einige besonders auffallende Pilze Brasiliens. 1898.

CHAPTER II

THE PERIODIC PHENOMENA OF VEGETATION WITHIN THE TROPICS

1. General Prevalence of Periodic Phenomena in the Functions of Plants. No solute period of rest. Rest only for some processes. Occurrence of periodicity in opical vegetation. **2. Periodicity in the Vegetative Domain.** i. *Leaf-fall.* Frequency periodic leaf-fall within the tropics. Diversity in appearance of trees during the dry asons. Seasons of the year and vegetation in the campos. ii. *Growth.* Periodic foliation in certain species independently of the season. Individual periodicity of the parate shoots of many tropical plants. iii. *Temperate Woody Plants in the Tropics.* **Periodicity in the Sexual Domain.** i. *General Considerations.* Separation in int of time of vegetative and reproductive activity. ii. *Constantly Humid Districts.* on-contemporaneous flowering of different twigs in woody plants. Simultaneous flowerg of all individuals of a species without relation to the season of the year. Connexion tween formation of flowers and leaf-fall. iii. *Periodically Dry Districts.* Abundance flowers in the dry seasons and at the commencement of the wet seasons. Poverty in wers at the height of the wet season. The wet season the period for ripening fruit. *Special Cases.* Climate and flowering season in Java, in North-west India, in Ceylon. British Guiana. **4. The Caesalpiniaceae in the Botanic Garden at Buitenzorg.**

. GENERAL PREVALENCE OF PERIODIC PHENOMENA IN THE FUNCTIONS OF PLANTS.

THE periodic phenomena of tropical vegetation have hitherto been vestigated only to a slight extent. As a result of the scanty and usually correct data supplied by travellers, the notion has been pretty generally sseminated that in constantly humid tropical districts vegetative and reproictive activity proceeds without interruption, whilst the well-defined dry asons of other districts cause their vegetation to undergo periods of rest.

Observations in tropical districts with abundance of rain at all seasons the year have taught me that there also *vital processes in plants exhibit rhythmic alternation of periods of repose and of activity.* This opinion, wever, depends on a conception of periods of rest that differs from the ual one.

The more recent investigations, especially those of Sachs and Muller-hurgau, have proved satisfactorily that there are *no periods of rest for the* *vital processes as a whole, but only resting periods for certain functions.* A plant during its hibernation is by no means inactive. In many trees, starch is converted into oil; the chlorophyll-corpuscles of conifers produce red colouring matter; the epidermis of the leaves of many herbs produces cyanophyll; the roots continue to grow in length; the winter-buds, by means of invisible processes, acquire the power of further development, which was lacking in them in the warm season, and so on. On the other hand, repose chiefly prevails as regards the inception, the growth in length and thickness of the shoots, although there are exceptions. Assimilation is weakened, yet suspended only in hard frosty weather.

At spring-time, in temperate latitudes, the period of rest for the processes of growth terminates; leafy shoots and flowers are formed; the functions of nutrition, especially the conversion of already assimilated material, break into stirring activity. On the other hand, functions depending on lower temperatures enter on a period of rest.

During summer, the greatest activity prevails in the domain of nutrition, especially as regards the assimilation of raw materials. Growth in thickness of stems, and in thickness and length of the roots, is in full activity; on the contrary, after the winter-buds have been completed, the meristems of the terminal buds are, as a rule, at rest. As regards the domain of reproduction, there may be activity or repose, according to species.

Autumn is a period of slackness, of the commencement of repose in most domains. In some species, however, reproductive activity for the first time awakens from rest.

There is therefore in the temperate zones no season of the year that does not tend to set in motion certain functions of plant-life, and to set others at rest. During autumn and winter repose predominates, and during spring and summer activity predominates, so that we may speak of relative seasons of rest and of vegetation, although at no season is either condition actually realized.

Tropical plants are just as subject to the periodic alternation of rest and of activity as are those of the cooler and cold zones. Wherever a sharp climatic periodicity prevails the functions of the plant-organism in the tropics also appear to be decidedly influenced by it. Thus dry seasons act like cold ones in many respects. *The less marked the periodicity of the climate is, the less dependent on its influence is the periodicity in the plant. Internal causes are mainly or solely responsible for the alternation of rest and of activity in a nearly uniform climate.* Such a rhythmic change is however never abandoned, for it arises from the nature of the living organism and not from external conditions; its connexion with external conditions is a secondary feature—an adaptation.

Hence the picture of general and continuous activity which most travellers have brought with them regarding the vegetation in constantly humid districts is an illusion. To the attentive observer repose is manifest everywhere side by side with activity, and both these conditions continually interchange like the parts of a kaleidoscope. The difference between such a vegetation and one exposed to the influence of alternately favourable and unfavourable seasons is confined to the fact, that in the constantly humid district the sum of repose and activity remains approximately constant in every season, whilst in districts with alternating seasons it periodically ncreases and decreases.

2. PERIODICITY IN THE VEGETATIVE DOMAIN.

i. *LEAF-FALL.*

In spite of numerous travellers' reports to the contrary, the notion still prevails that tropical forests are for the most part evergreen, and essentially occupy constantly moist districts only, whereas districts with markedly dry easons are supposed to produce forest growth only along the margins of water-courses. This incorrect idea is connected with the no less ncorrect assumption that dry seasons are unsuitable for forests.

In reality the case has quite a different aspect. *The tropical forest is for he most part composed of periodically leafless trees*, and, as has already been hown[1], is by no means excluded from districts with very dry and hot easons. Indian forest-botanists, especially Brandis and Kurz, were the rst to make us acquainted with the distinctive characters of tropical forests that are evergreen and forests that are green in the rainy season. Woodland in districts with periodic and well-marked dry seasons has uring the dry season a greater resemblance to Central European woodland uring winter than to the dense luxuriant rain-forests which are usually regarded as the typical tropical forests. The picture of repose, however, hat is evoked by the dry season, is much less uniform than that of a winter andscape in temperate zones.

Thus, in many cases, woodlands near the water retain all their foliage or large part of it during the dry season, and form green strips and spots n the landscape which is otherwise mainly brown and grey in tint. In ddition, outside the reach of water-infiltration, differences in the chemical nd physical nature of the soil affect the time and extent of the leaf-fall. A greater amount of moisture in the soil delays defoliation and accelerates he opening of the leaf-buds. Warming has also observed that woody lants growing on a calcareous soil become barer of foliage than on other inds of soil.

Specific differences in woody plants also come into play. Under identical

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[1] See p. 165.

external conditions, some of them lose their foliage even before the end of the rainy season, others shed their leaves at the commencement of the dry season, others again do this quite gradually in the course of several months. and lastly others remain in full leaf until the opening of the resting buds. In some trees even, according to Warming, leaf-fall is entirely suspended in many of the years. The variety in the scene is further increased by the fact that isolated evergreen trees are frequently scattered about the deciduous forest.

Such distinctions, however, are only exhibited in places where the dry seasons are either not very long or not quite without rain. I found the dry savannah-forest bordering on the llanos of Venezuela (Province of Maturin), except for a little evergreen tree, Rhopala complicata, just as bare of foliage as a German broad-leaved forest in winter: it formed the most striking contrast to the narrow but dense strips of forest which had retained their foliage along the water-courses.

Grasslands within the tropics, occurring chiefly in the form of savannah[1], during the dry season, if not burned by the usual fires, appear clad with dry straw-like grasses, among which only isolated plants are green and flowering. A striking contrast to such a grassy covering is formed by dry blocks of rock, which are burning hot in the sun, with their vegetation of succulent plants, and other evergreen xerophytes, such as Cactaceae, Bromeliaceae, Orchidaceae, which indeed usually blossom in the dry season[2].

Warming describes the connexion between vegetation and the season of the year in the campos of Minas Geraes in Brazil, in the following manner:—

Winter (May to July. Coldest and driest). Grass on the campos like straw. Leaf-fall begins, but continues into the spring months. Some trees already lose all their foliage, but some do not do this until the spring. Leaf-fall is much more complete and general in the campos (savannahs) than in the forests.

Spring (August to October). Increase of humidity and heat: in October the rains usually begin. The leaf-fall continues and becomes more general. During these months most trees lose all their foliage, but display the young leaves simultaneously, or even a little earlier, so that the forest always remains green. Most of the leaves remain for twelve to fourteen months on the trees, somewhat longer in the forest than on the campo. Some stems retain their foliage for twenty-four months, or even longer. Considered generally, the production of foliage continues for half a year; longer in some species, shorter in others. The new leaves develop before the commencement of the rain.

Summer (November to January). Rainy season. The leaf-fall has stopped Many species produce a second crop of leaves. Some appear to produce three generations of shoots annually.

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[1] See p. 162.

[2] I observed this in Venezuela.

Autumn (February to April). Continuation of the rainy season, after an interruption of dry weather in January to February. The leaf-fall begins in March, before the end of the rainy season.

The greater the precipitations during the rainy season, the more do the evergreen trees predominate over those that periodically shed their leaves. In the dense forests of constantly humid districts, defoliation occurs only in the gigantic trees, whose crowns rise like cupolas above the general leaf-canopy and are therefore more exposed to drought. Among these periodically leafless giants may be reckoned fig-trees in particular; also the rasamala. Altingia excelsa, the tallest tree in the dripping forests of Java, is bare of foliage in a short time after the commencement of the dry east wind.

In all tropical districts with very weak climatic periodicity, there are *woody plants that shed their leaves at longer or shorter intervals (one to six times a year), without any connexion with the season of the year*, so that trees of one and the same species, under the same external conditions, acquire fresh foliage and shed their leaves at times that do not agree. Thus, for instance, I saw at Singapore trees of flame-of-the-forest, Poinciana regia, growing together with and without foliage, and I have noticed the same behaviour in Terminalia Catappa at many places. Haberlandt makes a similar statement regarding Palaquium macrophyllum at Buitenzorg. The period during which such trees remain leafless is usually very short—one to two days, for instance, for Excoecaria Agallocha. Acer niveum, many species of Urostigma[1].

In the botanic garden at Buitenzorg I have carefully observed Urostigma glabellum, a gigantic tree which sheds its leaves and produces new foliage about every two months. On December 10, 1889, the whole foliage fell during the day while still perfectly green, so that the tree that appeared quite verdant in the morning became bare of leaves by evening. On December 20 the foliage had been almost completely renewed. One of the young shoots which had been formed in the interval and was plucked haphazard was 26 cm. long from its base to the tip of its topmost leaf, the axis alone 12 cm. long, and the blade of the third oldest leaf 13 cm. long: that of the youngest 8 cm.

Such cases of the loss and restoration of the leaves independently of the season of the year can only be due to internal causes. Frequently such a leaf-fall is a sign that the tree is preparing to blossom. In Urostigma glabellum and in many other species such a connexion does not exist, or not necessarily so.

It suggests itself that in such cases the swelling buds draw the transpiration-current to themselves; but no experiments have been made in relation to this.

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[1] Koorders and Valeton, op. cit.

In the cases described above all the parts of the crown of the tree exhibited the same behaviour. In other cases *individual twigs shed their leaves and acquire fresh ones at different times.* I have observed this in tropical trees only in connexion with the flowering time, and will therefore not discuss the matter till later on.

ii. *GROWTH.*

Evergreen woody plants in districts with precipitations at all seasons of the year are not endowed with continuous growth, but, like deciduous woody plants, experience periodic alternations of rest and activity. The ebb and flow of vegetation is very striking in the case of trees whose foliage in youth is very light in colour, but assumes a dark hue in old age. In such a case a tree remains for weeks, even for months, in its dark foliage; all its terminal buds are at rest. Suddenly the dark ground appears to be tipped with white or bright red, the foliage-buds have flushed. *More frequent than simultaneous rejuvenescence of the whole crown is the awakening at different times of the terminal buds of individual twigs, or systems of twigs,* from the resting to the active condition. In such cases, however, the trees, regarded as a whole, give the impression of emitting shoots without interruption: yet, even if it be more concealed, there occurs in them the alternation of rest and activity that is common to all vital processes.

The independence of individual systems of shoots, for instance, is very strikingly exhibited by the mango-tree. Its reddish young foliage does not appear at once all over the surface of its immense dark green crown, but only at one or at two points, corresponding to the system of branches of a longer bough, the terminal buds of which all sprout together, whilst those of other boughs remain at rest.

Usually, however, the individuality of the twigs goes still further. As a typical instance of the majority of evergreen woody plants in the constantly humid tropical districts we may select Amherstia nobilis, which is frequently cultivated and belongs to the Caesalpiniaceae. In this, as in many other trees, all the members of the system of branches are independent of one another, so that twigs with resting terminal buds and others with growing shoots in all stages of development are intermingled in the greatest confusion.

iii. *TEMPERATE WOODY PLANTS IN THE TROPICS.*

All text-books repeat Humboldt's statement that at Cumana in Venezuela the vine is in foliage and bears fruit throughout the year. I do not throw any doubt on the correctness of this observation; but, on the other hand the notion derived from it, that the vine has become evergreen, in the same sense as a silver-fir, is most probably incorrect.

I have had an opportunity of studying closely the periodic phenomena exhibited by trees from the temperate zones in a climate that may be reckoned as the most uniform in the world, namely, in the constantly humid and cool mountains of West Java. The botanic garden at Tjibodas, situated at about 1,500 meters above sea-level, contains woody plants from Europe, from temperate Asia, and from North America, which at home are leafless during winter, but here, like the far-famed vine of Cumana, have become 'evergreen.' I studied them in December and January, that is to say at a time when they would have been leafless under their own natural conditions; they were, however, all well provided with foliage, and in some cases with flowers and fruit. These trees have nevertheless retained their periodicity, but *the individual branches have become more or less completely independent of one another*, so that at the time of my visit many trees were simultaneously bearing winter, spring, summer, and autumn shoots, and the remaining trees, at least most of them, had branches presenting the appearance characteristic of two seasons of the year.

In young trees transplanted into the tropics, the indifference of the rhythmic alternation of foliation and defoliation to the time of the year, and the independence of action on the part of the several systems of shoots, appears only gradually during the course of the year; the influence of the seasons on the periodic phenomena that has already been experienced persists for a long time, as an after-effect, only to vanish by degrees by the different branches exhibiting dissimilar variations from the original behaviour.

The north temperate trees cultivated in the garden at Tjibodas, at the time of my visit, so far as my observations went, were as follow: Magnolia Yulan, Magnolia sp., Liriodendron tulipifera, Diospyros Kaki, Pyrus Malus, P. communis, Quercus pedunculata, Rhus succedanea, Olea europaea, Amygdalus communis.

Magnolia Yulan, for instance, presented the following appearance: some defoliated twigs with leaf-buds and sometimes flower-buds; others with young leaves and open flowers; still others with full-grown leathery leaves and the dried remains of flowers—there was no fruit formed; others, again, with a few 'autumn-tinted' leaves, that fell off easily when touched.

In Magnolia sp. the 'summer'-twigs bore fruit. The tree, represented by several fine specimens, exhibited a less marked difference in its separate twigs; these were more dependent on one another. But the individual trees were at different stages of seasonal development. Some were in the array of early spring, with quite young leaves; others in that of early summer, with still fresh leaves and young fruits: others again bore ripe fruits and old leaves.

Liriodendron tulipifera and Quercus pedunculata reflected winter, spring, and summer on their separate boughs. With Pyrus Malus and P. communis, which moreover the climate apparently did not suit, all four seasons were represented on the same little trunk. A shrub of Rhus succedanea was in spring-condition at its base, in summer-condition at its summit; a larger plant of the same species displayed on some branches light-red vernal tints and dark-red autumnal ones, whilst others were bare as in winter. Amygdalus communis was in purely spring attire.

In less uniform tropical climates, the periodic phenomena of woody plants coming from the temperate zones seem to adapt themselves to the new seasons. Then the phenomena naturally occurring in winter and spring take place in the dry season, and those characteristic of summer and autumn come to pass in the rainy season. Mr. Nock, the Curator of the experimental garden at Hakgalla in Ceylon at about 1,800 meters above sea-level, told me that European trees lose most of their foliage during the wet south-west monsoon, whilst during the moderately moist autumn months they produce young leaves and flowers. More precise observations on these interesting phenomena are not available.

3. PERIODICITY IN THE SEXUAL DOMAIN.

i. *GENERAL CONSIDERATIONS.*

In the majority of plants, flower and foliage exhibit a certain antagonis and are usually separated in their development in time or in space. I herbaceous plants, devoid of tubers or bulbs, vigorous development of th reproductive organs is generally attained only after the foliage has bee completely or almost completely formed. In this case, at all events, on may interpret the phenomenon by ascribing to the foliage the work o forming nutritive material for the production of flowers and fruits. In th case of plants with rhizomes, and of woody plants, there is no such direc dependence, and we see in fact the formation of flowers often precedin that of foliage, when it takes place at the expense of the previous year' reserve-material. This precedence of flower seems to occur frequentl when flower and foliage are at some distance from one another, as i cauliflorous plants.

In zones with cold winters, the development of blossom in many plant especially in woody ones, stretches over two periods separated by a seaso of rest, the first period being one of inception, and the second, one of growt It is not known to what extent this also occurs in the tropics. Th following remarks therefore concern only the later stages of developme that are easily discernible by the naked eye. Flowers have received f more attention than have fruits, as the former have been more minute investigated by earlier observers as well as by myself. What is state below is therefore merely fragmentary.

Woody plants may be considered in the first place, as in them a external influences on the development of flowers are more clearly reveal than in most herbaceous plants, in which the direct dependence of t reproductive functions on the assimilatory activity of the foliage interfer with the expression of any such external influence.

The separation in point of time of the blossoming and of the purely vegetative condition is due to the fact that both are associated with different seasons of the year. In the tropics also, an influence on the part of the season occurs wherever a sharply marked change of climate prevails, but this influence is usually weaker than in zones with a cold winter. The number of species in blossom throughout the whole year is greater, and the period during which blossoming individuals of one species are found is, in general, longer in the tropics than in places where the seasons of the year exhibit very great differences of temperature; in fact, repeated blossoming at short intervals, which in the temperate climate is almost always anomalous, is a normal and regular phenomenon with many tropical plants. Such distinctions are most striking when the woody plants of the temperate and tropical zones are compared with one another.

ii. *CONSTANTLY HUMID DISTRICTS.*

The less marked the climatic differences of the seasons are, the less dependent upon the season of the year is the blossoming period of tropical plants. We find therefore the same relationships as in the vegetative system. Species that blossom throughout the year are commonest in districts with a nearly uniform climate. The remark frequently met with in tropical Floras, 'blossoms throughout the year,' is however as a rule not to be interpreted as meaning that one and the same plant is always in flower, but merely that blossoming individuals are to be found at any time. Among the species belonging to the category of plants that are constantly in bloom, many occur the individuals of which bear blossoms only once a year, or not even annually. This is especially the case with many trees of moist virgin forests that are seldom found in blossom. On the other hand, there are species, individuals of which possess a blossoming period that is very long or recurs at short intervals, so that the number of their blossoming plants at any time of the year exceeds that of those out of blossom. This condition occurs in particular in open sunny situations and in littoral forests. Species of Rhizophora and Avicennia, but especially Hibiscus tiliaceus, have remarkably long blossoming periods and are usually found in bloom. I cannot state whether there are any long-lived plants, individuals of which are uninterruptedly in bloom, since observations extending over years would be required to determine it, and no one has thought of doing this. I do not however consider such a condition impossible, especially in the case of richly branched woody plants: some widely cultivated species of Hibiscus that seemed to me to be continuously in blossom, and Ricinus, should prove adapted for an easy solution of the problem. But even then, there could not fail to be an alternation of periods of rest and activity in blossoming. We have seen in the phenomenon of the production of foliage to what a high degree the separate branches of many tropical woody plants are individualized. The same truth often holds good in the production of flowers. Frequently a single bough is in blossom, while the other boughs remain in a condition of mere vegetative activity but bear flowers at other times. The phenomenon is very striking in the mango-tree and in the silk-cotton-tree Eriodendron anfractuosum, in which an area of the crown of about the extent that would be occupied by a large branch alone bears flower at one time, and then subsequently other similar areas bear flower. Fritz Müller mentions a gigantic fig-tree growing at Blumenau, the different boughs of which bear fruit at different seasons[1]. In other cases this phenomenon is less obvious, as it is not all the branches of a thick bough at one time but smaller systems of branches of a higher order, or even individual twigs that exhibit alternate rest and activity in the reproductive processes. One and the same shoot never blossoms and bears fruit uninterruptedly.

Most of the plants whose flowering period is independent of the season produce their flowers, as may readily be understood, at different times, and therefore a tree decked in full floral array may frequently be seen close to another tree of the same species bearing ripe fruit only.

Yet in a few species with a short blossoming period it strangely happens, *that within a more or less extensive district, frequently comprising many square miles, all the individual plants of one species come into blossom on the same day.*

The first to recognize a fact of this nature, as in the case of so many other features of tropical plant-life, was Fritz Müller, who noticed it in three species of the iridaceous genus Marica flowering at different times Subsequently Mr. Ridley at Singapore informed me that a local epiphytic orchid (Dendrobium crumenatum, Sw.) behaved in a similar way. Finally during my visit to Buitenzorg Dr. Treub drew my attention to the habit o this orchid, which is common everywhere in West and Central Java. On December 13, 1889, all the individual plants that I saw in Buitenzorg (which is in West Java) and its vicinity were opening the whole of their flower-buds On January 19, 1890, I met with the same phenomenon at Samarang in Central Java; and as I learnt, the Dendrobium had also blossomed a about the same time at Buitenzorg. On February 19 I saw the same thing at Garut, on the high plateau of Preanger, and again on March at Buitenzorg. Some other less common orchids appear also to act in a similar way.

Comparable perhaps with the above strange phenomena is the behaviour of certain bamboos that blossom only after cycles of a number of years and then all simultaneously within an extensive province. Thus the bamboos in the South Brazilian provinces of St. Catherina and Rio Grande

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[1] Fritz Müller, op. cit., p. 392.

lo Sul blossom at intervals of about thirteen years. Bambusa arundinacea, n the west coast of Cisgangetic India, blossomed at intervals of thirty-two ears—1804, 1836, 1868 [1]. According to Ridley, two species of Hopea, I. intermedia and H. Mengarawan, and four species of Shorea, S. leprosula, S. parvifolia, S. pauciflora and S. macroptera, blossom with great egularity every sixth year. These cycles are said to coincide with very ry years [2].

In most cases, *during the greater part of the reproductive period, there is retardation or even a stoppage in the vegetative domain,* and this may xtend to the whole crown, when its habit is to break simultaneously into ower, or it may be confined to the larger or smaller branches, according o their degree of individuality. The effect on the vegetative region is requently limited to the discontinuance of the formation of foliage-shoots; he vegetative buds rest. In many cases, the antagonism between the egetative and reproductive functions goes further. *A tree or shrub prearing to blossom throws off its foliage, chiefly however from the flowering ranches, whereas the purely vegetative ones usually retain their leaves.*

At what stage of the development of blossom this phenomenon happens I have nfortunately omitted to determine, and the literature of the subject has nothing say about it. In this case, as in the shedding of the foliage of Urostigma glaellum [3], the effect possibly depends on the diversion of the transpiration-current wards the flower-buds. The fresh foliage sometimes shoots out at the comencement, sometimes at later stages of the formation of the fruit.

Crüger had already observed in Trinidad that Erythrina blossomed hen bare of leaves and that twigs that remained flowerless retained their liage. I have frequently had an opportunity of seeing this statement onfirmed and have observed the same fact repeatedly in Schizolobium iganteum in Java. I met with similar phenomena in the botanic garden Tjibodas, where I paid more attention to it, in Parasponia parviflora, e richly flowering twigs of which threw off the greater part of their liage, whilst those that bore only a few flowers retained considerably ore leaves. I also noted it in an Ardisia and in Juannuloa aurantiaca, here the blossoming twigs were altogether or nearly leafless, whilst a duction in the foliage was not exhibited on the purely vegetative twigs.

I found also in many otherwise deciduous trees *that the flowering twigs quired their leaves later than did the purely vegetative ones.* Thus, on ovember 21, 1889, in the botanic garden at Buitenzorg, I saw two trees Firmiana colorata with young leaves and flowers. The flowers were undant on one of the trees and scanty on the other, but in both cases ere confined to separate systems of branches. On the flowering boughs

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[1] Brandis, II, p. 90.

[2] Ibid. p. 20.

[3] See p. 245.

the leaves were still small and pale, but on the sterile ones they wer already large and bright green. On December 13, after the flowerin period, the tree that had flowered abundantly could be easily distinguishe from the other by its less developed foliage. In Meliosma lanceolata, i the same garden, on November 21, I saw young foliage only on steri boughs, whilst the twigs provided with infructescences or young inflo escences still showed no signs of foliage.

Many trees in their youth, so long as they do not produce flowers, a evergreen, whilst later on they shed their leaves before the impendi blossoming period. This is the case, for instance, with Schizolobium giga teum, at least in Java.

It is evident from the foregoing remarks that, like leaf-formation ar leaf-fall, the development of flowers depends on a periodically recurrin internal condition of the plant. Shoots that flower continuously no mo exist than do those that are continuously forming foliage. *In the repr ductive domain, then, there occurs a rhythmic alternation of rest and activi depending on internal causes.*

iii. *PERIODICALLY DRY DISTRICTS.*

The rhythm that is witnessed in leaf-formation is observable also the flower. *The production of flowers exhibits a correlation with t seasons of the year, whenever the seasons display sharply defined differenc* In the reproductive domain this dependence is likewise a seconda feature—an adaptation to external factors on the part of physiological necessary processes. In the tropics an influence associated with variatio in temperature is exhibited only in border-districts, and consequently ne not be considered here. Over the greater part of the torrid zone, t difference in the seasons, as far as these concern plant-life, is express only in the atmospheric precipitations, and in particular in the rainfall a the atmospheric humidity.

The blossoming of woody and tuberous plants everywhere within the trop is most abundant during the dry season, or immediately after it; and the are precisely plants in which the production of flowers is not direct dependent on the foliage. We frequently find it stated in the accou of travellers, as a remarkable phenomenon, that many trees blosso precisely in the dry season. Belt makes this statement concerni Nicaragua, Crüger concerning Trinidad, Schweinfurth concerning Nub and Kurz says of the deciduous forests in Pegu, that most of the tre blossom during the hot dry season, that a number of plants with rhizom and tubers—for instance, Scitamineae, Amaryllidaceae, Orchidaceae, Och suffruticosa—at the same time burst into blossom, and finally that t leafless dried branches of the trees are covered with flowering orchids.

I became personally acquainted with the abundance of blossom duri ropical dry seasons in the savannah-forests of Venezuela. Most of the rees were leafless during my visit in March, 1883; not a trace of egetative activity was visible on them, and yet many of them, in particular pecies of Cassia and other Leguminosae, were completely covered with owers. Epiphytic bromeliads and orchids were also in full blossom. n the other hand, the vegetation on the ground was almost flowerless; was however chiefly composed of grasses and other herbaceous plants, he plastic substances of which accumulate chiefly in the foliage and nsequently must be expended for the production of flowers during the egetative season, that is to say, during the rainy season. In March their liage was as dry as straw.

A show of flowers often even richer, particularly of perennial herbs, ccompanies the first rain after the dry season. But this continually ecreases as the rainy season proceeds, especially as regards woody and uberous plants, and sinks to a minimum at the close of the rainy season; hilst the growth of the foliage-shoots still continues for a long time, he secondary growth in thickness attains its greatest intensity, and ssimilation as well as other nutritive processes are at a maximum.

The fruits of many woody plants that have blossomed in the dry season pen during the ensuing rainy season; others require a longer time. et the ripening season for most fruits, so far as it is confined to any articular season, appears to be chiefly the rainy season. Accordingly here is very little fruit during the dry season.

The favourable influence of the dry season on flowering is not at all urprising. On the contrary, it is more a matter for surprise that certain pecies of plants should blossom at the height and towards the end of he rainy season. Such species are however very much in the minority, pecially when only woody plants are taken into consideration. It has een shown in a former chapter[1] that poverty of water in the soil and in e atmosphere favours the inception and growth of flowers. Blossoming the dry season, or soon after it, is a phenomenon that is intelligible on hysiological grounds. Why on the contrary it should in other cases, re however, be induced by the great humidity of the rainy season, ay perhaps be correlated in the case of woody plants with certain laptations, for example with special pollinating agents and the like. hat, however, many herbaceous plants without persistent stores of reserve aterial should blossom during the rain, is a necessary consequence of e direct dependence of the flowers on the foliage.

iv. *SPECIAL CASES.*

In order to obtain reliable and sufficient results regarding the influence the tropical seasons on the formation of flowers, I have collected from

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[1] See p. 26.

several 'Floras' the data bearing on this question for individual species. Only works that are founded on local experience extending over a number of years can be utilized; in others, one will usually find that month given as the flowering period in which particular specimens happened to be collected. However, the occasional use of such collectors' data in part of the works that I have used is not excluded; but Brandis' data in his Forest Flora of North-West and Central India may be accepted with absolute confidence; Koorders and Valeton also, the editors of a Tree-Flora of Java, now coming out in parts, have paid critical attention t this question. Besides these works, the three published volumes o Trimen's Flora of Ceylon and Schomburgk's catalogue of the Flora o Guiana have been utilized. *In all these works, the favourable influenc of the dry seasons on the development of flowers could be most clearl recognized.* The flowering time of most of the species, and especially, fo reasons already given, that of woody plants, coincides with the end o the dry season and the very commencement of the rainy season.

Koorders and Valeton's work promises when completed to afford the mos important material for investigating the connexion between the flowering tim and the season of the year, on the one hand, because of the care with which th data were collected, and on the other, because differences of temperature are o no concern in Java. So far, therefore, as the climate in Java influences th flowering time, it can act only by differences in the atmospheric precipitations.

Of 228 species whose flowering time is given, in 53 species it is uniformly distributed throughout the year, in 12 it commences in the wet season (Decembe to March) and continues into the dry season; therefore in 65 species, or abou 29 %, atmospheric precipitations have no decided influence on the flowering time In 142 species, or about 63 %, the flowering time is limited to the dry seaso (April to November), either entirely or for the most part. Only about 18 specie or not quite 8 %, blossom solely during the rainy season.

The annexed table gives a summary of these data:—

CLIMATE AND FLOWERING TIME IN JAVA.

Mean temperature.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug	Sept.	Oct.	Nov
Batavia (annual 25·8)	25·6	25·3	25·4	25·8	26·3	26·4	26·0	25·7	26·0	26·3	26·4	26·
Rainfall in % West Java	11	19	12	13	8	5	6	4	3	5	6	9
East Java	16	22	18	12	8	5	7	3	1·4	0·5	2	4
	Rainfall 61·5 %				Rainfall 38·2 %							
Flowering time in % of species	8 %				63 %							
Flowering time independent of the rainfall	29 %											

The district dealt with in Brandis' book is less instructive, because, especial n the parts relating to North-west India, the differences of temperature during he seasons of the year are not inconsiderable. But yet during the hot dry season nd during the rainy season they are at all events never very great, whereas he difference in the flowering seasons is largely in favour of the hot dry season. n the following table the heading 'Flowering Time' gives the number of species hat were found in flower during the month in question. The small number of lowers during the winter may be due to the low temperature. One and the same pecies is therefore included in several months, if its flowering period extended ver several months:—

TEMPERATURE, RAINFALL, AND FLOWERING TIME IN NORTH-WEST AND CENTRAL INDIA.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
North-West India.												
Peshawar (Punjab). Rainfall in mm.	42	40	40	50	18	5	44	65	17	7	25	19
Lahore. Rainfall in mm. .	14	34	26	18	20	41	177	124	55	17	4	15
Delhi. Rainfall in mm. . .	22	16	21	11	19	72	213	183	112	18	2	11
Agra. Temperature . . .	15·6		24·7	31·1	34·3		30·6		29·1	26·4	20·9	
Central India.												
Nagpur. Rainfall in mm. .	17	12	16	13	22	218	322	229	190	54	8	10
Indore. Rainfall in mm. .	8	9	0	2	8	154	289	255	218	17	1	4
Jabalpur. Rainfall in mm. .	16	13	12	6	10	198	450	357	217	36	7	5
Jabalpur. Temperature . .	16·6		24·3	29·3	32·6		26·0		25·4	23·4	18·7	
Mean rainfall of the six places	20	21	19	18	16	115	249	202	135	25	8	11
Flowering Time	64	113	231	293	269	189	111	78	49	43	49	54
Rain %	2·4	2·5	2·3	2·2	1·9	13·7	29·7	24·1	16·0	3·0	1·0	1·3
Flowering Time %	4·1	7·3	14·9	18·9	17·4	12·2	7·2	5·0	3·1	2·1	3·1	3·4

I have selected from Trimen's Flora of Ceylon species from the lowlands only, ecause reliable meteorological data were available to me only for this region. he island may be divided into two parts, a smaller western and south-western ortion with heavy rainfall, and a larger eastern and northern portion with less lentiful rain. More detailed data regarding the climate are given in the ccompanying tables:—

CLIMATE OF CEYLON: LOWLANDS.

(From Meteorol. Zeitschr. 1886, p. 272.)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
I. *Humid District.* A. West—Colombo.												
Temperature	26·1	26·7	27·8	28·3	28·1	27·3	27·0	26·9	27·1	26·8	26·5	26·2
Relative Humidity	78	77	77	80	81	83	82	83	81	82	82	80
Cloudiness	4·9	4·1	4·0	5·5	6·8	7·4	6·8	7·0	6·8	6·8	6·3	5·6
Rainfall in mm. (annual 2,219 mm.)	81	47	142	233	328	191	137	120	121	316	334	169
B. South—Galle.												
Temperature	25·3	26·1	27·1	27·6	27·4	26·7	26·3	26·4	26·4	26·2	25·9	25·5
Relative Humidity	89	87	86	86	88	91	90	91	91	91	91	90
Cloudiness	5·6	4·9	5·0	6·0	6·7	7·0	6·5	6·6	6·5	6·7	7·0	5·6
Rainfall in mm. (annual 2,273 mm.)	109	89	124	232	284	200	137	142	191	313	291	161
II. *Dry District.* A. East—Batticaloa.												
Temperature	24·9	25·7	26·8	28·1	28·6	28·4	28·3	27·9	27·7	27·0	25·7	24·8
Relative Humidity	88	85	85	84	82	79	79	82	83	87	89	92
Cloudiness	6·9	5·9	5·4	5·6	5·9	6·8	6·8	6·8	6·5	6·7	7·2	6·8
Rainfall in mm. (annual 1,332 mm.)	206	91	85	42	41	32	17	72	52	146	331	217
B. North—Jaffna.												
Temperature	25·3	26·2	28·1	29·5	29·3	28·7	28·1	27·9	27·8	27·4	26·1	25·2
Relative Humidity	81	77	79	82	85	86	85	86	87	86	88	87
Cloudiness	4·3	3·0	2·6	3·7	3·9	5·4	5·4	5·6	5·0	5·6	6·4	6·0
Rainfall in mm. (annual 1,215 mm.)	51	34	34	58	53	11	14	31	65	227	375	262

CEYLON.

DISTRIBUTION OF THE RAINFALL IN PERCENTAGES.

(After Woeikof, Die Klimate der Erde, I, p. 392.)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
East Ceylon	12	5	4	2·7	3	2·7	2·5	6	6	11	22	23
West Ceylon	4	3	6	10	14	9	6	6	7	14	14	7

CEYLON.

MEAN TEMPERATURES IN CENTIGRADE.

(After Woeikof, Die Klimate der Erde, I. p. 379.)

	Jan.	Mar.	Apr.	May	July	Sept	Oct.	Nov	Year
Jaffna (dry)	25·6	28·6	29·9	29·7	28·4	28·2	27·8	26·6	27·9
Galle (humid)	25·7	27·3	27·8	27·7	26·6	26·7	26·6	26·2	26·7

It may be seen, here as in Java, that the influence of temperature can be eglected.

I consider it not unlikely that in Trimen's Flora the 'flowering seasons' repre-nt frequently merely the dates of collection of the specimens. Nevertheless ey attest in the clearest manner, especially in woody plants, the favourable fluence of the dry season, and, indeed, corresponding to the two dry seasons e two maxima of flowering seasons, a larger one in spring, a smaller one late the summer.

The flowering periods, so far as they do not continue throughout the year, are stributed in Ceylon over the different months, as is shown in the following table, which the figures indicate number of species:—

CEYLON.

DISTRIBUTION OF FLOWERING PERIODS.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1. *Humid District.*												
A. Woody plants	81	126	183	159	88	67	74	66	104	36	38	62
B. Herbaceous plants . . .	86	109	83	50	40	41	52	60	67	49	51	80
2. *Dry District.*												
A. Woody plants	57	92	97	77	49	48	83	79	61	20	25	39
B. Herbaceous plants . . .	117	147	105	45	34	35	59	73	57	37	48	89

The three published volumes of the Flora of Ceylon include the Dicotyledones, cept the Euphorbiaceae, Urticaceae, and Cupuliferae. Twenty-five woody plants d seventy-two herbs are given as blossoming throughout the year, but these ures are certainly too small. It is indeed not a rare phenomenon in the tropics, at whilst the great majority of individuals of a species are not blossoming, a small mber are in flower. The seasons of the year are not followed so strictly. In orders' careful reports we therefore find a relatively greater number of species at flower throughout the year, but often with the proviso that they blossom chiefly a definite season, usually during the east monsoon. Of 107 Javanese trees ated in the first two parts of the book, the flowering seasons of which may be nsidered as certainly established, I find 22 stated as blossoming throughout the year. According to Schomburgk, in British Guiana 172 dicotyledonous an 36 monocotyledonous plants flower throughout the year.

In Schomburgk's catalogue of the Flora of Guiana the Dicotyledones of th forest-district only are considered, because the Monocotyledones are nearly a herbaceous. The relations between climate (Georgetown) and flowering perio are shown in the following table:—

CLIMATE AND FLOWERING SEASONS IN BRITISH GUIANA.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec
Temperature	25·8	25·8	26·1	26·4	26·3	26·1	26·1	26·5	27·2	27·3	26·9	26·
Rainfall	174	148	185	186	357	353	274	189	66	63	142	27
Flowering period	164	174	73	191	108	115	79	170	184	168	81	58

The wettest months, May, June, July, and December, are poor in flowers whe compared with the moderately moist months January, February, and April, an with the dry months September and October. The poverty of blossom in Marc cannot be attributed to the climate.

4. THE CAESALPINIACEAE IN THE BOTANIC GARDEN AT BUITENZORG.

As an example of the bewildering phenomena associated with periodicit in the tropics, the following extracts are given from my note-book regar ing the *Caesalpiniaceae in the botanic garden at Buitenzorg*:—

November 11, 1889. Although the family is one of those that posse a large number of periodically deciduous trees, yet nearly all the trees a more or less in leaf. The section stands out from a distance as a ma of foliage in several shades of green. On examining it more closely o sees for the first time a picture to which no European garden can affo an analogy—a peculiar intermingling of all seasons.

From the midst of the mass of foliage formed by the majority of t trees, others stand out bare and leafless. To the latter belongs one two specimens of the Brazilian Schizolobium excelsum, which howev bears one quite young sterile branch in leaf, whilst the other branch possess inflorescences but are leafless. The other tree is in full folia and bears some old fruits. In its home in South Brazil the tree is ba of leaves during winter and blossoms at its conclusion.

Few trees are in a condition comparable with that of our own tre Among such trees are Phanera maculata and P. Richardiana, which, wi their quite young foliage and their large rosy-red flowers, present a pictu of spring. Near them stand several tall trees, Hymenaea Courbaril a H. verrucosa, whose appearance may be described as autumnal: the s beneath them is thickly covered with dead leaves; their foliage is for t nost part yellowish or copper-coloured; the round ripe fruits, on long talks, appear all over the crown. In many places the fresh green of oung shoots glistens through the yellowish foliage. Pileostigma acidum resents a similar appearance. Maniltoa gemmipara is dark green over he greater part of its crown, but has a few white young shoots drooping s in a flaccid condition. Resembling it are Jonesia declinata and ynometra sp. Amherstia nobilis exhibits all possible conditions, from a ud that is resting to one that hangs flaccidly; likewise from a red young hoot to one that is hardened and green; also all stages of inflorescence re present; but fruit is absent, being never formed here. The leafy crown f Jonesia minor resembles that of Amherstia; on the stem one sees nflorescences in all stages, from the earliest bud to the mature orange-ellow umbels, and fruits from the moment they protrude beyond the orolla-tube to the over-ripe burst pods.

SELECT LITERATURE.

elt, Th. The Naturalist in Nicaragua. 2nd edition. London, 1888.

randis, Sir D. I. The Forest Flora of North-West and Central India. London, 1874.

— II. Bambuseae in Haekel, Gramineae. Engler und Prantl, Die natürlichen Pflanzenfamilien. Theil II, Abth. 2. 1887.

— III. Die Familie der Dipterocarpaceen und ihre geographische Verbreitung. Sitzb. d. niederrhein. Gesellschaft. 1896.

rüger, H. Westindische Fragmente. I. Ueber Periodicität in der Pflanze. Botanische Zeitung. Bd. XII. 1854.

rnst, A. Botanische Miscellaneen. Botanische Zeitung. Bd. XXXIV. 1876. p. 38.

aberlandt, G. Eine botanische Tropenreise. Leipzig, 1893.

ohow, Fr. I. Zur Biologie der floralen und extrafloralen Schauapparate. Jahrb. des königl. botan. Gartens zu Berlin. Bd. III. 1884.

— II. Vegetationsbilder aus Westindien und Venezuela. III. Ein Ausflug nach der Höhle del Guacharo. Kosmos. Bd. II. 1885.

oorders, S. H., en Valeton, Th. Bijdrage tot de kennis der boomsoorten van Java. I–IV. Mededeelingen uit 's Lands Plantentuin. 1894–1897. Batavia.

üller, Fr. Bemerkungen zu Hildebrand's Abhandlung über die Lebensdauer und Vegetationsweise der Pflanzen. Engler's Jahrbücher. Bd. II. 1882.

chomburgk, R. Versuch einer Fauna und Flora von Britisch-Guiana. Leipzig, 1848.

chweinfurth, G. A. Several papers relating to the Sudan. Zeitschr. für allgemeine Erdkunde. Berlin. XIX. 1865.

rimen, H. A Handbook to the Flora of Ceylon. I–V. London, 1893–1900.

arming, E. Lagoa Santa. Skrifter a. d. kgl. danske Videnskabernes Selskab. 1892.

CHAPTER III

WOODLAND CLIMATE AND GRASSLAND CLIMATE IN THE TROPICS

1. The Kinds of Climatic Formations in the Tropics. 2. High-Forest Climate in the Tropics. Climate of the Malay Archipelago according to Woeikof. Conditions of rainfall in other tropical high-forest districts. Rain-forest and monsoon-forest in Cis-gangetic India. Atmospheric humidity and temperature. Climatic tables taken from tropical high-forest districts. **3. Thorn-Forest Climate in Cis-gangetic India 4. Woodland Climate and Savannah Climate in Brazil.** Coast mountain-ranges and campos of São Paulo. Campos and forests in Minas Geraes. Xerophilous woodland climate of the Sertão. **5. Climate of Northern South America and of the Antilles 6. Climate of Tropical Africa.** West coast. Savannah of the central African plateau. **Summary.**

1. THE KINDS OF CLIMATIC FORMATIONS IN THE TROPICS.

Tropical woodland, so far as its character depends on climate and no on definite effects of the soil, may be divided into four kinds—*Rain-forest* *Monsoon-forest*, *Savannah-forest*, *Thorn-forest*. Close shrub-formations are rare under favourable physical and chemical conditions of the soil wherever the climate is too dry for forests, they are replaced by open half-desert and desert-like formations, in which xerophilous shrubs play the chief part, but trees are not always absent.

The *Rain-forest* (Fig. 124) is evergreen, hygrophilous in character at least thirty meters high, but usually much taller, rich in thick-stemmed lianes, and in woody as well as herbaceous epiphytes.

The *Monsoon-forest* (Fig. 125) is more or less leafless during the dr season, especially towards its termination, is tropophilous in characte usually less lofty than the rain-forest, rich in woody lianes, rich in herbaceous but poor in woody epiphytes.

The *Savannah-forest* (Fig. 127) is more or less leafless during the dr season, rarely evergreen, is xerophilous in character, usually, often much less than twenty meters high, park-like, very poor in underwood, lianes and epiphytes, rich in terrestrial herbs, especially in grasses.

The *Thorn-forest* (Fig. 128), as regards foliage and average height, resemble savannah-forest, but it is more xerophilous, is very rich in underwoo and in slender-stemmed lianes, poor in terrestrial herbs, especially i grasses, and usually has no epiphytes. Thorn-plants are always plentiful.

The different types of forest are connected by intermediate forms, an besides these, transitions are very frequent between savannah-forest and savannah as well as between thorn-forest and open bush-formations, which as intermediate forms connect the formations of woodland and desert.

Tropical grassland, wherever it has not been modified by human agency, occurs chiefly as *savannah*, more rarely as *steppe*. The occurrence of *meadow*, by which we understand hygrophilous or tropophilous grassland, s rare in the tropics and is always due to factors that are merely local.

Tropical desert has a vegetation consisting of scrub, that is to say, of stunted trees and shrubs or of shrubs only, also of succulent plants and perennial herbs. Most tropical deserts are near the tropics of Cancer and Capricorn, and are allied to the far more extensive warm temperate deserts. The climate of the tropical deserts will be treated of in a subsequent chapter together with that of the temperate deserts.

2. HIGH-FOREST CLIMATE IN THE TROPICS.

Brandis declares that really *successful forests occur only where the rainfall attains forty inches, and that a luxuriant rich vegetation is limited to zones where the annual rainfall is much greater*.

The available meteorological tables for tropical districts show, in regard o land that is covered with or has been covered with high-forest (rainorest or high monsoon-forest), an annual rainfall of at least 180 cm., xcepting near large sheets of water where telluric moisture replaces ain. Within the most extensive forest-district of the tropics, the Indo-Malayan, including New Guinea, an annual rainfall of over two meters is he rule; wherever much less than two meters of rain falls, the indigenous egetation, so far as is known, forms less lofty woodland, as at many spots in East Java, or creates savannah, as in Timor (Koepang in Timor as a rainfall of 145 cm.). On the other hand, at many spots the rainfall xceeds 300 cm.; at several it exceeds 400, at Buitenzorg, for instance, eaching 499 cm.

Thanks to the excellent records of the numerous meteorological stations in Dutch Malaysia, Woeikof[1] has been able to compare the conditions of rainfall of a great umber of localities there. In Java the annual rainfall is given for 62 stations; it is ess than 200 cm. for twelve of them only, for five it is less than 150 cm., for none is it ess than 100 cm., the minimum (113 cm.) being at Probolinggo. Several of the above ocalities are known to me personally, for instance Probolinggo, where the rainfall is owest. Probolinggo is in East Java, far from any forest, and there, except manroves, I found in the wild state only thorny brushwood, xerophilous in character. The vegetation near Pasoeroean, where the rainfall is quite as small, is just like that f Probolinggo. It cannot now be ascertained what kind of indigenous vegetation ormerly occupied these parts of the country, which are now covered with planta-

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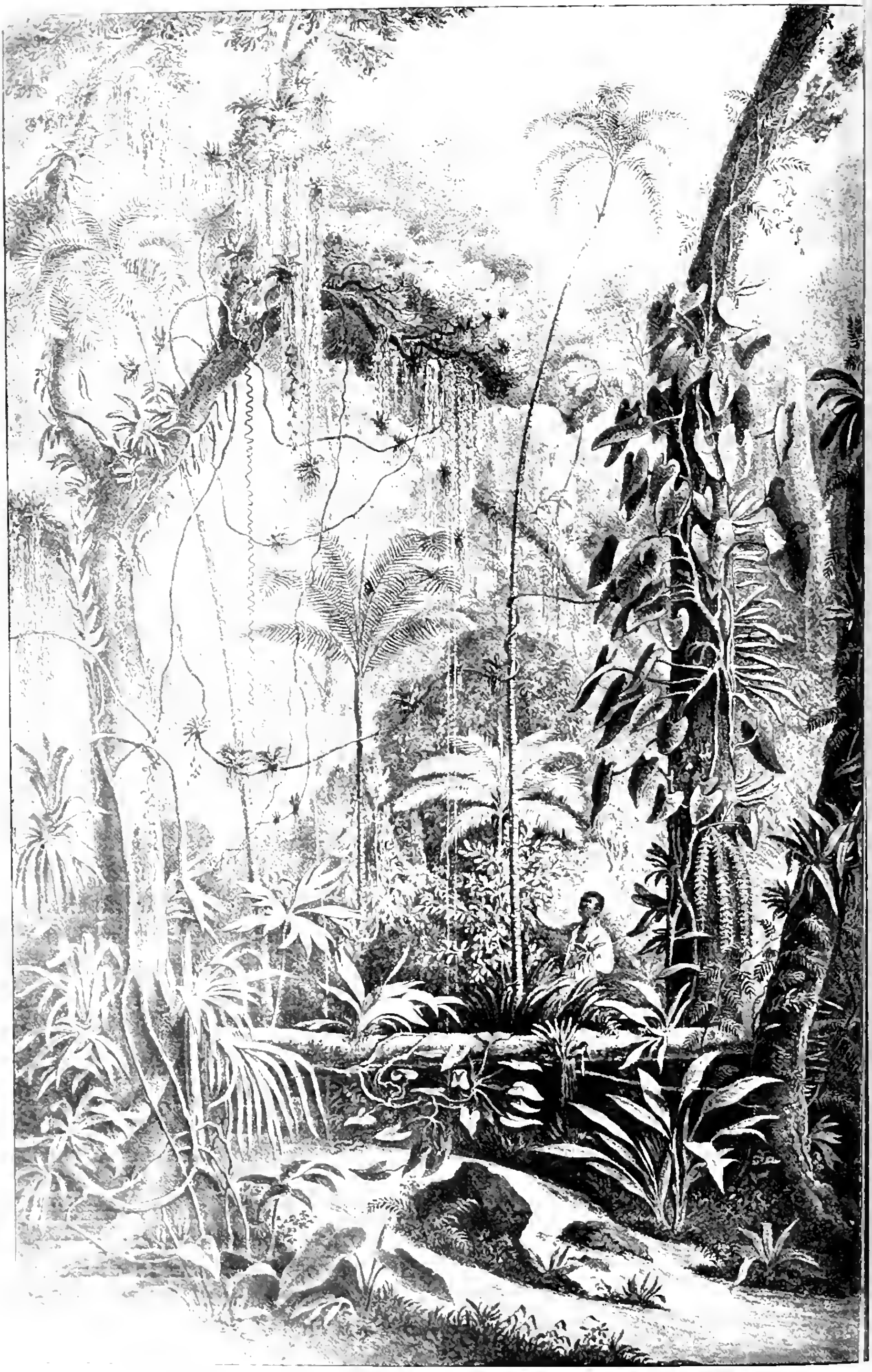
[1] Woeikof in Zeitschr. d. österr. Gesellsch. f. Meteorol., 1885.



[illegible] in the tropics. Virgin forest near Pedro da Onza, Brazil. Somewhat diagrammatic. After Martius.

Fig. 125. M[illegible] forest in Burma. Ewet Reserve, Tharawadi, Burma. *a* Schleichera trijuga. *b* H[illegible] *c* Xylia dolabriformis. *d* Bambusa. From a photograph by J. W. Oliver.

tions of sugar-canes. Cultivated trees are frequently met with in both localities. The country round Buitenzorg (rainfall 499 cm.), Malang (450 cm.), Tjilatjap (463 cm.) is also bare of forest-growth, but trees planted there show the greatest vigour. Near Depok (334 cm.) some forest is retained, but is not very luxuriant. It is well known that Borneo and Sumatra are completely under forest. Of 22 stations in Sumatra, only one, Kota Badja, has a rainfall of less than 200 cm. (175 cm.). On the other hand, four stations have more than 400 cm. The seven stations given for Borneo all have more than 200 cm., some of them more than 300 cm. Celebes, except its south coast (Kema 163 cm.), the Moluccas, except Timor (145 cm.), and Sumbawa (109 cm.), have just as heavy a rainfall as have the larger islands. Of Timor, Forbes says[1], 'I can scarcely say that we had any true forest, for the trees rarely entwined their crowns overhead and the ground was covered with sparse grass sufficient to give it a park-like look.' This description corresponds to the picture of a typical savannah-forest.

New Guinea, according to the present scanty data, does not appear inferior as regards rainfall to the Malayan islands. Thus for Hatzfeldhafen, 248 cm., for Constantinhafen, 296 cm., for Finschhafen, 288 cm. are given[2].

The peninsula of Malacca also has probably a similar rainfall. Singapore, on a small island separated from the peninsula by a narrow arm of the sea, has an annual rainfall of 240 cm. The island has been deforested except for an eminence, on which the rainfall may be even greater. Trees planted anywhere in the island show a very luxuriant growth. Kwala Lumpor, in the State of Selangor, on the peninsula itself, has an annual rainfall of 243 cm.

The precipitations in the Malayan forest-district are nowhere uniformly distributed throughout the year, but a wet season (in summer) and a dry one (in winter) may be distinguished, or even two rainy seasons. The difference between the seasons is sometimes greater and sometimes less, but never so marked as in Cis-gangetic India :—

DISTRIBUTION OF THE RAINFALL IN PERCENTAGES OF THE TOTAL ANNUAL RAINFALL IN THE MALAY ARCHIPELAGO.

(After Woeikof.)

	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
W. Java (Gedeh group)	9	10	9	10	10	7	7	5	5	6	9	12
NE. Java	16	22	18	12	8	5	7	3	1·4	0·5	2·4	4
Sumatra (Paday) . . .	12	10	9	11	8	8	5	4	7	7	9	9
W. Borneo	10	9	8	9	8	8	7	5	7	6	12	11
SW. Celebes	23	25	16	12	5	3	4	2·2	0·8	0·7	0·3	5

The other tropical districts with high-forest have rainfalls similar to that of the Malay district. Thus in *Asia*: Rangoon, 250 cm.; Colombo, 222 cm.; Kandy, 212 cm.; Ratnapura (Ceylon), 384 cm.; Mahabaleshwar in the Western Ghats, 723 cm. (according to Woeikof, 657 cm.); Mangalore,

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[1] Forbes, op. cit., p. 422.

[2] Meteorol. Zeitschr., 1891, p. 277.

338 cm.: Saigon, 211 cm.; Kilung in Formosa, 305 cm.—in *Africa* Kamerun, 388 cm.; Gabun, 226 cm.; Sierra Leone, 319 cm.—in *America* North-East Jamaica, 281 cm.; Hayti (Sanchez), 206 cm.; Colon, 289 cm. Georgetown (British Guiana), 214 cm.; Paramaribo, 228 cm.; Bahia, 22 cm.; Santos, 250 cm.—in *Australia*: Cape York (North Australia), 220 cm. Papeete (Tahiti), 218 cm.; Samoa (Utumapu), 212 cm. At certain spot in the districts of tropical high-forest we find the rainfall as low as abou 150 cm., but no lower. Only on the Amazon are rainfalls of 200 cm. an more the exception; there the forest owes its luxuriant growth to th water in the soil, and it consequently does not form an extensive continuou area, but is confined to the river-banks.

The distribution of precipitation throughout the months of the year ma be given in millimeters for a few non-Malayan stations in the district of th tropical high-forest :—

DISTRIBUTION OF THE RAINFALL THROUGHOUT THE MONTHS O THE YEAR IN MILLIMETERS IN SOME NON-MALAYAN STATIONS.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Kandy (Ceylon)	144	64	79	148	210	357	357	240	228	268	241	204
Kamerun . . .	54	97	214	292	164	407	1050	473	473	406	175	73
Colon	42	28	40	54	296	444	398	259	215	354	561	196

In tropical districts with precipitations at all seasons the forest is evergree and is developed as rain-forest. In districts with a marked dry season t forest is either less rich in foliage during the dry season, for instance in Ea Java, or is defoliated like typical monsoon-forest, for instance in the great part of Cis-gangetic India.

The meteorological data at my disposal do not permit of a very preci statement of the conditions that occasion the leaf-fall in the great part of Cis-gangetic India. Besides the distribution of the rain, oth factors certainly intervene, such as quantity of rainfall, temperature, ar humidity of the air.

DISTRIBUTION OF THE RAINFALL PER MONTH IN MILLIMETER IN CIS-GANGETIC INDIA.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Ratnagiri, 34 meters above sea-level	27	0·2	0	4	36	795	839	511	384	86	20	8
Mahabaleshwar, 1,380 meters above sea-level	10	1	10	23	32	1802	2575	1742	860	137	28	10

Ratnagiri on the west coast of Cis-gangetic India, at the foot of the Ghats, ituated in a district where the forests are leafless in the dry season. The tal shows that the dry season is far more marked than in the Malayan forest-distri or even than in East Java; forests actually leafless by reason of drought are wanting even in the latter district. Mahabaleshwar is surrounded by evergreen forest. Yet at this place there is a long well-marked dry season, which, however, is less poor in precipitation than it is in the lowlands. Lower temperatures and abundance of moisture in the soil must also essentially co-operate in maintaining the foliage.

Of further significance to the district of tropical high-forest is, in addition to the large amount of rain, the great *atmospheric humidity*, which at night approaches saturation, but even during the hours of midday scarcely falls below 70 °/₀, at any rate in tracts where evergreen forests occur.

The importance of *temperature* as a factor in the formation and maintenance of tropical high-forest is much less than that of atmospheric precipitations. It fluctuates between degrees (25–30° C.) which, if the necessary humidity be present throughout the year, favour all kinds of vegetative activity. Provided the soil is sufficiently moist, it is never high enough to occasion a disproportion between the outgo and intake of water and to bring about consequent wilting or shedding of the foliage. Leaf-fall indeed occurs only where prevalent great heat is associated with a scanty supply of water in the soil and air.

Tropical High-Forest Climate.

BATAVIA.

6° 11′ S., 106° 50′ E., 7 meters above sea-level.
(From Meteorol. Zeitschr., 1893, p. 355.)

1866–1890.	Temperature.		Relative Humidity.		Cloudiness.	Rainfall.	
	Mean.	Daily Range.	Mean.	Daily Range.		Amount in mm.	Days.
January . .	25·3	5·2	87	24	7·4	356	22·6
February .	25·4	5·2	87	23	7·3	317	20·4
March . .	25·8	5·9	86	26	6·7	204	17·3
April . . .	26·3	6·4	85	28	5·8	117	13·6
May . . .	26·4	6·6	84	29	5·4	85	9·7
June . . .	26·0	6·7	83	30	5·4	88	9·2
July . . .	25·7	7·2	81	32	4·7	57	6·0
August . .	26·0	7·7	78	35	4·1	39	5·3
September .	26·3	7·6	78	35	5·0	76	7·9
October . .	26·4	7·5	79	34	5·7	108	10·1
November .	26·1	6·8	82	31	6·8	122	13·4
December .	25·6	6·0	85	27	7·2	233	18·9
Year . .	25·9	6·5	83	29	6·0	1803	155·3

NORTHERN INDIA (SIBSAGAR).

26° 59′ N., 94° 40′ E., 101 meters above sea-level.

Vegetation in Upper Assam : dense forest. (From Meteorol. Zeitschr., 1894, p. 411.)

	Mean Temperature.	Relative Humidity.	Cloudiness.	Rainfall. Amount in mm.
January . .	14·3	89	5·2	30
February .	16·1	84	6·1	55
March . .	19·7	83	6·6	116
April . . .	22·9	86	7·7	249
May . . .	25·2	86	8·4	295
June . . .	27·7	87	9·0	371
July . . .	28·3	86	9·2	396
August . .	28·1	86	8·7	394
September .	27·1	88	8·2	301
October . .	24·8	87	6·1	100
November .	19·7	87	4·6	31
December .	15·5	88	4·2	14
Year . .	22·4	86	7·0	2381

MANILA.

14° 35′ N., 127° 11′ E., 14·2 meters above sea-level.

(From Meteorol. Zeitschr., 1893, p. 73.)

1890.	Temperature.			Relative Humidity.	Rainfall.		Evaporation.	Days.	
	Mean.	Max.	Min.		Amount in mm.	Days.		Bright.	Dull.
January .	25·6	32·3	17·8	78	14	8	162	7	1
February	25·9	32·8	18·2	74	16	5	179	6	2
March .	27·3	34·8	20·5	69	16	5	257	16	15
April . .	27·9	35·6	21·9	73	77	8	251	11	6
May . .	27·9	25·7	22·9	79	70	14	221	2	24
June . .	27·3	34·7	22·2	82	255	15	208	4	9
July . .	27·3	33·1	22·4	83	502	18	150	0	17
August .	27·4	33·3	22·3	82	131	13	163	0	12
September	26·5	32·2	22·5	87	539	27	118	0	26
October .	26·1	33·2	20·4	86	205	25	145	2	18
November	25·4	32·2	18·4	80	210	15	145	9	15
December	25·2	32·1	17·8	79	45	8	159	20	2
Year .	26·6	35·7	17·8	79·5	2080	161	2157	77	147

SANDAKAN (BRITISH NORTH BORNEO).

6° N., 118° E.
(From Meteorol. Zeitschr., 1889, p. 316.)

1888.	Temperature.					Rel. Humidity.		Rainfall. Amount in mm.	Cloudiness.
	9 a.m.	3 p.m.	9 p.m.	Mean Max.	Mean Min.	3 p.m.	9 p.m.		
January . .	26·1	27·8	25·2	28·6	23·3	74	86	280	5·7
February .	27·4	28·5	25·7	29·0	23·4	68	82	48	5·3
March . .	28·5	29·7	26·3	30·3	23·8	66	82	101	3·3
April . . .	29·4	30·4	27·9	32·2	24·6	63	84	47	2·7
May . . .	29·3	30·8	27·1	33·0	24·7	63	85	72	2·0
June . . .	27·6	31·5	26·4	31·8	23·9	62	85	236	5·0
July . . .	27·8	31·6	26·9	31·9	24·3	62	81	81	5·0
August . .	28·3	31·4	26·5	32·4	23·8	60	83	300	3·3
September .	28·0	30·0	26·7	31·4	23·5	67	85	339	4·0
October . .	28·6	30·2	25·7	31·9	23·9	69	88	239	3·3
November .	28·2	30·0	24·8	30·9	23·8	70	86	343	3·0
December .	28·1	29·3	26·1	30·1	24·1	72	87	496	4·7
Year . .	28·1	30·1	26·3	31·1	23·9	66	84	2582	3·9

GABUN (SSIBANGE FARM).

0° 25′ N., 9° 35′ E., 90 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1881, p. 427.)

1880.	Temperature.		Rel. Humidity.		Mean Cloudiness.	Bright Days.	Rainfall.		Strength of Wind. 2 p.m.
	7 a.m.	2 p.m.	7 a.m.	2 p.m.			Amount in mm.	Days.	
January . .	23·6	29·6	98	72	5·3	2	170	18	2·2
February .	23·6	29·3	95	73	7·0	1	271	21	2·2
March . .	23·8	28·4	95	77	7·9	0	490	28	1·9
April . . .	24·1	28·9	95	77	7·5	0	331	25	2·3
May . . .	23·8	28·4	94	72	7·9	0	64	17	1·9
June . . .	20·9	26·3	94	73	7·6	2	30	3	1·9
July . . .	21·3	25·2	91	75	9·2	0	1	10	1·7
August . .	21·7	26·2	93	77	8·6	0	27	18	1·7
September .	22·8	27·6	92	70	8·4	0	108	21	2·2
October . .	23·3	27·7	95	73	8·5	0	198	26	2·0
November .	23·0	27·3	97	70	8·3	0	619	25	1·7
December .	22·9	28·1	97	79	7·9	0	299	24	1·6
Year . .	22·9	27·8	95	74	7·8	5	2608	236	1·9

In July 14, in August 15, cloudy days—heavy dew.
Vegetation: Virgin forest. A few huts 1,000–8,000 paces from the forest.

KAMERUN.

4° 3′ S.., 9° 42′ E.., 12 meters above sea-level.
(From Meteorol. Zeitschr.. 1893, p. 435.)

1890–1891.	Temperature.		Mean Rel. Humidity.	Mean Cloudiness.	Rainfall.	
	2 p.m.	Absol. Max.			Amount in mm.	Days.
April . . .	28·3	31·2	88	8·4	292	16
May . . .	27·9	31·2	88	8·2	164	19
June . . .	26·2	29·4	88	9·4	407	24
July . . .	25·3	27·7	92	9·3	1050	26
August . .	25·6	28·4	89	8·8	473	27
September .	26·3	29·0	92	9·1	473	25
October . .	26·1	29·4	94	8·8	406	26
November .	27·6	30·8	90	8·2	175	22
December .	28·2	30·0	90	7·8	73	12
January . .	28·6	30·8	89	5·5	54	14
February .	29·3	31·0	88	4·7	97	12
March . .	28·8	31·2	88	5·6	214	15
Year . .	27·3	31·2	90	7·8	3878	238

COLON (PANAMA).

9° 22′ N., 79° 55′ W., 50 meters above sea-level.
(From Meteorol. Zeitschr., 1886, p. 367.)

	Temperature.			Relative Humidity.	Cloudiness.	Rainfall.	
	6 a.m.	1 p.m.	Daily Range.			Amount in mm.	Days.
December .	25·3	28·3	6·8	82	4·1	196	15
January . .	25·7	28·0	5·5	78	5·0	42	11
February .	25·2	27·8	6·2	77	5·0	28	12
March . .	25·5	28·0	4·9	76	3·8	40	10
April . . .	26·2	29·0	7·6	77	4·2	54	14
May . . .	25·0	28·7	8·1	84	5·9	296	21
June . . .	25·0	28·4	7·3	87	7·1	444	26
July . . .	25·4	28·3	7·4	87	7·3	398	26
August . .	24·5	28·0	8·1	88	6·9	259	24
September .	24·4	28·2	8·5	88	6·3	215	21
October . .	24·2	28·1	9·1	88	6·2	354	25
November .	24·4	28·0	8·2	87	6·6	561	23
Year . .	25·1	28·2	7·3	83	5·7	2887	228

3. THORN-FOREST CLIMATE IN CIS-GANGETIC INDIA.

The peninsula of Hindustan affords the amount of rainfall necessary or high-forest (rain-forest and monsoon-forest) only on its west coast, nd a small part of its north-east territory in the monsoon district of he Ganges and Brahmaputra. In the central parts of the peninsula he rainfall is mostly 760–1,900 mm., and according to Hann's map here is an extensive district lying between 80° and 88° E., the tropic of ancer, and 18° N., in which the rainfall is about 125 cm. The southern nd north-western parts of the peninsula are, on the whole, much drier 380–760 mm.); the north-western part borders on the western district f India.

All these districts experience summer and winter rain, except the outh-eastern (Madras), where autumnal rain prevails. They are covered ith thorn-forest and semi-desert, according to the rainfall. Tree-growth s nowhere entirely excluded (Fig. 126).

The climate is everywhere suitable for woodland, never for grassland: uring the vegetative season it is extremely hot, usually very dry, the atter especially during the cool winter and spring months.

Tropical Xerophilous Woodland Climate.

ROORKEE.
29° 52′ N., 77° 56′ E., 270 meters above sea-level.

PATNA.
25° 37′ N., 85° 14′ E., 56 meters above sea-level.

(After Woeikof in Meteorol. Zeitschr., 1894, p. 411.)

	Roorkee Temperature.		Relative Humidity.	Rain-fall.	Patna Temperature.		Relative Humidity.	Rain-fall.
	Mean.	Range.			Mean.	Range.		
January . .	13·0	13·7	70	52	15·9	10·2	69	18
February .	15·4	12·9	62	37	18·4	13·6	57	12
March . .	21·6	14·8	52	24	25·1	14·2	43	59
April . . .	28·0	15·7	36	9	30·1	14·0	40	7
May . . .	29·0	13·8	42	28	31·2	11·5	55	46
June . . .	32·2	10·5	54	124	30·8	7·6	72	181
July . . .	28·8	6·0	80	329	29·0	4·5	83	280
August . .	28·2	6·3	81	316	28·7	4·2	84	258
September .	27·7	9·4	76	140	28·6	5·3	81	201
October . .	22·5	15·2	65	15	26·2	8·5	72	70
November .	16·8	16·5	63	5	21·0	11·7	65	5
December .	12·8	14·4	71	9	16·9	12·0	69	4
Year . .	23·1	12·3	63	1088	25·2	15·9	66	1090

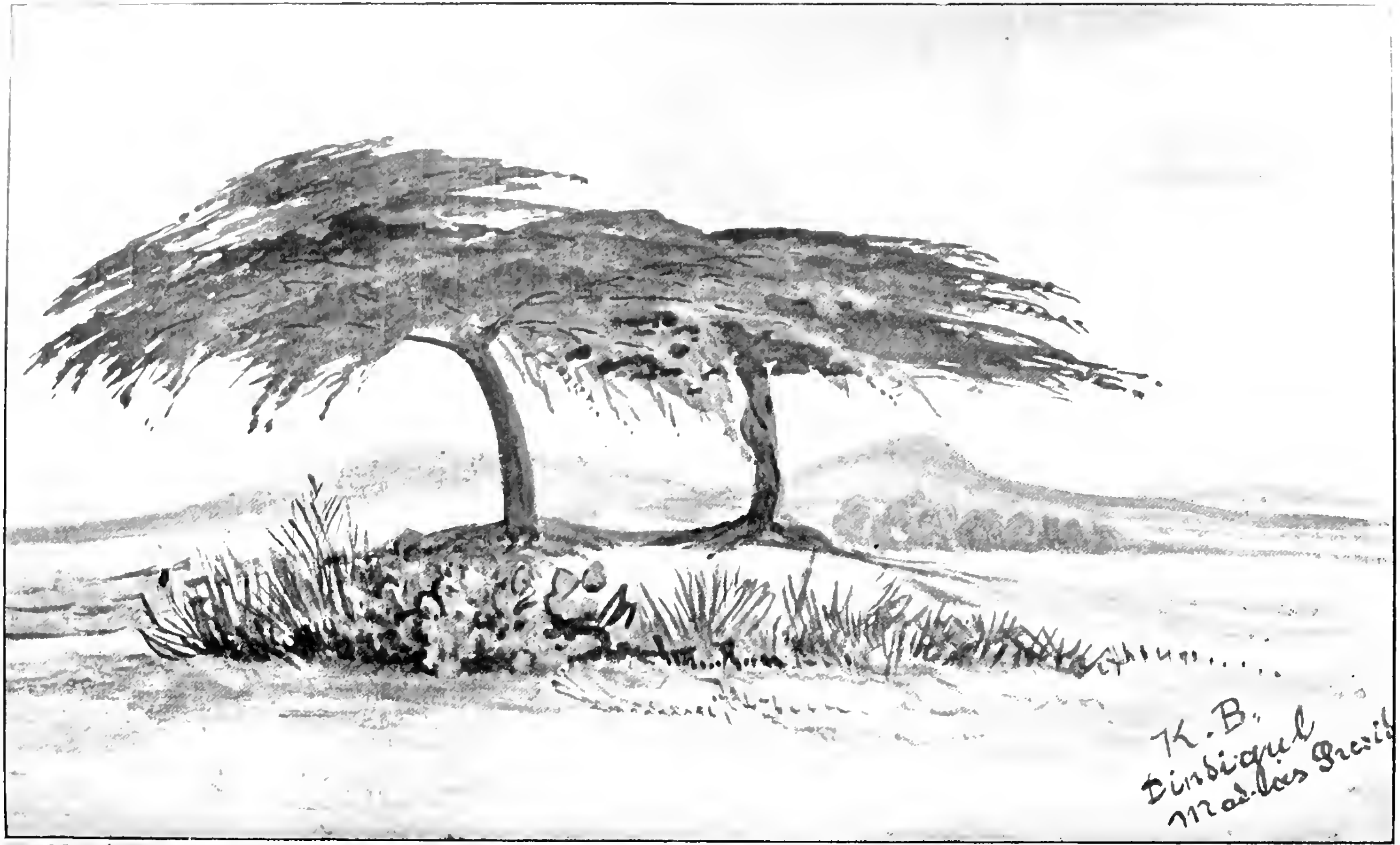


FIG. 126. Acacia planifrons in Southern India. After a water-colour drawing by Lady Brandis.

4. WOODLAND CLIMATE AND SAVANNAH CLIMATE IN BRAZIL.

The difference between woodland climate and grassland climate is exhibited very instructively after crossing the mountain-range Serra do Mar on the coast of South Brazil, which, stretching from north to south, deprives the sea-breezes of so much of their moisture as to render them considerably drier as they blow over the Brazilian plateau as far as the Andes, which constitute a mighty barrier that condenses their remaining aqueous vapour.

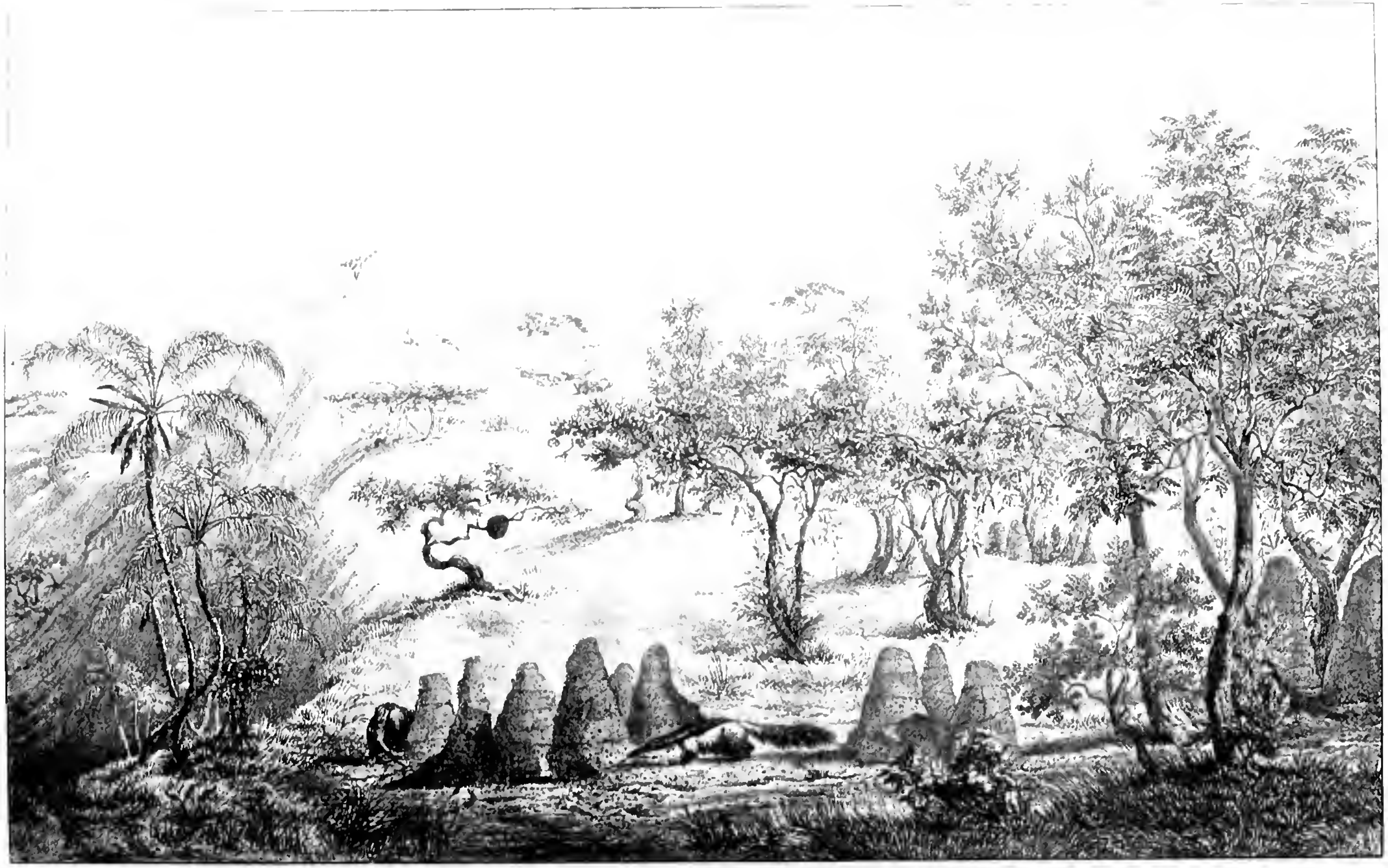
East of the Serra do Mar stretches the immense evergreen forest of the Brazilian coast, usually exhibiting only such interruptions as cultivation has caused; to the west savannah predominates. The forest is restricted as fringing-forest to the river-banks, or frequently in the form of open low savannah-forest, but also as high-forest, clothes the eastern slopes of the mountain-ranges that are exposed to the sea-breeze; it also appears in depressions in the ground, where water accumulates in the soil. It is only on the slopes of the Andes that true evergreen lofty rain-forest reappears for the first time, because, thanks to their great altitude, the mountain-slopes rob the wind of its remaining moisture.

If we land, for instance, at the seaport of Santos in the province of São Paulo we soon perceive from the fine growth of evergreen trees, from the abundance of epiphytes, and from the stately lianes, that we are within the district of the high-forest, even though this has been cleared near the town. Santos has in fact an annual rainfall of 250 cm.

Raiz de la Serra, at the foot of the Serra (21 meters above sea-level), has a still greater rainfall, namely 280 cm., than has the seaport Santos, and Alto da Serra on the mountain-range (800 meters above sea-level) has as much as 336 cm. Once the mountain-crest is passed, however, the rainfall sinks below that necessary for high-forest, and savannah, not bushwood, becomes the predominant vegetation. At the foot of the Serra on the west side lies São Paulo (740 meters above sea-level) with still 120–150 cm. of rain, but the rainfall diminishes as we pass inland and the coast-mountains become more distant—naturally leaving out of account the mountain-ranges in the interior. Porto Ferreira (531 meters above sea-level) has for instance 1,042 mm. The rainfall in the province of São Paulo apparently does not fall below 100 cm.

According to Saint-Hilaire the province of Minas Geraes lying to the north of São Paulo is subdivided by the Serra do Espinhaço into an eastern district of high-forest, and a western district of savannah (*campo*) and of deciduous savannah-forest. In the high-forest district the annual rainfall exceeds 200 cm.; in the savannah district it usually ranges between 100 cm. and 150 cm., and on the average does not attain 170 cm.

Towards the south, the region of savannah, together with the savannah-



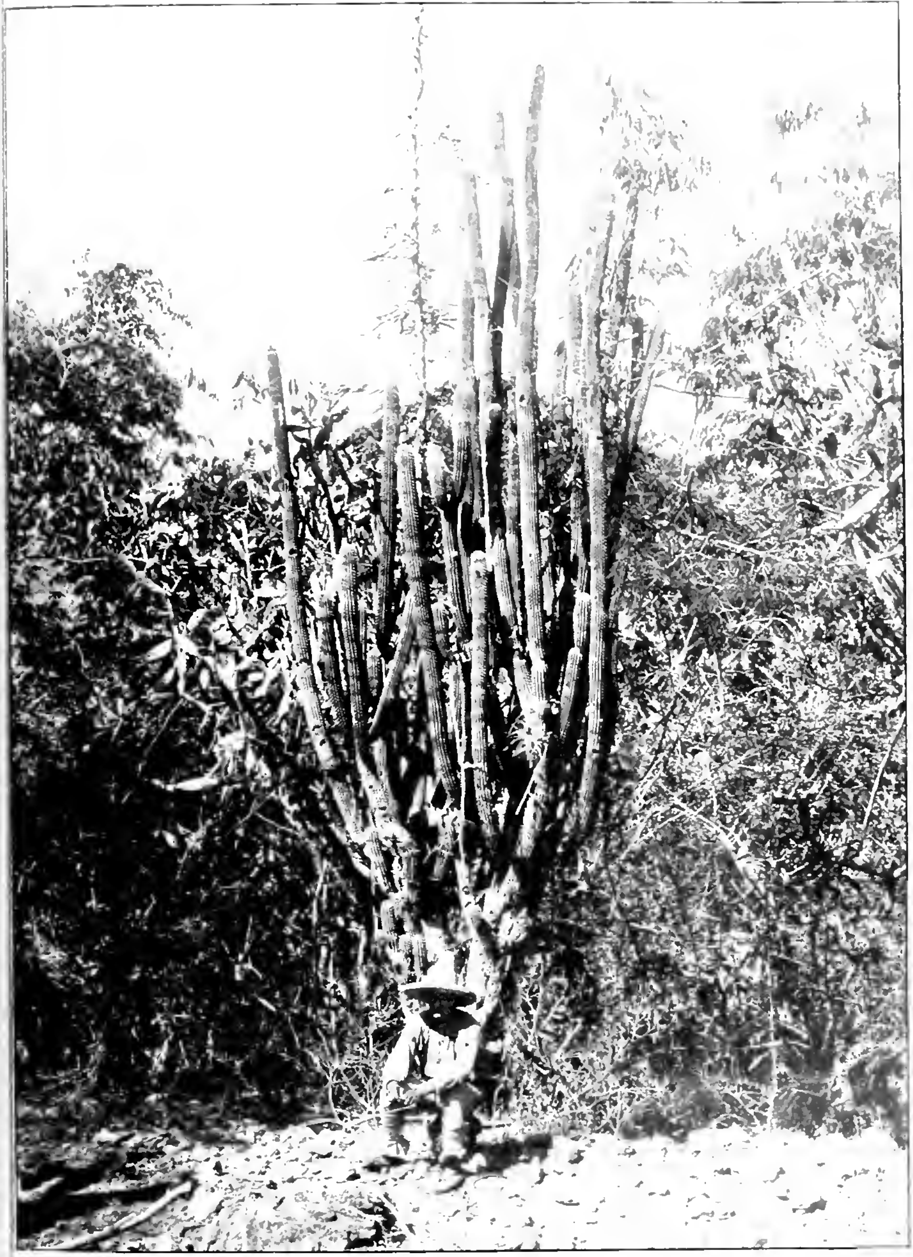


FIG. 128. Tropical thorn-forest, Mexico. S^ta Maria, tierra caliente, State of Vera Cruz. In the middle: Cereus polylophus, DC.; behind this, Acacia cornigera. From a photograph by Stahl.

To face p. 272.]

forest that replaces it on moister soil, extends over the interior of the provinces of Parana and Santa Catarina (*Araucaria-savannah*) to Rio Grande do Sul, where, owing to the cessation of tree-growth, it passes over into a purely grass steppe, the *pampas*.

To the north-west, on the other hand, in the Sertão district, which occupies the interior of Brazil between Minas Geraes and the basin of the Amazon, the savannah gradually gives way more and more to *thorn-forest* and *thorn-scrub*. Whence arises this difference between the vegetation of the southern and northern provinces in the interior? why in the southern provinces does grassland predominate—although in the form of savannah it is not quite destitute of trees and is interspersed with savannah-forest—whilst in the northern provinces woodland predominates? The climatic differences afford a decided answer.

The campo-district has a climate admirably suited to grassland, in particular, frequent precipitations and moderate heat during the vegetative season; on the other hand, the climate includes a factor unfavourable for woodland, in the *dry cold winter*[1].

Tropical Grassland Climate.

BRAZILIAN CAMPOS (SÃO PAULO).
23° 36′ S., 46° 25′ W., 745 meters above sea-level.
(From Meteorol. Zeitschr., 1891, p. 146.)

1887.	Temperature.			Relative Humidity.	Rainfall.		Bright Days.
	Mean.	Max.	Min.		Amount in mm.	Days.	
January . .	21·4	34·2	15·3	88	300	21	7
February .	21·7	32·2	11·6	82	158	16	8
March . .	19·8	31·3	14·3	87	134	22	6
April . . .	18·6	28·8	8·8	87	114	19	9
May . . .	15·4	26·7	6·6	88	64	13	10
June . . .	15·1	26·0	6·8	88	17	4	21
July . . .	14·0	25·0	5·4	86	23	10	14
August . .	13·9	30·4	6·3	74	6	6	20
September .	17·3	33·2	8·8	93	177	22	7
October . .	18·5	33·0	5·7	86	137	16	13
November .	19·0	32·8	8·5	80	79	15	15
December .	21·3	32·1	13·5	83	288	24	7
Year . .	18·0	34·2	5·4	85	1497	188	137

Evaporation: 1887, 545·2 mm.; 1888, 454·0 mm.

According to the five years' observations of Joyner (Meteorol. Zeitschr., 1886, p. 312) the mean lowest temperatures are—May, 2·7; June, 1·7; July, 2·1; August, 0·7.

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[1] See p. 174.

BRAZILIAN CAMPOS (TATUHY, PROVINCE OF SÃO PAULO).

23° 20′ S., 48° 10′ W., 600 meters above sea-level.
(From Meteorol. Zeitschr., 1891, p. 146.)

1888.	Temperature.			Relative Humidity.	Rainfall.		Days of complete Sunshine.
	Mean.	Max.	Min.		Amount in mm.	Days.	
January . .	21·8	33·6	12·0	75	103	7	18
February .	20·7	35·5	14·5	76	124	17	10
March . .	21·4	33·9	13·9	81	105	12	13
April . . .	16·3	30·9	7·0	90	8	4	16
May . . .	16·3	27·7	2·2	90	206	13	12
June . . .	14·8	25·6	4·0	82	26	4	19
July . . .	14·2	25·0	4·0	83	18	4	26
August . .	16·1	27·7	5·3	82	135	8	19
September .	18·6	29·7	10·7	85	152	11	11
October . .	21·8	34·0	7·8	85	211	15	8
November .	21·4	34·3	16·0	85	285	17	9
December .	23·4	35·7	11·0	85	20	15	9
Year . .	18·9	35·7	2·2	83	1393	127	170

Evaporation: 736 mm.

RAINFALL IN MILLIMETERS OF THE CAMPOS OF MINAS GERAES.

(After Draenert in Meteorol. Zeitschr., 1886, p. 390.)

	UBERABA. 19° 33′ S., 48° 5′ W., 750 meters above sea-level. 3 years.	CONGONHAS-DE-SABARA. 19° 47′ S., 44° 19′ W., 695 meters above sea-level. 25 years.	QUELUZ. 20° 40′ S., 44° 17′ W., 982 meters above sea-level. 1$\frac{2}{3}$ years.
December .	211·3	390	339·1
January . .	308·3	299	301·7
February .	321·3	221	303·1
March . .	142·3	192	94·5
April . . .	109·3	52	29·2
May . . .	31·3	36	31·2
June . . .	25·0	15	12·0
July . . .	13·7	11	22·3
August . .	29·3	13	19·5
September .	59·7	53	109·0
October . .	137·3	121	87·5
November .	172·0	234	104·0
Year . .	1560·8	1637	1453·1

RAINFALL IN MILLIMETERS OF THE HIGH-FOREST IN MINAS GERAES.

GONGO SOCO.

19° 58′ S., 43° 33′ W., 1,090 meters above sea-level. Two years' observations.
(After Draenert in Meteorol. Zeitschr., 1886, p. 390.)

Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Year
369·6	604·3	537·7	253·0	172·0	57·9	55·1	34·0	20·3	93·2	169·7	573·5	2939·3

The climate, however, is not so unfavourable for tree-growth as to prevent small xerophilous savannah-trees from establishing themselves n the prairie and thus lending to it the character of a savannah. At he points where water is more plentiful in the soil, where the winds blow less strongly especially during winter, where atmospheric humidity s greater, woodland prevails over grassland, so that the whole district hows the alternation of both formations in its park-like features.

In contrast with its southern portion, the middle part of Central Brazil, he so-called Sertão district, possesses a xerophilous woodland climate.

Here the year is hot throughout, at times very hot, and there are no dry cold winter months that are so injurious to woodland; on the other hand, the climate includes factors unfavourable to grassland in the more onsiderable heat and the small amount of precipitation over the greater part of the district, except the coast. Finally, the vegetative season is much interrupted by hot dry periods.

The Sertão district is therefore much richer in woodland than is the outhern cooler campos district. Tree-growth is richer in the savannah, xtensive tracts are covered by savannah-forest and thorn-forest, in general woodland strongly predominates over grassland. To explain in detail why woodland occurs in one place, and why grassland in another, is at present only partially possible, for there is a lack of accurate data of the meteorology and local constitution of the soil, and the soil plays an mportant part in such mixed districts[1].

Quite a narrow strip of coast in the province of Pernambuco possesses a very eavy rainfall, a real high-forest climate (Pernambuco, 297 cm.). Tree-growth is xtremely luxuriant in the public grounds of the principal town, but there is no nformation available regarding the indigenous vegetation.

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[1] See Part III, Sect. I, Chap. V.

T 2

Tropical Xerophilous Woodland Climate.

THE SERTÃO.

(After Draenert in Meteorol. Zeitschr., 1886, p. 390, and 1889, p. 28.)

	COLONIA ISABEL (PROV. PERNAMBUCO). 8° 45′ S., 35° 42′ W., 229 meters above sea-level, about 80 kilom. from the coast. 6½ years' observations.			VALLE DO ALTO PARNAHYBA. About 6° S. 43° 30′ W., 124 m. above sea-level.	FORTALEZA OR CEARA. 3° 44′ S., 38° 31′ W., at sea-level.	SANTA ANNA DO SOBRADINHO on the lower river. About 9° 26′ S., 40° 47′ W., about 321 meters above sea-level, 800 kilom. from the coast. R. San Francisco. 3 years' observations.		
	Mean Temp.	Relative Humidity.	Rainfall. Amt. in mm.	Rainfall. Amount in mm. 1 year's observations.	Rainfall. Amount in mm. 28 years' observations.	Relative Humidity.	Rainfall. Amount in mm.	Rainfall. Days.
January .	25·0	68	36·1	219·0	68·6	67	78	3·7
February	24·4	69	46·6	109·8	200·0	73	40	6·0
March .	25·2	74	77·7	234·4	291·9	77	148	7·0
April . .	24·5	76	144·7	81·4	372·6	77	11	1·3
May . .	23·4	79	193·0	55·4	276·8	84	5	1·0
June . .	22·3	81	144·8	0·0	137·5	77	7	1·7
July . .	21·4	81	154·7	0·0	48·9	78	1	0·5
August .	21·3	79	124·9	0·0	15·3	70	0	0·0
September	22·2	75	49·9	0·0	12·7	64	12	0·2
October .	23·6	68	19·2	93·8	14·3	64	38	2·5
November	24·8	64	19·5	91·0	14·4	66	11	1·5
December	25·1	65	25·9	80·8	38·6	67	22	2·3
Year .	23·7	73	1037·0	965·6	1491·5	72	373	27·7
						Rainfall in 1884 = 399, 1885 = 527, 1886 = 186 mm.		

5. CLIMATE OF NORTHERN SOUTH AMERICA AND OF THE ANTILLES.

Between the richly forested districts of the Amazon basin and of th southern part of the Orinoco basin lies the small savannah district c Guiana, regarding the climate of which there are no data. North of th Orinoco, up to the wooded mountainous coasts of the Caribbean Se stretches the wide prairie district of the *llanos*, usually a typical savanna in some places with very scattered trees, in others with more densel crowded trees. According to my own observations, high-forest occu as fringing-forest along the water-courses; savannah-forest occurs at th foot of the Cordilleras on the coast, *pari passu* with an increasing rainfa and also in moist depressions in the ground, in the same way as in the campos.

Only general facts are known regarding the climate of the llanos; accurate meteorological data are wanting. Yet, from the available material, the climate may be described as one *hostile to woodland*. The year is divided into a quite rainless dry season of five months, which is contemporaneous with our winter and early spring, and into a rainy season, which begins at the end of April. In the climate of the llanos *it is the dry season that is hostile to woodland*, for during the greater part of its duration the dry easterly trade-wind blows almost continuously, and usually with extreme intensity, and is associated with great heat and excessive dryness of the air.

A windy dry season is unfavourable to woodland, whereas it does no harm to the thoroughly dried up prairie, whose existence is maintained only in the subterranean parts of its plants, except when the season is immoderately prolonged. Such abnormally long periods of drought are not rare, but they are far more fatal to woodland than to grassland.

In the llanos, according to Humboldt, *it rains continuously during the rainy season. This directly favours the prairie*, whose existence, as we know, depends more on very frequent showers than on heavy ones during the vegetative season.

The following extracts from Hann's 'Klimatologie' give the characteristics of the climate of the llanos:—

'"The clearness of the air from December until February is incomparable. The sky s continuously cloudless, and the presence of a single cloud is a phenomenon that ngages the attention of all the inhabitants. The wind blows strongly from the east nd north-east" (Humboldt).

'C. Sachs stayed at Calabozo (9° N., 150 m. above sea-level) in the dry season (Dec. 876 until Feb. 1877). He found a morning temperature of 22–25° C. before sunrise, nd 34–35° between 1 and 2 p.m. In February, the mean temperature between 1 and p.m. is 35·9°, and the relative humidity 30%, and sometimes only 16%. The east rade-wind blows constantly from sunrise until noon. Complete drought prevails or five months, during which there is no dew. In April the rainy season begins, nd the land that has been parched into a desert becomes clothed once more with ense vegetation' (pp. 365–6).

The small western islands of the West Indian archipelago are occupied y woodland, which is favoured by the great humidity of the air. The oodland is composed sometimes of rain-forest, as in Dominica, sometimes f thorn-forest, as in St. Kitts, according as the rainfall is greater or less han about 150 cm.

I am personally acquainted with the vegetation of the two islands, regarding the ainfall of which data are given below. The rainfall in Dominica, as I know from xperience, is considerably heavier in the mountains, where the high-forest shows the greatest luxuriance of growth, than at Roseau, or on the coast generally. St. Kitts does not possess such lofty mountains as Dominica.

RAINFALL IN THE LESSER ANTILLES.

(From Meteorol. Zeitschr., 1886, p. 462.)

Rainfall at Roseau in Dominica.

The mean of 21 years (1865–1885) is 1,901 mm.; the minimum during this period 1,309, the maximum 2,690.

Monthly mean:	mm.
December	145
January	148
February	71
March	56
April	61
May	73
June	207
July	266
August	274
September	223
October	176
November	200

Rainfall in St. Kitts.

The mean of 30 years (1856–1885) is 1,292 mm.; the minimum 895, the maximum 2,111. 200 cm. exceeded only in one year.

Monthly mean:	mm.
December	96
January	103
February	48
March	55
April	90
May	98
June	92
July	105
August	144
September	154
October	173
November	134

The Greater Antilles, Jamaica, Hayti, and Cuba possess partly high-forest, partly thorn-forest or perhaps savannah. It is impossible to give from the available literature any distinct impression of the vegetation of these islands.

6. CLIMATE OF TROPICAL AFRICA.

A frequent alternation of forest and savannah reveals itself on the west coast of tropical Africa.

True desert stops a little south of the tropic of Cancer and is replaced by a still very scanty open woodland vegetation, with Adansonia digitata and Borassus flabelliformis (Saint Louis, 16° N., 16° 33′ W., with rainfall 42 cm.; Goree, 14° 39′ N., 17° 24′ W., with rainfall of 53 cm.). Tree-growth becomes richer and more luxuriant further south. Round Sierra Leone (rainfall of 319 cm.) plains and mountains are covered with high-forest. On the Ivory and Gold coasts (Elmina, 5° 4′ N., 1° 20′ W., with rainfall of 72 cm.; Christiansborg, 5° 32′ N., 0° 8′ W., with rainfall of 58 cm.) the vegetation is again poorer. East of Akra, in the Gulf of Benin, true savannah with fan-palms prevails (Lagos, 9° 26′ N., 3° 30′ E., with rainfall of 172 cm., from two years observations); the country at the mouth of the river Niger (4° 17′ N., 6° 4′ E.) and that of Kamerun (4° N., 9° 40′ E., with rainfall of 249 cm.) and Gabun (0° 22′ N., 9° 23′ E. with rainfall of 226 cm.) are all covered with rain-forest; in the highlands of Gabun, however, savannah rich in trees predominates. South of the Ogowe (0° 40′ S., 9° E. the savannah gains the mastery even along the coast, and rain-forest is found by rivers and lagoons only. In Jumba, forest (rain-forest?), interrupted by savannah, reappears up to the mouth of the Kiulu, south of which savannah with fan-palms and baobab-trees predominates (Chinchosho, 5° 9′ S., 12° 4′ E., with rainfall of 108 cm.). The last great forests, possibly rather as fringing forests, clothe the plains at the mouth of the Congo (9° 4′ S., 12° 15′ E.), whilst the highlands on the lower Congo (San Salvador 6° 17′ S., 14° 53′ E., with rainfall of 998 mm.) are covered with savannah. South of the mouth of the Congo, again, we at once find savannah with gigantic Adansonia. In the southerly direction the savannah becomes continually poorer, and at Kinsembo a desert character is assumed, where succulent plants like Euphorbia and Aloe predominate. North of Mossamedes (15° 11′ S., 12° 8′ E.), Welwitschia mirabilis first shows itself, the grass vegetation becoming constantly scantier, and beyond the Kunene (17° 30′ S., 14° E.), the river bounding Lower Guinea, only scattered tufts of grass and accommodating thorn-plants grow on the parched and stony ground.

In the preceding remarks, the distribution of high-forest—possibly rain-forest throughout—and of savannah is shown in the clearest manner to be dependent on the amount of rainfall. Everywhere high-forest alone predominates when the rainfall attains 200 cm. in the year, but is entirely supplanted by savannah when the rainfall does not exceed 170–180 cm. Finally savannah gradually dwindles into desert at a rainfall of 30–35 cm.

Here and there in fertile districts, especially where there is much atmospheric humidity, savannah alternates with savannah-forest, which appears to be absent from other districts, for instance the high plateau on the Congo and to the south of the mouth of the Congo.

Should the inquiry be made, why districts that are too dry for high-forest are occupied by savannah, which is grassland, and not by scrub, we may reply that the frequency of the precipitations shown by the great number of rainy days, as well as the not very high temperature, are favourable to grassland. Pechuel-Lösche mentions the by no means rare occurrence of prolonged periods of drought on the Congo coast, for instance years with only 20 centimeters of rainfall, and, as has been explained already, such droughts are much less fatal to the continued existence of grassland than to that of woodland. The heavy dew of the normal dry season will possibly continue during these periods of drought to moisten the surface of the ground, but is of no value to the roots of woody plants. Our meteorological table for San Salvador, on the savannah-clad highlands of the lower Congo, shows that strong winds prevail there, especially during the dry season. This circumstance, unfavourable to woodland, favours grassland. Our present knowledge of the African climate is, however, still too incomplete to afford a completely satisfactory answer to the question postulated.

Our meteorological knowledge of the savannah districts on the elevated plateau of central tropical East Africa is still very incomplete, but the available data, for instance the tabular statement given below, exhibit a typical savannah climate, with a moderately hot vegetative season, during which the rainfall is about 100 centimeters in very frequent showers, as the number of rainy days tells.

Tropical Grassland Climate.

WEST AFRICAN SAVANNAH (LOANGO, CHINCHOSHO).

5° 9′ S., 12° 4′ E., 12 meters above sea-level. 2 years.
(After Danckelmann, op. cit.)

	Temperature (1874).		Rel. Humidity. Mean (1874).	Days (1875).		Rainfall in 1875.	
	6 a.m.	2 p.m.		Bright[1].	Cloudy[2].	Days.	Amount in mm.
January . .	22·79	27·04	87	0	6	13	311
February .	24·17	28·45	84	0	5	14	301
March . .	23·77	28·44	82	1	8	16	267
April . . .	22·92	26·24	88	0	5	17	202
May . . .	21·56	24·70	86	1	2	8	107
June . . .	20·50	23·99	86	11	2	0	0
July . . .	19·06	22·84	84	5	4	0	0
August . .	19·37	22·01	88	1	13	4	8
September .	21·79	23·91	83	1	18	4	11
October . .	23·26	25·94	84	0	8	7	10
November .	23·88	27·69	85	0	9	9	170
December .	23·49	27·75	85	8	3	3	25
Year . .				28	83	95	1412

The rainfall is extraordinarily variable, and in some years has apparently been as low as 200 mm., but accurate observations are not forthcoming. Heavy dews in the dry season often correspond to a precipitation of 3 mm.

WEST AFRICAN SAVANNAH (CONGO, SAN SALVADOR).

6° 17′ S., 14° 53′ E., 579 meters above sea-level (high plateau).
(From Meteorol. Zeitschr., 1888, p. 394.)

1883–1886.	Temperature.		Rel. Humidity.		Cloudiness.		Rainfall.		Mean Strength of Wind.	Evaporation.
	9 a.m.	3 p.m.	9 a.m.	3 p.m.	9 a.m.	3 p.m.	Amount in mm.	Days.		
January . .	23·4	27·8	80	61	7·8	6·4	59	11·0	5·4	147
February .	24·0	28·9	80	59	7·5	6·9	118	11·7	5·8	150
March . .	24·3	28·4	79	60	7·3	5·6	132	10·7	6·0	129
April . . .	24·0	28·2	84	67	7·8	7·2	271	17·3	4·4	100
May . . .	22·5	27·7	88	65	8·3	5·3	87	9·3	5·4	88
June . . .	19·9	26·6	87	58	8·4	2·9	8	5·0	5·1	59
July . . .	18·7	25·5	84	53	7·7	2·3	0	1·5	10·1	110
August . .	19·2	25·9	81	52	7·6	4·6	0	3·5	8·3	130
September .	20·3	27·1	80	56	8·5	5·3	0	3·0	8·9	143
October . .	21·8	27·5	84	59	8·8	7·3	42	9·5	8·4	158
November .	22·3	27·0	86	66	9·2	7·3	194	16·5	6·7	120
December .	22·8	27·0	85	66	8·9	6·8	77	12·0	5·7	120
Year . .	21·9	27·3	83	60	8·1	5·6	988	111·0	6·7	1454

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[1] Cloudiness = 2 and less.

[2] Cloudiness = 8 or more.

SAVANNAH ON THE CENTRAL AFRICAN PLATEAU (KAKOMA AND IGONDA).

5° 40′ S., 32° 35′ E., 1,120 meters above sea-level.
(From Meteorol. Zeitschr., 1887, p. 421.)

1881–1882.	Temperature.			Rel. Humidity.		Cloudiness.	Rainfall.	
	7 a.m.	2 p.m.	Mean.	7 a.m.	2 p.m.		Amount in mm.	Days.
March . .	19·0	26·8	21·6	95	58	8·0	293	27
April . . .	18·6	27·3	21·4	94	55	5·7	114	17
May . . .	16·7	29·0	20·8	91	43	2·6	13	4
June . . .	12·0	28·5	18·0	90	28	1·1	0	0
July . . .	11·9	29·5	18·8	86	24	1·3	0	1
August . .	15·4	30·5	21·7	72	23	2·4	0	0
September .	20·4	31·5	25·7	52	23	3·0	0	2
October . .	21·6	33·2	26·8	52	18	2·4	0	0
November .	22·3	32·1	25·9	60	26	3·9	73	9
December .	20·3	27·7	23·1	82	52	6·0	124	22
January . .	20·0	28·2	23·0	81	45	5·3	115	15
February .	18·4	24·1	20·4	93	69	7·3	265	15
Year . .	18·0	29·0	22·3	79	38	4·5	997	112

The months of June to November (dry season) are very windy; the south-east wind greatly predominates. Savannah fires begin in May.

Tropical Xerophilous Woodland Climate.

LADO ON THE UPPER NILE.

5° 2′ N., 31° 44′ E., 465 meters above sea-level.
(From Meteorol. Zeitschr., 1890, p. 109.)

1878–1884.	Temperature.		Rel. Humidity.		Mean Cloudiness.	Rainfall.		Velocity of Wind.
	7 a.m.	2 p.m.	7 a.m.	2 p.m.		Days.	Amount in mm.	
January . .	23·4	34·7	62	29	2·3	0·5	0	2·0
February .	24·6	35·2	62	30	4·1	3·7	0·2	2·1
March . .	26·5	35·1	74	43	5·0	10·5	27·0	1·9
April . . .	26·4	32·9	74	50	6·2	16·2	135·6	2·1
May . . .	25·0	30·9	85	60	6·0	15·2	86·8	2·0
June . . .	23·6	29·5	91	60	6·3	19·0	151·4	2·0
July . . .	23·0	28·8	90	62	6·4	17·0	217·8	1·9
August . .	23·0	28·6	88	65	5·9	18·4	128·8	1·9
September .	23·0	29·1	88	56	6·0	15·8	122·8	1·9
October . .	22·6	30·2	79	57	5·7	14·0	56·5	1·9
November .	22·5	31·8	75	51	4·5	8·7	20·0	2·0
December . .	22·7	33·7	55	24	3·2	2·7	1·6	2·0
Year . .	23·9	31·7	77	49	5·1	141·7	948·5	2·0

SUMMARY.

If we summarize the results of this chapter, we arrive at the following conclusions:—

1. With at least 180 cm. of rainfall, the high-forest alone predominates. In regard to rainfalls of 150–180 cm. no data are available.

2. With 90–150 cm. of rainfall there is a struggle between xerophilous woodland and grassland. Xerophilous woodland gains the victory when greater heat and more prolonged rainless periods prevail during the vegetative season: grassland succeeds when a milder temperature, a more even distribution of rainfall during the vegetative season, and windy dry or frosty seasons prevail.

3. With a rainfall below 90 cm., xerophilous scrub, in particular thorn-forest and thorn-bush, prevails; both of these, if the precipitation be less pass over into open scrub (semi-desert).

SELECT LITERATURE.

Bebber, W. J. van. Die Regenverhältnisse Indiens. Meteorol. Zeitschr. 1885.
Brandis, D. I. On the Distribution of Forests in India. Ocean Highways. 1872.
—— II. Influence of Forests on Rainfall. Indian Forester. Vol. XIV.
—— III. Regen und Wald in Indien. Meteorol. Zeitschr. 1887. p. 369.
Danckelmann, A. v. Die meteorologischen Beobachtungen der Gussfeldt'schen Loango-Expedition. Leipzig, 1878.
Draenert, F. M. I. Die Vertheilung der Regenmengen in Brasilien. Meteorol. Zeitschr. 1886.
—— II. Das Küstenklima der Provinz Pernambuco. Meteorol. Zeitschr. 1887.
Engler, A. Ueber die Flora der deutschen Schutzländer in West-Africa. Gartenflora. 1885.
Forbes, H. O. A Naturalist's Wanderings in the Eastern Archipelago. London, 1885.
Gardner, G. Travels in the Interior of Brazil during the Years 1836–1841. London, 1846.
Kurz, S. Preliminary Report on the Forest and other Vegetation of Pegu. Calcutta, 1876.
Pechuel Lösche, E. Die Vegetation am Kongo bis zum Stanley-Pool. Das Ausland. 1886. Nos. 20, 21.
Sachs, Carl. Aus den Llanos. Leipzig, 1879.
Saint-Hilaire, A. de. Tableau de la végétation primitive dans la province de Minas Geraes. Annales des sciences naturelles. Tome XXIV. 1831.

Schweinfurth, G. Allgemeine Betrachtungen über die Flora von Socotra. Engler's Jahrbücher. Bd. V. 1884.

Trimen, H. On the Flora of Ceylon, especially as affected by Climate. Journal of Botany. Vol. XXIV. 1886.

Woeikof, A. I. Die Regenverhältnisse des malayischen Archipels. Zeitschr. der österr. Gesellschaft für Meteorologie. 1895.

—— II. Der tägliche Gang der Temperatur und der Hydrometeore in Nordindien. Meteorol. Zeitschrift. 1894. p. 403.

The climatic tables are taken from:—

Zeitschrift der österreichischen Gesellschaft für Meteorologie. Bd. I-XX. 1866-1885.

Meteorologische Zeitschrift der deutschen und österreichischen Gesellschaft für Meteorologie. 1884-1896.

Also utilized without special reference:—

Hann. Atlas der Meteorologie. Gotha, 1887.

CHAPTER IV

TROPICAL DISTRICTS CONSTANTLY MOIST

1. **Distribution of the Tropical Rain-Forest.** 2. **General Character of the Tropical Rain-Forest.** i. *External Aspect of the Forest.* Surface and profile. ii. *Interior of the Forest.* Variable density. Frequent and widespread constituents of the flora. Woody plants. Herbs. Lianes. Epiphytes. The struggle for light. Atmospheric humidity. iii. *Tropical Rain-Forest in Asia.* Vegetation and flora on the Gedeh and Salak in Java. Characteristic forms. Occurrence of brightly-coloured flowers. Rain-forest in Pegu, according to F. Kurz. iv. *Tropical Rain-Forest in Africa.* The forest of the Loango coast according to Pechuel-Lösche. Rain-forest in Usambara. v. *Tropical Rain-Forest in America.* vi. *Tropical Rain-Forest in Australia and Polynesia.* 3. **Oecological Characteristics of Plants growing in the Rain-Forest.** i. *Trees and Shrubs of the Rain-Forest.* The stems of the trees. Plank-buttresses. Bark. Branching. ii. *Terrestrial Herbs of the Rain-Forest.* Coloured foliage. The Hymenophyllaceae. iii. *Lianes of the Rain-Forest.* Palm-lianes. Scrambling bamboos. Root-climbers. Cyclanthaceae and Pandanaceae. Araceae. Their absorbing and attaching roots. Twiners. Tendrillous plants. Species of Bauhinia with ribbon-shaped, wavy stems. iv. *Epiphytes of the Rain-Forest.* Occurrence. Subdivision according to their mode of life into Proto-epiphytes, Hemi-epiphytes, Nest-epiphytes, Tank-epiphytes. Characteristics of the groups. Water-reservoirs. Velamen of orchids and aroids. Aphyllous orchids. The banyan. Humus-collecting orchids. Ferns with collecting funnels and with pocket-leaves. Bromeliaceae. Absorption of water through the leaves. Illumination of epiphytes. Epiphylly. Distribution of epiphytes on an individual tree. v. *Buds in the Rain-Forest.* Unprotected buds. Protective devices of active buds. The sprouting of leaves. Pendent leaves and pendent shoots. Flower-buds under water. Flower-buds with water-calyces. vi. *Cauliflory in the Rain-Forest.* Cauliflory on stem and branches. Aphyllous fertile twigs. vii. *Saprophytes and Parasites in the Rain-Forest.* Plants without chlorophyll belonging to the Orchidaceae, Burmanniaceae, Triuridaceae, Gentianaceae. Balanophoraceae. Rafflesia. Loranthaceae.

1. DISTRIBUTION OF THE TROPICAL RAIN-FOREST.

In his map showing the distribution of precipitation according to the seasons, Hann subdivides the tropical zone into districts with a dry season—that is to say, with months in which the normal frequency of rain falls below 0·20, in other words with six rainy days in a month—and into districts without any dry season proper. Districts without any dry season may be described as constantly humid regions. Precipitation in them, however, is not uniform throughout the year, but is distributed over more humid and less humid periods, the alternations of which are not without influence on vegetation, for, as was shown in the previous chapter, this influence frequently makes itself felt, especially as regards the times of flowering.

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Fig. 129. Tropical rain forest in the Province of Chiapas, S. Mexico. On the stems to the left and right are climbing Araceae.

FIG. 130. Recently thinned part of a forest in the interior of Samoa, 300 meters above sea level. Palms. On the branch to the right, an epiphyte, Astelia sp., in flower. In the background the intact rain-forest. From a photograph.

To follow Fig. 129]

On the whole, the vegetation of the constantly humid districts is clearly marked off from that of the periodically dry districts. *Constantly humid districts, whenever undisturbed by cultivation, are nearly always covered with evergreen rain-forest; periodically dry districts are occupied by deciduous woodland and savannah.* If precipitation be very slight even during the rainy season, the character of vegetation becomes that of desert.

Hann's tropical district without a dry season includes, passing from east to west: 1. In *Australia*, New Guinea with its neighbouring archipelagos, the Bismarck and Solomon Islands, and most of the Pacific islands. 2. In *Asia*, the Philippines, the Moluccas (for the most part), West Java, Celebes, Borneo, Sumatra, and the southern end of Malacca. 3. In *Africa*, the Mascarenes, Eastern Madagascar, Zanzibar with the neighbouring continental coast, and the district of the great African lakes. 4. In *America*, the Brazilian coast district to the south of 15° S., the northern part of the basin of the Amazon, Guiana, the Lesser Antilles (for the most part), and the east coast of Central America.

In general, the boundaries of the district designated above coincide with those of the tropical rain-forest. Wherever it has not been cleared, the tropical rain-forest covers the lowlands and ascends the highlands as far as the tropical climate extends. Here and there the tropical rain-forest slightly oversteps the boundaries of the tropical climate proper, both in the horizontal and vertical directions. Tropical rain-forest also occurs within the range of the district with marked dry seasons, chiefly among mountains that condense moisture, in districts of limited extent, where the climate is constantly humid and occasions the appearance of the rain-forest, as in the eastern Himalayas, in Burma, on the western slopes of the Nilgiris, in West Ceylon, in Kamerun, and on the east coast of tropical Australia.

A similar, but usually less luxuriant, evergreen forest frequently, but not always, fringes the rivers of the periodically dry district. Such *fringing forests*, as has been already stated, are independent of atmospheric precipitations and will be discussed in the chapter dealing with the edaphic influences.

2. GENERAL CHARACTER OF THE TROPICAL RAIN-FOREST.

i. *EXTERNAL ASPECT OF THE FOREST.*

When the rain-forest is viewed from outside, say from a ship sailing by a forest-clad coast, or from the summit of an elevated point rising above a tract of forest, many distinctions between it and forest in temperate regions meet the eye. The upper surface never exhibits a uniform tint, but forms a richly varied mosaic, in which every shade of green is represented: least frequent of these is the fresh green, say like that of beech-woods in early summer, whereas yellowish, brownish, grey, olive-like tints compose a picture somewhat gloomy but one tinted with innumerable shades. Here and there on the duller ground glows the bright patch of the flowering crown of a tree. When I was approaching the coast of Trinidad in winter, the flowering erythrinas resembled so many fires in the dark forest. So, in Java, I could recognize the puspa-tree (Gordonia Wallichii) at a great distance by its snow-white flowers. By the mere tints of their foliage a native can recognize valuable trees in the richly figured tapestry of the canopy of the forest. Thus, the cascarilleros of the Andes look for an elevated point from which they can fix the position in the forest of the scattered quinine trees.

Fig. 131. Profile view of the tropical rain-forest near Blumenau, Brazil. The palm is Euterpe edulis. From a photograph by H. Schenck.

Even the side view of the tropical rain-forest differs essentially from that of a European forest; it is not as with us bounded above by a nearly level line, but is irregularly jagged, crested, and furrowed (Figs. 131, 132). In a natural condition, for instance on the bank of water-courses, such side views of the forest are so overhung with lianes and epiphytes that the stems are quite invisible and even the crowns appear veiled. In an artificial side view, due to a forest-clearing, the great diversity in the tree-trunks, the irregular tangle of lianes, and the variety in the forms of the foliaged crowns forcibly strike the eye (Fig. 130).

FIG. 132. Profile view of the tropical rain-forest at Tjibodas, in Java, behind the botanic garden, which may be seen in the foreground. From a photograph.

ii. *INTERIOR OF THE FOREST.*

The picture afforded by the interior of the rain-forest varies greatly in individual cases. Many forests display a dense mass of foliage from the ground up to the tops of the trees, through which we can only laboriously cut our way with a bill-hook (Fig. 129); others are like immense, dark-columned halls, which afford a free passage and a clear outlook in all directions, where only a few ferns on the ground and on the stems of the trees here and there relieve the monotony of brown tints. As a matter of course these extreme forms are connected by intermediate ones.

The dense rain-forest with abundant underwood appears, at least from my own observation, to be the commoner of the two (Fig. 133). In all my tropical expeditions I have seen extensive tracts covered by it. The light column-forest I know in particular on the mountains of Dominica, where it is chiefly formed by a species of Canarium; the same in a less pure form with many tree-ferns I know in Trinidad. Kurz describes similar open forests in Pegu. There appears to be less variety among the trees in it than in the closed forest.

Within the forest, the botanist will at once endeavour to obtain a clear idea of its systematic composition. As regards the large trees that produce the general covering of the forest the labour is usually in vain. Only felling the trees would secure the object in view, and to do this is much more difficult than with us, for the trees are bound together by a tangle of lianes. It does not moreover always lead to decisive results, for not all trees are sufficiently characterized by their foliage, and many of them blossom but seldom or do so only for a short period. I have very rarely seen a useful result obtained by knocking down twigs.

The cries of flocks of parrots will often denote trees with ripe berries, and in particular fig-trees, and then a search on the ground usually leads to the discovery of some fruits. Occasionally, the area of ground corresponding to the particular tree is pretty thickly covered with fruits that have fallen or have been thrown down, for instance with berries of Myrtaceae and Meliaceae, and the easily recognizable seeds of a Myristica. In other cases corollas or petals are found. One must always remembe the possibility of such fruits and flowers coming from epiphytes o lianes. No doubt indeed can arise regarding caulifloreus species; they ar however quite exceptional, in particular among the tall trees.

The bark of most trees shows much that is characteristic. In one cas it is smooth, in another furrowed; in many Myrtaceae the bark peels off i thin flakes or scales, in certain Leguminosae the surface is green; in othe cases it is armed with thorns or with corky warts, or if it be wounded latex or resin exudes. Accurate investigation of such features woul certainly lead far towards identification. This is proved by the circum-

FIG. 133. From the South Mexican rain-forest. Underwood with tree-ferns. From a photograph by G. Karsten.

To face p. 288.]

stance that frequently natives can correctly name individual species of trees by merely observing the characters that can be seen from the ground, such as the nature of the bark, the thickness of the trunk, the occasional plank-buttresses, which will be subsequently dealt with, and, at times, the mode of branching. Analytical tables founded upon such characters, which however are often very difficult to describe, would be of immense value.

Most lianes—the woody climbing plants which usually occur in such abundance in every virgin tropical forest—also withdraw their crown of foliage from the view of the naturalist, who is confined to the ground, and an attempt to pull them down is as a rule as useless as to fell them. But in their case the anatomical structure of the stem exhibits so much that is characteristic, that the determination, at least of the genus, is possible, thanks to the excellent works of Radlkofer, Bureau, and Schenck[1].

In order to obtain an idea of the systematic composition of the forest-canopy, the botanist, even if he has frequently traversed and carefully searched the virgin forest, must rely on 'Floras,' which, prepared chiefly from collections made by natives, usually convey very incomplete information. Much more useful are the works of the foresters, but these unfortunately are still entirely wanting in respect to tropical America and tropical Africa. The works of Brandis, Kurz, and Koorders and Valeton are sources of information regarding the systematic composition of the forests of India and further India. Apart from the lianes and herbaceous flora, it is comparatively easy to acquire the necessary knowledge of the systematic composition of the underwood, without which a work on the physiology of the virgin forest is valueless. Not only is the variety of foliage much greater than in Europe, but a number of species bear flowers and fruit, though often in small quantities, for months if not throughout the year. At the first glance, in a damp, cool forest, the tree-ferns strike the eye, and these, like the ferns in general, can be easily determined from the available herbaria. Small palms are seldom absent; for instance, in Brazil species of Geonoma occur, in Java species of Pinanga. Here and there appear thickets of bamboos, or of climbing ferns like Lygodium, or of species of Selaginella. The main mass of the underwood and bushes, however, is formed by Dicotyledones. The Urticaceae are seldom absent, for instance species of Boehmeria, and in Asia also species of Laportea, which are easily recognizable, even when not flowering, by the form of their leaves and their hairs. In company with these, shrubby Piperaceae will be found, in particular species of Artanthe, and species of Ottonia with knotty stems and vertical, white, taper-like spadices; also the varied species of Croton, with inconspicuous flowers and leaves with scales beneath. Less abundant, but highly characteristic, are

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[1] See p. 196.

the Araliaceae, with their rosettes of large leaves on a stem that is eithe simple or but slightly branched.

Although the above-mentioned types of shrubs or small trees are usuall provided with inconspicuous flowers, a fine show is made, especially i tropical America, by a number of Melastomaceae with flowers of incomparable beauty. The most varied kinds of Rubiaceae, such as Pavetta an species of Psychotria, frequently bear their beautiful thyrsoid inflorescence of coral-red or white flowers on axes glistening in the same tints. If a sepa is large, or blood-red in colour, we are dealing with a Mussaenda (Asia or a Warszewiczia (America). Certain Rubiaceae of the Javanese forest have a highly repulsive but characteristic odour of excrement, for instanc Lysianthus purpureus. Among shrubs or small trees may also readil be found, in America, flowering specimens of Vochysiaceae, Malvacea (Abutilon), Samydaceae (Casearia), Mutisiaceae (Stifftia), Solanacea Mimoseae (Inga, Calliandra), and the beautiful species of Brownia (Caesalpiniaceae) with their bright red cauliflorous clusters of blossom. In tropic Eastern Asia, again, besides the types already mentioned, in particula species of Anonaceae, Ternstroemiaceae (Saurauja) and Myrsineae (Ardisi are conspicuous by their flowers, by which they can easily be determine But nearly always such species with abundant and beautiful blossoms are f less numerous than those whose flowers are few or inconspicuous, as the case amongst Urticaceae, Piperaceae, Euphorbiaceae. One will als find, especially at the height of the rainy season, very many shrubs an small trees without either blossom or fruit.

The herbaceous vegetation is very poorly developed in the darkest pa of the virgin forest; in the better-lighted portions, however, it is ofte surprisingly luxuriant. The Scitamineae are certainly its most promine representatives, not only because of their dimensions and their large brightl coloured inflorescences, but also frequently because of their great abundan (Fig. 135). On the Lesser Antilles I frequently saw Heliconia Bihai, H caribaea, and other species taller than a man (Fig. 178) and formin a dense thicket with their long-stalked leaves, between which the larg inflorescences projected with distichous, red keel-shaped bracts. Sti more striking, and at all events more varied in their appearance, ar in the East Indies, the Zingiberaceae, several genera of which, such Elettaria, Hedychium, Zingiber, Costus, Alpinia, and many species for little woods in the high-forest. Thus, in the forests of Java, one frequentl sees dense expanses of such Zingiberaceae taller than a man, with the stiff distichous shoots allowing no other vegetation to grow between, an their strange inflorescences, like bright red cabbage-heads, as in Cost globosus, Elettaria sp., or like fiery stars, as in Elettaria coccinea, restin with broad bases on the bare soil.

It is in fact a frequent phenomenon in tropical virgin forest that a wid tract of ground should be essentially occupied by one herbaceous species to the exclusion of all others, so that there exists a far greater uniformity in the herbaceous than in the woody vegetation. In the forests of Ceylon and Java I saw certain species of the acanthaceous genus Strobilanthus with juicy brittle stems forming delicately foliaged bushes far exceeding man's height and alone constituting the herbaceous vegetation over immense tracts. I have seen many other herbaceous plants growing socially, though not in such great multitudes, for instance species of Impatiens, Cyrtandra, Elatostema, Selaginella. Grasses are quite insignificant as components of the tropical forests.

Among the more scattered plants, yet seldom absent from the rain-forest, mention may be made of begonias (Fig. 136), which both in America and Asia show great diversity of form, being sometimes small and erect, sometimes climbers reaching high up tree-trunks and rocks; also Aroideae growing on the ground, with their variegated petioles, often reminding one of snakes; finally, as rare features, parasitic Balanophoraceae, saprophytic orchids and Burmanniaceae.

The stems of the trees are covered with a rich flora of the most diverse species of lianes and epiphytes, to which detailed reference will be made hereafter. The most varied forms, often characterized by large expanses of foliage or by splendid flowers, form these epedaphic gardens.

If we attempt to form a general conception of the changing aspects of a virgin forest, the first point that strikes one is the *struggle for light*, and the possibility of carrying on this struggle almost without hindrance is afforded by the *great and incessant humidity*.

The struggle for light indeed prevails in the forests of every zone. Everywhere it drives the vegetation from the shady depths in an upward direction, but this struggle is nowhere so pronounced as in the evergreen forests of tropical districts, in which individuals with slender stems and erect weakly branched boughs eagerly strive after the light and at the same time convey to the light a crowd of guests, including lianes whose weak stems cling firmly to the scaffolding of the trees, and epiphytes which germinate on the branches and thus from the very first secure a suitable degree of illumination.

In the epiphytic vegetation, the struggle for light is the most thoroughly successful, for it clothes the branches of the trees up to their extreme tips with frequently large and even tree-like plants; nor are the leaves spared, for on them both mosses and Algae grow, and occasionally also flowering orchids.

With the epiphytic vegetation also the struggle for light is the most pronounced, and results in great destruction. One may frequently hear a branch of a tree crack and break under the burden of its epedaphic garden which has become too luxuriant (Fig. 134): and the trellis-work of coalescent roots of epiphytic figs or species of Clusia forms often the living coffin within which many a stately tree moulders away.

cinetia and epiphytic Astelia. On the moist ground, Colocasia sp. In the background, across the lake, virgin forest. From a photograph.

Whilst the demand for light draws vegetation upwards, the need fo moisture draws it downwards. Where humidity is decreased, the con formation of the woody plants becomes massive, the crowns of foliag

Figs. 135 and 136. Undergrowth in the South Mexican rain-forest. Upper figure: in the centre, a rubiaceous plant with variegated velvety leaves; to the right and left, Scitamineae. Lower figure: in the centre, Begonia sp. From a photograph by G. Karsten.

To face p. 292]

denser, the foliage-leaves smaller, and all plants, except accommodating mosses and lichens, remain attached to the ground. *The abundance of moisture is the physiological factor of all that is characteristic in the plastic form of the tropical rain-forest.*

As a matter of fact, all rain-forest districts receive not only precipitations at all seasons of the year, but also very large quantities of rain. The rainfall of rain-forest climate amounts to at least 200 cm. annually, but frequently to very much more; 300–400 cm. are not at all rare. The atmospheric humidity is correspondingly great. It seldom sinks much below 80 %, and at night and in early morning it approaches complete saturation.

G. Haberlandt made some observations regarding the humidity of the air at the edge of the virgin forest near Tjibodas. According to these observations, the relative humidity there, even during the bright forenoon, was 80–90 % at 7 a.m.. and in the afternoon always 97–99 %. The lowest relative humidity I observed was on February 12 at noon, with a clear sky, when it was 79 %. The humidity is naturally still greater within the forest, where for weeks together it probably never sinks below 90 %[1].

iii. *TROPICAL RAIN-FOREST IN ASIA.*

An account of an excursion in the tropical virgin forest may afford a clearer picture of the general character of such a forest than any merely general remarks on the subject. I extract from my notebook the following sketch, made on the spot, of a virgin forest on the Gedeh in Java, with occasional references to the forest of Salak, which is close by[2] (Fig. 137).

Compared with a forest of Central Europe the picture is one of marvellous luxuriance but also of confusing disarray. The stems of the trees are very unequal in thickness, they are sometimes supported at their base by plank-buttresses; lianes, the stems of which are seldom thicker than the fist, traverse the air in confused serpentine coils. Between the trees the brush-wood of large-leaved and often gaily flowered shrubs is frequently interrupted by gaps, which are occupied by very juicy herbaceous plants often taller than a man. What at first glance distinguishes the physiognomy of such a forest from that of a European or North American forest is the crowding of the space with foliage and the overpowering preponderance of green colour. The surface of the stems of the trees is almost completely concealed beneath a green envelope of plants. This covering is in places chiefly formed by Freycinetia insignis, an ivy-like climbing species of Pandanaceae, the shoots of which, pendent in elegant festoons and thickly covered with flaccid riband-like leaves, penetrate the crowns of the trees. From the

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[1] Schimper, op. cit., p. 792.

[2] The Gedeh forest lies in a cooler region, at about 1,500 meters, yet still preserves a tropical aspect.

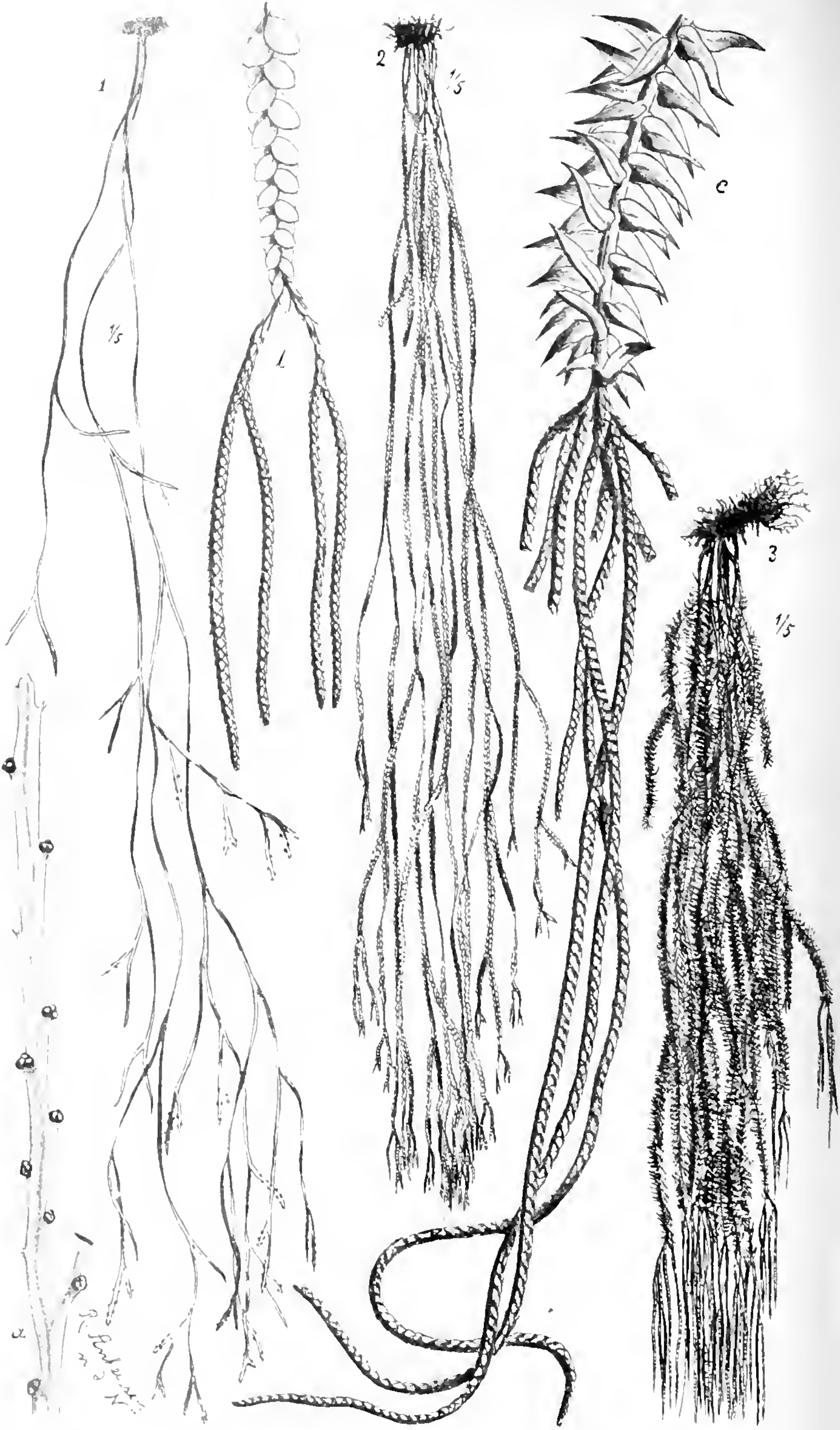

FIG. 138. Epiphytic Lycopodiaceae hanging from the branches of trees in the tropical rain-forest on the Gedeh. 1. Psilotum flaccidum. 2. Lycopodium nummulariaefolium. 3. Lycopodium Phlegmaria. The figures *a*, *b*, *c* show the natural size.

boughs there hang wisps of Lycopodium Phlegmaria, Psilotum flaccidum, and other species of Lycopodiaceae (Fig. 138), two to three meters in length, and mingled with them the pectinate riband-leaves of a Nephrolepis; associated with them are crowds of small ferns. The upper surface of the boughs is an aërial flower-garden, where from amid a low carpet of small orchids, of creeping Peperomia and ferns, and of scarlet-flowered species of Aeschynanthus, there rise shrubby species of Medinilla with rosy panicles of flowers. On the tops of the highest trees often blazes Rhododendron javanicum, visible from afar as a tuft of flaming flowers, but only discoverable within the virgin forest by its fallen corollas. This beautiful plant becomes commoner at higher elevations and is then less restricted to the tops of the trees.

FIG. 139. Asplenium Nidus in the botanic garden at Buitenzorg. Much reduced. From a photograph by Treub.

In many places it is not Freycinetia, but the far more remarkable Asplenium Nidus (Fig. 139) that gives character to the scene within the forest. On all the tree-stems, thick or thin, even on the lianes, its huge funnel-like rosettes are fixed in series one above the other. They fill up all interstices, they prevail over the entire landscape, they are the real victors in the struggle for existence; the rest of the vegetation appears to have no other object than to serve as supports for their funnels and to fill these with dead leaves, until stems break under their weight, or perish—and this the more frequently—owing to disturbances in the metabolism.

Many other types of plants also establish themselves on the bark of the trees. The bases of the trunks are free from large epiphytes, but are wrapped in a thin veil of delicate Hymenophyllaceae. Vaccinium lucidum produces from a tuberous stem its twigs with box-like leaves and small flowers; Ficus diversifolia attracts attention by its leaves, which are ochre-coloured beneath, and by its bright yellow figs of the size of peas. At many other places in Java, but always at a lower altitude, Myrmecodia and Hydnophytum (Figs. 85, 86)—the widely known myrmecophytes with shoots swollen like turnips—are attached to the stems and thicker branches. Mosses and lichens, as epiphytes, are poorly developed in such low-lying forests; their true home is the higher cool, misty region.

In comparison with green, other colours are feebly represented. The tropical rain-forest is however by no means so poor in plants with beautiful flowers as is usually stated, possibly in accordance with Wallace, who probably had in his mind an English meadow, and did not compare forest with forest. Rather is the tropical forest in general richer in colours than a European forest, especially in America, where varied and abundant epiphytic Bromeliaceae are frequently provided with brightly coloured flowers, fruits, or bracts.

Rhododendron javanicum and species of Medinilla have been already mentioned as beautifully flowering plants of the Javanese forest. Many terrestrial shrubs merit the same description, for instance species of the rubiaceous Pavetta, with coral-red umbellate panicles, which in parts of the Salak are quite common. Species of Mussaenda, belonging also to the Rubiaceae, are commoner; in them one of the sepals is developed into a larger dazzling white leaf, whilst the small corollas stand out in perfect orange-yellow. Beautiful beyond comparison is Dichroa Cyanites with its lovely sky-blue and snow-white inflorescences; and the species of the ternstroemiaceous Saurauja, which may be described rather as small trees than as shrubs, recall our cherry-trees by their delicate flowers. The numerous Melastomaceae are more remarkable in Java for their peculiar foliage than for the beauty of their flowers, which, except for Medinilla, are far behind the tropical American species in brightness of colour and size. Tolerably inconspicuous in the low-lying forests are Ardisia semidentata, A. polyneura, and other species, whilst the well-named Ardisia decus-montis forms one of the chief attractions of the more elevated temperate rain-forest[1].

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[1] See Sect. IV.

Species of Rubus, for instance R. glomeratus, R. chrysophyllus, R. alceaefolius, are more remarkable for the beauty of their foliage than of their flowers; in addition they first appear as essential components of the vegetation in forests situated higher up. Small trees and shrubs with quite inconspicuous flowers, on the other hand, are very strongly represented both as regards number of species and number of individuals. To these belong representatives of the Urticaceae with loose pendulous greenish inflorescences, such as species of Boehmeria and of Laportea; species of Piper with erect taper-like inflorescences; Euphorbiaceae, like species of Croton and Phyllanthus; and Lasianthus purpureus with small violet flowers. Finally, as essential constituents of the vegetation in the shade, may be mentioned small palms of the genus Pinanga, Pandanus furcatus, and numerous tree-ferns.

The herbaceous vegetation displays a marvellous wealth of forms. Its most prominent constituents are the social Zingiberaceae, the thickets of which have already been described. Here and there appears a fine Musa not in blossom. Wide tracts are covered by a dense shrubby Strobilanthus, the transparent stems of which break like glass as one passes among them, and the delicate foliage of which is rendered gay by fairly large bright red flowers. In other places the herbaceous vegetation is hardly up to the knee, and is chiefly composed of Cyrtandra nemorosa and a species of Elatostema; from the dark green level surface there rise up isolated taller plants, such as the large-leaved Begonia robusta, Pollia thyrsiflora, more conspicuous for its cobalt-blue berries than for its white inflorescences, Dianella montana, which agrees with the last-named plant in the rare colour of its fruit and in that of its flowers, Disporum multiflorum with pendent violet campanulate flowers, Polygala venenosa with large yellow flowers, and many others.

If with the hand we push aside the leaves of the herbs clothing the soil, we can see, between the turgid brittle stems, the soil covered with decayed sodden leaves. The gaps between the plants appear large, though they are completely arched over by the canopy formed by the foliage of the herbs, and they support no vegetation that is visible to the naked eye. One is however surprised to find a flora of flowers which are invisible from above the leafy roof, and spring in particular from the stalks of Cyrtandra nemorosa, but also from the stems of Saurauja cauliflora, which produces its dense red and white bunches of flowers only at its base, quite hidden among the herbage.

Trees are the least striking constituents of the rain-forest; the plank-buttresses alone distinguish many of them at first glance from the trees of a European forest. The finest tree in these forests is Altingia excelsa, one of the Hamamelidaceae, the rasamala of the natives, which attains a maximum height of about 60 meters and a diameter of stem of 112 centimeters, but is usually from 40 to 45 meters in height [1]. This tree is best appreciated from a distance, when the forest is viewed from above, as its crown far overtops the other trees. The puspa, Gordonia Wallichii, one of the Ternstroemiaceae, is also very common, and, when in flower, appears from a distance like a mass of snow; in the interior of the forest it betrays its presence by its numerous fallen petals. Species of Ficus, which mainly grow in the forests situated at the lowest levels, are easily recognized by their aërial roots, and are frequently cauliflorous.

According to Junghuhn, the tallest trees in these forests are Canarium altissimum, Thespesia altissima, Dipterocarpus trinervis and D. retusa, Epicharis altissima and E. cauliflora. The smaller species of trees are much more diversified. As especially common Junghuhn mentions representatives of the Myristicaceae, Tiliaceae, Sapotaceae, Compositae (Vernonia javanica), Rubiaceae, Euphorbiaceae, Byttneriaceae, Lauraceae (Cinnamomum), Mimosaceae [2].

Kurz distinguishes two forms of rain-forest in Pegu, *closed* and *open* forest, corresponding to two grades of humidity:—

The *closed evergreen forest* forms a dense mass of vegetation 150-200 feet high, in which four or five tiers may be distinguished:—

Of the loftiest trees overtopping the general leaf-canopy of the forest, some shed their leaves during the dry season, for instance species of Sterculia, some Datiscaceae (Tetrameles), Leguminosae (Parkia, Albizzia, Acrocarpus, Pterocarpus, Xylia), Anonaceae (Guatteria), Anacardiaceae (Swintonia), Lythraceae (Duabanga), Artocarpaceae (Artocarpus), Tiliaceae (Pentace). Evergreen species of giant trees are among the following: Dipterocarpaceae (Dipterocarpus, Parashorea, Hopea, Anisoptera), Sapotaceae (Payena), Guttiferae (Garcinia), Urticaceae (Antiaris).

The large trees of the middle tier are for the most part evergreen. Among these in particular appear single species of Anonaceae (Mitrephora), Sterculiaceae (Pterospermum), Burseraceae (Bursera), Meliaceae (Amoora, Cedrela, Disoxylum, Sandoricum), Celastraceae (Kurrimia), Cornaceae (Marlea), Bignoniaceae (Stereospermum), Verbenaceae (Vitex), Leguminosae (Pithecolobium, Adenanthera, Dalbergia, Albizzia), Sapindaceae (Sapindus), Lythraceae (Lagerstroemia), Anacardiaceae (Mangifera, Semecarpus), Guttiferae (Xanthochymus), Moraceae (Ficus), Diospyraceae (Diospyros), Lauraceae (Litsea), Euphorbiaceae (Bischofia, Trewia), Malvaceae (Hibiscus), Sterculiaceae (Sterculia, Pterospermum), Tiliaceae (Elaeocarpus), Podocarpus, and many others.

The third tier is composed of small evergreen trees, at the most thirty feet high, and exhibits a still more confusing systematic composition than the higher tiers. Among them are Violaceae (Alsodeia), Lauraceae (Litsea, Phoebe, Cinnamomum), Bixaceae (Hydnocarpus), Hippocrateaceae (Siphonodon), Euphorbiaceae (Cleistanthus, Ostodes, Baccaurea, Aporosa, Excoecaria, Ântidesma), Rutaceae (Micromelum), Bignoniaceae (Spathodea), Tiliaceae (Elaeocarpus), Sapindaceae (Erio-

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[1] Koorders en Valeton, op. cit., I, p. 204. The tallest tree measured by these authors was 58 meters, and the height to the first branch 40 meters.

[2] Junghuhn, op. cit., I, p. 315.

glossum, Lepisanthes, Cupania, Euphoria), Meliaceae (Aglaia, Heynea), Anacardiaceae (Drimycarpus, Semecarpus), Myrsinaceae (Maesa, Ardisia), Urticaceae (Celtis), Moraceae (Ficus), Leguminosae (Millettia, Erythrina, Dalbergia), Myrtaceae (Eugenia), Melastomaceae (Memecylon), Anonaceae (Cyathocalyx, Goniothalamus, Saccopetalum), Cupuliferae (Castanopsis), Diospyraceae (Gunisanthus, Diospyros), Guttiferae (Garcinia), Ternstroemiaceae (Eurya), Tiliaceae (Grewia), Rutaceae (Zanthoxylum, Glycosmis, Murraya), Simarubaceae (Picrosma), Ochnaceae (Ochna), Ilicineae (Ilex), Celastraceae (Euonymus), Verbenaceae (Vitex), Myristicaceae (Myristica), and many others. Various palms, bamboos, and Pandanus furcatus also belong to this tier.

Among lianes appear Malvaceae (Hibiscus), Combretaceae (Illigera, Calycopteris), Anonaceae (Artabotrys), Leguminosae (Dalbergia, Acacia, Bauhinia), Rhamnaceae (Colubrina, Zizyphus, Gouania, Ventilago), Araceae (Pothos, Scindapsus), Ranunculaceae (Naravelia), Acanthaceae (Thunbergia), Convolvulaceae (Porana), Orchidaceae (Vanilla), Oleaceae (Jasminum), Menispermaceae (Tinospora), Rubiaceae (Ancistrocladus, Uncaria), Vitaceae (several species of Vitis), Palmae (three or four species of Calamus), and many others.

Among erect shrubs appear Violaceae (Alsodeia), Rubiaceae (Mussaenda, Morinda, Ixora), Urticaceae (Boehmeria), Verbenaceae (Clerodendron), Anonaceae (Unona), Capparidaceae (Capparis), Myrsinaceae (Maesa, Ardisia), Diospyraceae (Diospyros), Connaraceae (Connarus), and many others.

Herbaceous plants are scanty. In the dense parts of the forest the soil is covered only with decaying leaves, stems of trees, and other débris; in lighter places, however, numerous individuals of species of Strobilanthus and other Acanthaceae, some Aristolochiaceae (Bragantia), Urticaceae (Elatostema), Piperaceae (Piper), Rubiaceae, Araceae, Liliaceae (Dracaena, Dianella), Commelinaceae (Pollia), a few Cyperaceae and Gramineae, many Scitamineae, and still more ferns. The trees support on their trunks and branches, as epiphytes, Orchidaceae, Cyrtandreae.

Mosses are in general very poorly represented except as epiphyllous plants, in which state they are plentiful.

Lichens occur on bamboos and on the top branches of the trees.

Fungi are numerous, in particular during the rains.

Some Algae (Chroolepus, Scytonema) occur as epiphytes on stems and leaves.

The *open evergreen forest* largely agrees with the closed forest as regards the composition of its flora, but is considerably poorer in forms. There are only three or four tiers of vegetation, and but few lianes and epiphytes occur, so that this forest is less impenetrable.

iv. *TROPICAL RAIN-FOREST IN AFRICA.*

The description of the *West African rain-forest* on the Loango coast given by Pechuel-Lösche is picturesque rather than scientific; yet it affords a vivid picture of the physiognomy of the West African forest (Fig. 140).

'In its fullest development it prevails over the mountain heights, slopes, and valleys, as well as over the plains along many water-courses; in particular it lends incomparable beauty to the banks of the Kuilu river, which are composed of very fertile alluvial land. It is equal to the grandest forests that I have marvelled at in

Fig. 140. In the West African rain-forest. Loango coast. After Pechuel-Lösche.

other countries. Yet it does not contain, as for instance do the forests of Brazil, Guiana, and the West Indies, large and small forms of plants crowded together in rich confusion, so as to utilize the available space to the utmost conceivable degree; in it there is rather a rich repetition of certain forms developed into giants which invest it with an imposing uniformity.

'It admits the visitor, as it were, into a vast, green, vaulted hall. The roof of foliage is raised aloft twenty meters above the ground by countless columns, often marvellous in shape. Huge stems, without a branch, straight as an arrow and cylindrical, and mingled with them weaker ones that are gnarled, bent, and repeatedly branched, all lose themselves overhead in the loose mass of leaves, which is traversed at many places by richly foliaged lianes. A subdued, mysterious light enfolds the bright-barked, silvery-grey or brownish boles, whilst here and there, as in a church, the sun's rays play in quivering golden beams. Evergreen trees as tall as our finest German trees constitute the chief mass of the forest, with their tops closely interlaced. Above this dense leaf-canopy that is interwoven with climbing plants, mighty deciduous trees, resembling our beech-tree, project and do not display their finely branched crowns before a height of thirty to fifty meters. Most of the trunks exhibit in most striking manner a tendency to produce buttresses at their base[1].'

After a detailed account of the buttresses and of the lianes, the author continues: 'Epiphytes never become attached to the bright smooth stems; even mosses are relatively uncommon. The underwood is scantily represented, only dense collections of one leafy plant with straight, very long, climbing stems occupy certain tracts. A layer of dry foliage covers the ground and, embedded in it, fallen pieces of wood lie mouldering. Wherever one of the towering giant-stems, in a crashing fall, has crushed all the forest-growth beneath, daylight streams through the wide gap in the leaf-canopy and humbler forms of plants have established themselves, whilst young trees struggle upwards in keen rivalry. . . . Even though the mass of foliage, formed of layers piled one above the other, appears to constitute a completely closed cover to all that stands beneath, yet its texture is loose; the leaves for the most part are arranged in tufts at the end of the twigs, and the latter are not so much subdivided as in our German forest-trees. Hence, everywhere, rays of light can pass through the leaf-canopy, and, even though repeatedly interrupted, eventually reach the ground.'

The *East African rain-forest* is more poorly developed than is the West African, both in expanse and luxuriance of vegetation; it appears to be chiefly confined to the mountain gorges. The flora of the rain-forest of Usambara has been studied by Engler:—

Among its already known trees, the following among others are remarkable for their height or other qualities:—Mesogyne insignis; Paxiodendron usambarense (Lauraceae); Albizzia fastigiata; Sorindeia usambarensis (Anacardiaceae); Stearodendron Stuhlmannii (Guttiferae); Chrysophyllum Msolo (Sapotaceae). These trees are 30 to 60 meters high. Smaller trees are, for example, Ficus Volkensii (15 meters); Myrianthus arborea (10 meters, Urticaceae); Dasylepis integra (up to 10 meters, Bixaceae); Oxyanthus speciosus (up to 10 meters, Rubiaceae). As

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[1] Pechuel-Lösche, op. cit., pp. 142, 145.

shrubs and dwarf trees of the underwood are found species of Piper, Cassia, Brucea (Simarubaceae); Pycnocoma (Euphorbiaceae), Allophylus (Sapindaceae), Alsodeiopsis (Olacaceae), Haronga (Hypericaceae), Oncoba (Bixaceae), Clerodendron (Verbenaceae), Whitfieldia (Acanthaceae), Pavetta, Chasalia and Psychotria (Rubiaceae), Vernonia (Compositae), and a low tree-fern (Alsophila Holstii). The herbaceous vegetation is chiefly formed of ferns, to which may be added a few Scitamineae, Urticaceae, Euphorbiaceae. Lianes are rare in the dense forest; epiphytes consist chiefly of ferns, in a less degree of orchids and species of Peperomia[1].

v. *TROPICAL RAIN-FOREST IN AMERICA.*

The tropical virgin forest of America has very properly acquired the highest reputation. The ordinary descriptions of tropical virgin forest chiefly refer to it and are taken from the works of Humboldt, Martius, Schomburgk, and St.-Hilaire. I have visited the virgin forest in several parts of tropical America, the Antilles, Venezuela, and Brazil. I found it, in many ways, far more majestic than in Java, owing to the larger dimensions of the trees, the greater thickness of the liane-stems, and the greater abundance of epiphytes. The essential features of the physiognomy are however, nearly identical in both lands, in accordance with the similarity of environment in both cases. Yet not only in the West Indies, but also in Brazil and South Mexico—and probably in other parts of America—there is an additional characteristic that I did not find in Java and which has not been recorded in regard to the Cis-gangetic Indian forests. This is the extraordinary wealth in aërial roots descending vertically and unbranched through the air, the 'cipos' of the Brazilians, which form tightly stretched cords connecting the climbing and epiphytic Araceae and Clusiaceae with the nutritive soil (Fig. 152).

Among the characteristics of the flora of the tropical American rain-forest, the most striking is the presence of Bromeliaceae, which are nearly always epiphytic and usually form an important constituent of the vegetation, remarkable for their peculiar forms and splendid colouring. The epiphytic Cactaceae, in particular species of Rhipsalis, are seldom absent and are easily recognizable.

In opposition to a widespread error, it must be insisted that palm-trees are by no means necessary as prominent constituents of the tropical rain-forests, in either the New World or the Old World. Representatives of the family are possibly present as a rule. These are, however, for the most part small forms, or prickly palm lianes. Tall erect palms are usually feebly represented in the forest, for instance in Java, but in Dominica I have seen Euterpe oleracea, and in South Brazil Euterpe edulis (Fig. 141), growing abundantly in the virgin forest. Fig. 130 shows a forest in Samoa, rich in palms.

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[1] Engler, op. cit., p. 82.

FIG. 141. From the tropical American rain-forest, Blumenau, Brazil. On the left: Schizolobium excelsum; leafless. On the right: Euterpe edulis. In the centre: a tree-fern. From a photograph by H. Schenck.

To face p. 302]

vi. *TROPICAL RAIN-FOREST IN AUSTRALIA AND POLYNESIA.*

A description has been written by Tenison-Woods of the tropical forest that extends from the northern coast of Australia towards the south-east along the coast mountains of Queensland (Fig. 142) beyond the tropic of Capricorn. Unfortunately I have been unable to see Tenison-Woods'

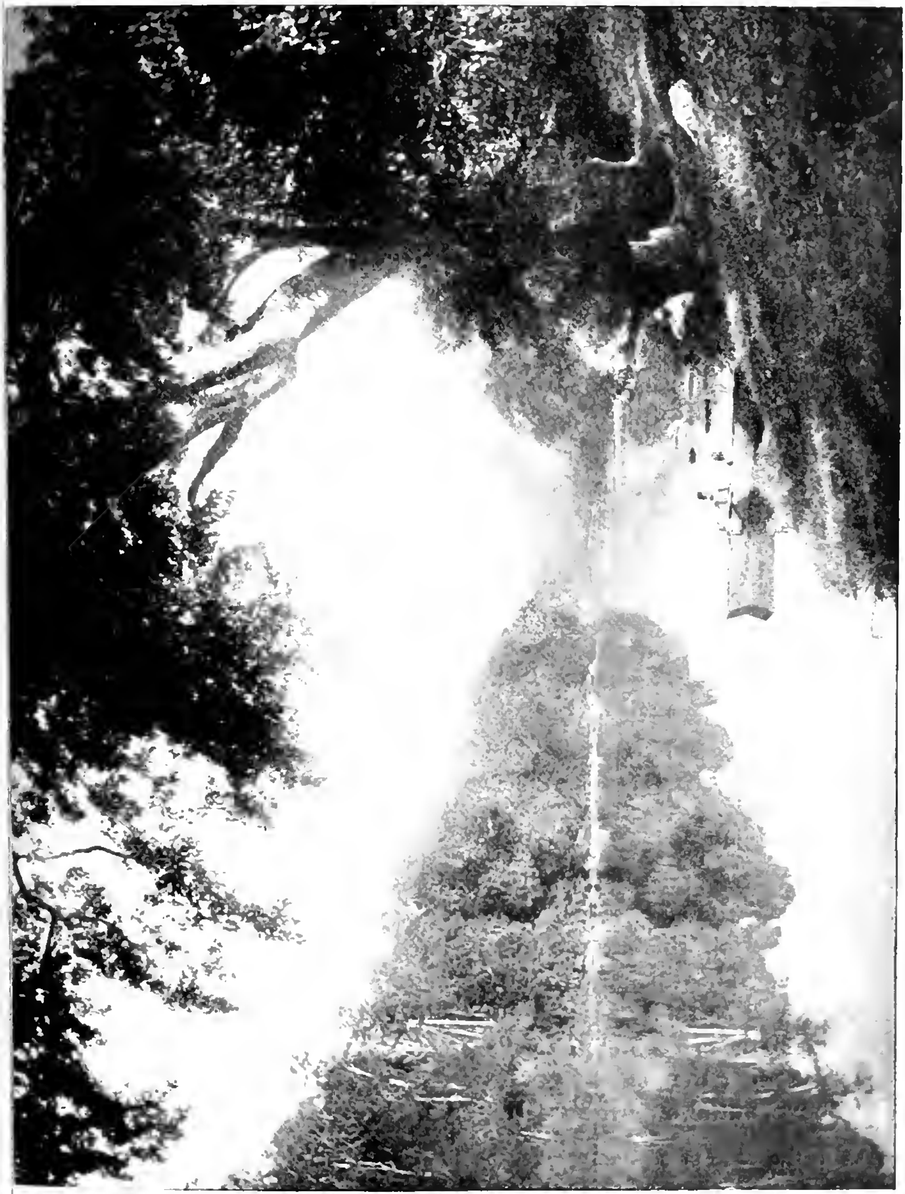

FIG. 142. Tropical rain-forest in Queensland. Musgrave River. From a photograph.

work, and know it only from the abstract given by Drude[1]. Of the luxuriance of the rain-forest in Samoa a vivid representation is given in Fig. 130.

3. OECOLOGICAL CHARACTERISTICS OF PLANTS GROWING IN THE RAIN-FOREST.

The plants of the evergreen tropical rain-forest are markedly hygrophilous, and, with the exception of some epiphytes which are exposed to quite peculiar conditions of existence, they possess a corresponding structure. All the features that in an earlier chapter we recognized as characteristic of the vegetation in a very moist climate, such as feeble formation of cork and of fibres in the axial parts, ombrophilous foliage, hydathodes, dripping-points to the leaves, are strongly marked in them. The last-mentioned peculiarities of hygrophilous plants appear to be more strongly developed in the tropics than in the temperate zones, and, for the most part, have been first observed there.

In the following paragraphs a description will be given of some of these peculiarities of the tropical rain-forest, which without being entirely absent from other zones yet in the tropics alone attain great importance and determine the oecological features of the vegetation.

i. *TREES AND SHRUBS OF THE RAIN-FOREST.*

The stems of the trees whose crowns form the leaf-canopy that is usuall invisible from below are of very unequal thickness, and usually thinner tha in less dense and humid virgin forests. Many of them are supported a their base by *buttresses*, which sometimes consist of *cylindrical roots* spring ing from the stem at some distance from the ground, as in species o Cecropia and Myristica: but much more frequently these buttresses assum the form of *plank-like outgrowths* of the base of the trunk and of the upper most roots, and they may be termed *plank-buttresses* (Fig. 143). Thes plank-buttresses, radiating from the base of many tree-trunks, reach up t a height mostly of one or two meters above the ground, and thus for deep niches, in which there is not infrequently ample space for two o three men. The thickness of the planks is often so small that they ca be employed as tables without any further manipulation. Such buttresse are by no means common to all the trees of the rain-forest, but to th minority only: they chiefly occur on very tall stems that are comparativel thin above, but also on the massive stems of fig-trees.

As in the case of so many other phenomena of tropical vegetation, the botani garden at Buitenzorg affords a splendid opportunity for studying plank-buttresse of different shapes, and indeed, as is not usually the case in the forest, on tree

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[1] Drude, Pflanzengeographie, p. 495.

f known systematic position. The most remarkable of these structures appear, s Haberlandt has already stated, on trees of the family of Sterculiaceae. In my otes I find Sterculia spectabilis, Miq., Firmiana colorata, R. Br., and Pterygota Roxburghii, Schott and Endl., as specially remarkable. I have also recorded as vorthy of note, Dysoxylum mollissimum and D. Kadoya (Meliaceae); Urostigma ltissimum and Cecropia cyrtostachya (Artocarpaceae); Spathodea campanulata Bignoniaceae); Vitex timorensis, V. Cofassus, V. leucoxylon (Verbenaceae); most pecies of Terminalia (Combretaceae). No plank-buttresses are possessed by tall rees belonging to the families Sapindaceae, Apocynaceae, Sapotaceae, or to species f Myristica. Many species of the latter genus have prop-roots. Brandis mentions ank-buttresses in connexion with Bombax malabaricum and species of Vitex, ntiaris, Lagerstroemia, Hymenodictyon, Nauclea, and others.

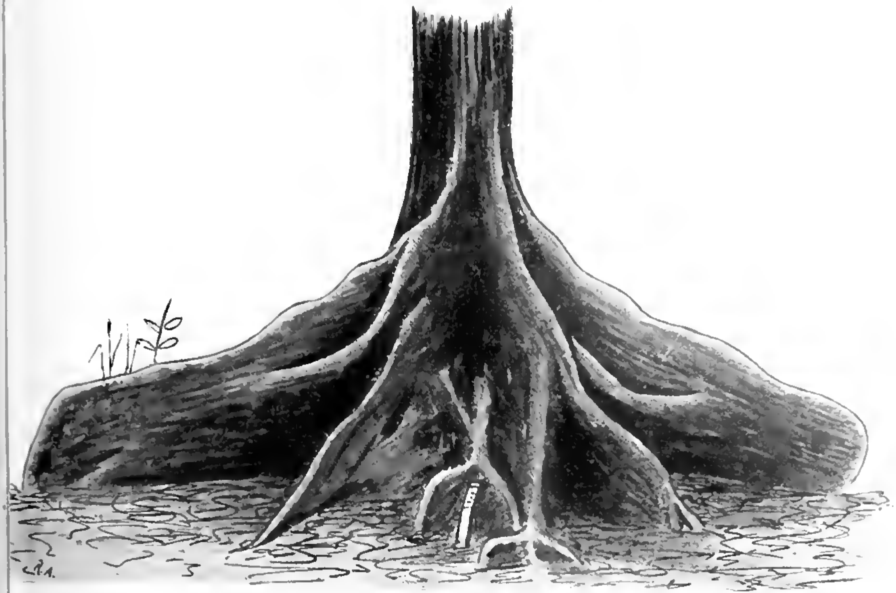

FIG. 143. Sterculia sp. in the botanic garden at Buitenzorg. Base of stem with plank-buttresses. After Haberlandt.

The plank-buttress is a peculiarity of trees in a tropical climate with undant rainfall. It is not limited to the evergreen rain-forest, for it also curs in the deciduous monsoon-forest (Fig. 189), but is not found in less mid districts. The amount of rainfall necessary for its appearance is not t ascertained. The physiological causes of the phenomenon and its gnificance to the life of the tree are still obscure.

Owing to the prejudicial effect of humidity on the formation of cork, *the rk is only poorly developed* on most of the tree-stems in the rain-forest. ems in the rain-forest never exhibit scales of bark of such surprising thickness as occur in dry tropical districts. They are, on the contrary, mor frequently quite smooth, or marked by shallow longitudinal and transvers fissures. Indeed, the formation of cork is often s poor that moderately thic stems are green owing to th chlorophyll of the cortica layers being visible throug it. It is possible that the phenomenon of cauliflory, whic will be described further o is connected with the feebl development of bark.

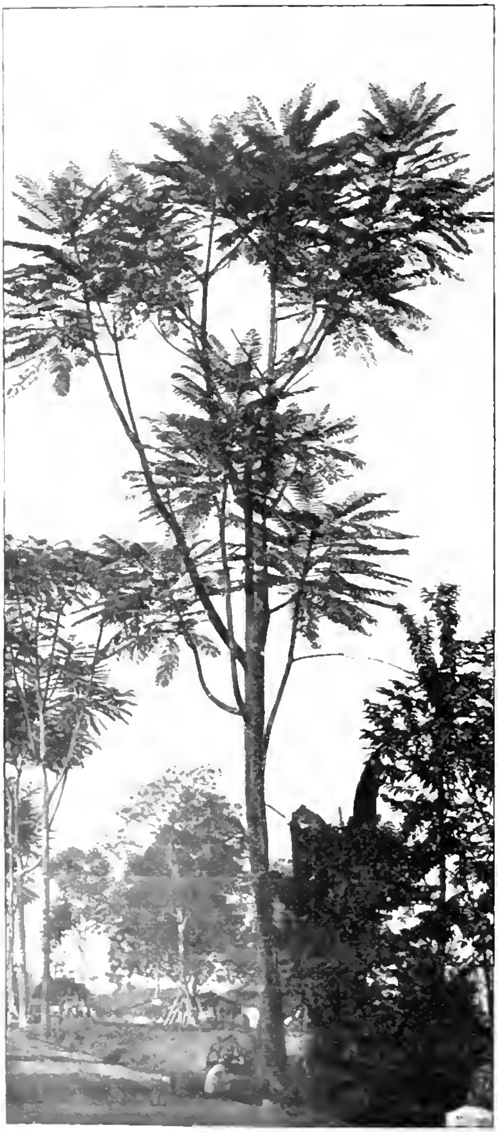

Fig. 144. Schizolobium excelsum. After a photograph by Treub.

Rarely in the forest ha one an opportunity of gaining an insight into the precise arrangement of th branches, for to achieve th the tree must be felle In this respect again th Buitenzorg garden giv ample opportunity for stud although it should alwa be remembered that, besid trees of the rain-forest, also contains trees of deciduous forest, of littor forest, and even of savanna The very striking forms umbrella-like trees are qu exceptional in the evergre virgin forest—and even th they are usually giants the forest, whose crow tower above the gene leaf-canopy—whilst the st more striking forms of t trees with their branches i tiers seem to be entir absent from them. Su forms of trees are far more characteristic of well-lighted, deciduous, m or less xerophilous forest, of savannah, and of the highest forest regi in the mountains, in short, of a dry climate. The crowns of the tr in the virgin forest are as a rule oblong, more or less ovoid in shape, or very irregular.

In the careful descriptions of Koorders and Valeton[1], the form of the crown is given in the case of the majority of the trees described. In nearly all trees of the evergreen forest of Java this is described as ovoid, or irregular. Trees with umbrella-shaped or flattened hemispherical crowns are represented by Parkia biglobosa (commoner in thin deciduous forests), Tarrietia (a rare forest giant with a somewhat flattened crown), Dysoxylum mollissimum (a rare forest giant reaching 58 meters in height, with an irregular umbrella-shaped crown), and Cedrela febrifuga (a forest giant with a hemispherical crown, also occurring in thin deciduous forests).

The trees of the tropical rain-forest are far less branched than those of forests in temperate zones. Many tropical trees remain quite unbranched, for instance tree-ferns, cycads, palms, and many small dicotyledonous trees, such as Carica Papaya, species of Theophrasta, and Araliaceae. Many commence to branch only when they are two or more meters in height and have a stem as thick as one's fist, as in species of Albizzia, Schizolobium and other Leguminosae, Cecropia, and the like; the branches that appear subsequently either remain unbranched, or produce merely a few simple lateral axes (Figs. 144, 145). Frequently, even in very lofty trees, only three grades of branches occur, for instance in species of Strombosa, Cinchona.

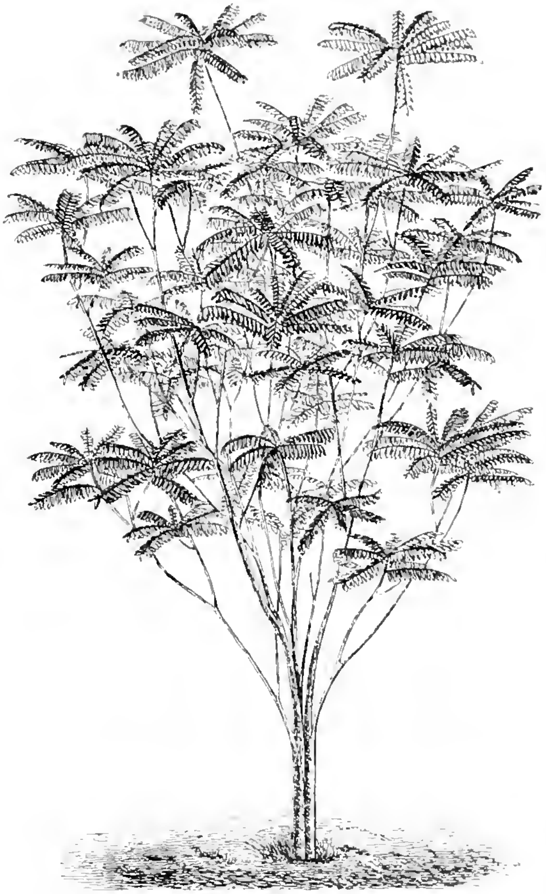

FIG. 145. Averrhoa Bilimbi. A tree-like oxalidaceous plant, about 8 meters high, in the botanic garden at Buitenzorg. From a photograph. Reproduced from Engler and Prantl's Die natürlichen Pflanzenfamilien.

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[1] Koorders en Valeton, op. cit., I-III.

Jagera, Hopea. In the case of European forest trees, on the other hand, higher grades, usually 5–8, of branches prevail (Wiesner).

> 'Even in the largest trees I have seen in the tropics, the number of grades of branches never exceeded five (Ficus elastica, which has often only two to four, F. religiosa, Pterocarpus indica, Altingia excelsa, Grevillea robusta). The numerous observations of Koorders lead to the same result; exceptionally, however, higher grades of branches occur. The complication of the branching concerns only the twigs that immediately bear the foliage. Those portions of the axes that have become leafless are throughout only feebly branched.'

The leaves of the trees in the rain-forest are highly diversified, frequently of firm leathery consistence and very glossy, but seldom are they finely pinnate or felted with hairs. They are, as Wiesner has explained in detail[1], usually set obliquely as regards the zenith, often aggregated in tufts at the ends of long bare axes (Fig. 145).

The *shrubs* of the rain-forest, like the trees, are for the most part sparsely branched when compared with the shrubs of the forests of Central Europe. Their leaves are usually large, delicately membranous, seldom coriaceous.

ii. *TERRESTRIAL HERBS OF THE RAIN-FOREST.*

The terrestrial herbs (Figs. 135, 136) are sometimes erect, sometimes creeping, feebly branched, and nearly always provided with elongated axes in accordance with the great humidity dense rosettes do not occur Wherever the shade is denser the soil bears only delicate weeds, which by their weak roots, their large and excessively delicate leaves, the scant development of fibres and of vessels in their turgid brittle stems, exhibit i the clearest manner the influence of moisture in both the soil and air Various Rubiaceae and Urticaceae are illustrations of these features.

Many herbs growing on the ground of the virgin forest are provided wit wonderful markings on their foliage, in the way of white, silvery, golden, o red spots and stripes, which have raised many of them to the rank of choic ornamental plants, like species of Begonia, of Marantaceae, of Orchidaceae Stahl considered these coloured flecks as devices for increasing transpiration. His discussion of this subject is sagacious and suggestive, but owing to the want of quite conclusive experiments, is still too hypothetica to merit detailed consideration.

Not unfrequently, particularly in very moist and shady spots, the foliag of the herbs exhibits the velvety surface (Fig. 24), the connexion of whic with the concentration of light and furtherance of transpiration has alread been described[2]. In similar places, the foliage of many plants, especiall species of Selaginella and Trichomanes, glistens with a metallic blu lustre.

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[1] Wiesner, op. cit., pp. 73-4.

[2] See p. 19.

A peculiar form of vegetation is produced by the Hymenophyllaceae (Fig. 146), never absent from the deepest shade of the forest, which, though they often clothe the bases of tree-trunks as epiphytes, yet also occur on the ground and on rocks, and in any case do not assume the peculiar characters of epiphytic plants. The Hymenophyllaceae (Hymenophyllum and Trichomanes) illustrate the great humidity of the virgin forest better than any other plants, as they have many features in common with aquatic plants. Their delicate leaves usually consist of only one layer of cells, excepting over the veins, absorb water by their whole surface, and shrivel up quickly whenever the atmosphere is not wellnigh saturated with water-vapour. As in aquatic plants, the greatly reduced roots play merely a subordinate part as organs of fixation, or may be entirely absent[1].

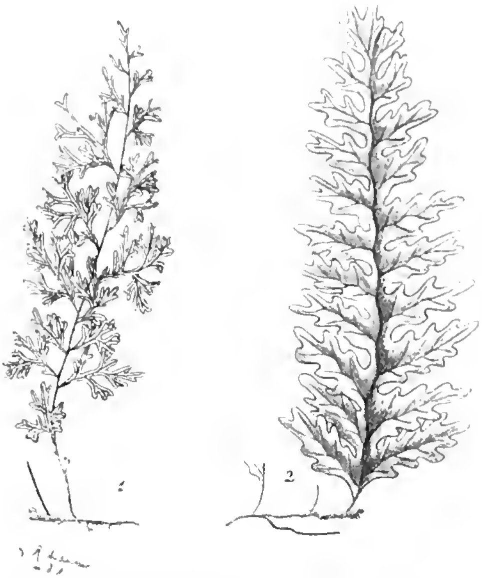

FIG. 146. Hymenophyllaceae which are epiphytic on tree-ferns in the tropical rain-forest of America at Blumenau, South Brazil. 1. Trichomanes angustatum, Carm. 2. Trichomanes sinuosum, Rich.

iii. *LIANES OF THE RAIN-FOREST.*

The most peculiar components of the rain-forest, those which first strike travellers and are most frequently mentioned by them, are *lianes* and *epiphytes*. Both these forms of vegetation, it is true, also occur in other forests, and are not confined to the tropics, but, as has already been shown[2], the tropical rain-forest is the original home of nearly all the higher epiphytes, even of those that occur in open dry tracts of country, and woody lianes have in the tropical rain-forest, if not their sole place of origin, yet certainly the site of their most luxuriant development and of their greatest diversity of form. Lianes and epiphytes exhibit a connexion, to this extent, that a forest rich in woody lianes is rich usually in epiphytes also, and the representatives of both these guilds frequently belong to the same families. The origin of both forms is to be traced back to the same factors, the struggle for light assisted by abundance of moisture; they are connected by intermediate forms, and many epiphytes have apparently been evolved from lianes.

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[1] See in particular the cited works of Prantl and Mettenius.

[2] See p. 198.

The oecological peculiarities of lianes, so far as their general features are concerned, have been described in a former chapter[1], but the few types, distinguished there according to their modes of climbing, give no idea of the rich diversity in the forms of tropical lianes, and the diagnostic characters which were considered are usually withdrawn from view within the forest, excepting in the case of root-climbers. Many lianes belonging to quite different oecological types closely resemble one another in their lower portions, which alone are visible, whilst others are easily recognizable by their mode of growth, and in particular by the shapes of their stems[2].

Fig. 147. Gnetum scandens on a coconut palm. From a photograph by G. Karsten.

Climbing palms form one of the most characteristic and frequent types among lianes of the tropical rain-forest; they include types of Calamus and some allied small genera in tropical Asia and Australia, species of Oncocalamus and other Raphieae in tropical Africa, and of Desmoncus in tropical America. The slender, tough, and often prickly stems, well known as 'rattans,' in many tropical forests form extensive confused masses (cane-brakes), which can be cut through only with the greatest trouble by means of the bill-hook, and which lie in immense coils on the ground. One portion of a stem that had been torn down was measured by Treub, and was 240 meters in length (Fig. 148).

Their manner of climbing is even more characteristic of palm-lianes than is their mode of growth. In Calamus and the Raphieae, the rachis of the leaf is prolonged into a long flexible flagellum, provided with hooked thorns, and this, as an organ resembling a tendril but not irritable, most effectively fixes the leafy end of the shoot to the branches of the supporting tree. When once the summit of the supporting tree has been reached by the liane, and hence its further growth upwards is prevented, the older

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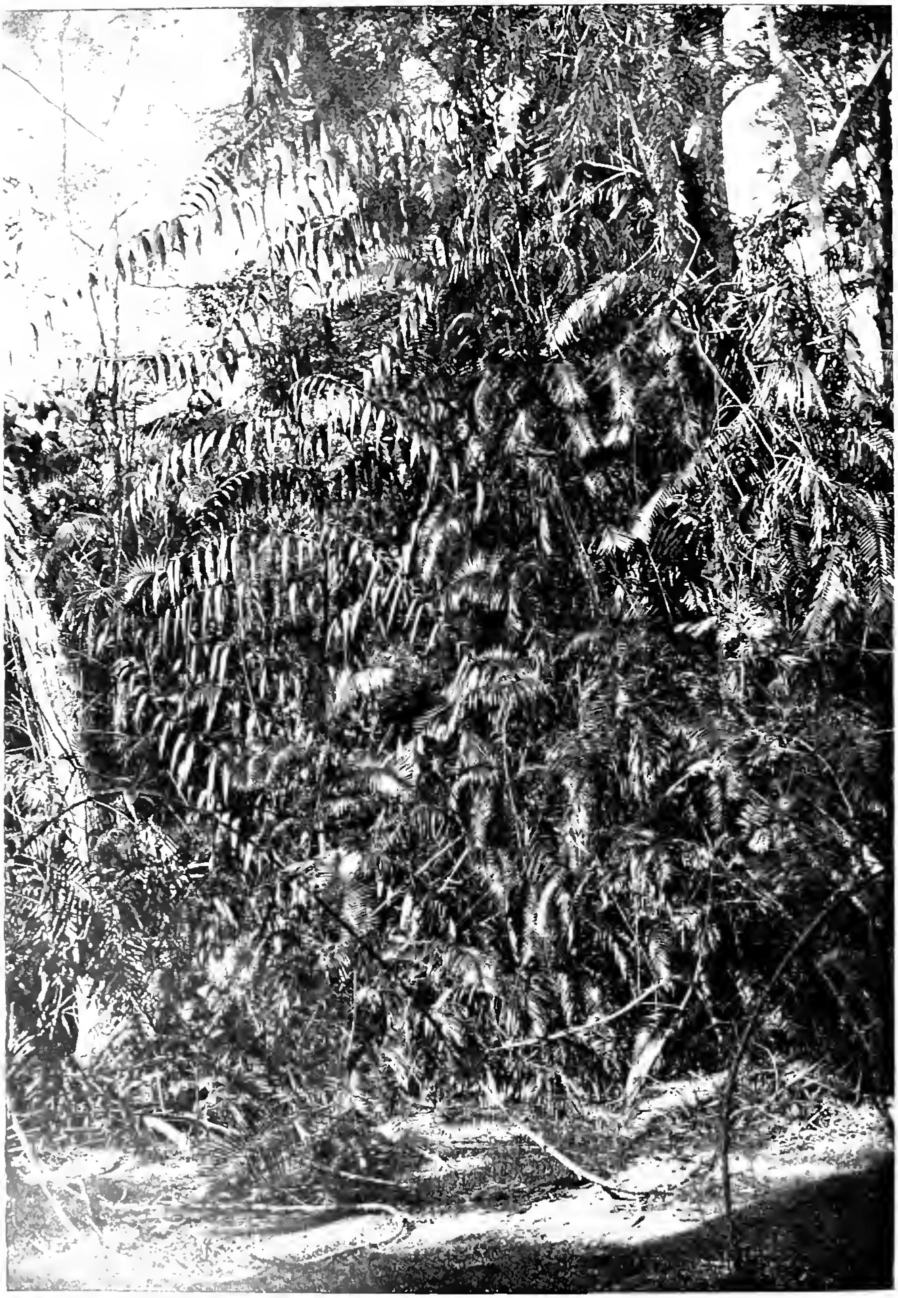
[1] See p. 192.

[2] See Schenck, I and II, regarding the subject of this and the following paragraphs.

FIG. 148. A liane in the botanic garden at Peradenyia. From a photograph.

To face p. [illegible]]



[illegible] the botanic garden at Buitenzorg.
From a photograph by M. Treub.

portions of its axis that have lost their leaves slip down owing to their weight, and finally rest on the tree in the form of the coils already mentioned. These coils are well seen in Fig. 149.

Still more peculiar are the climbing devices of the American species of Desmoncus, which I studied closely, particularly in the forests of Trinidad. In this case the topmost pair of pinnae are converted into long, powerful, recurved thorns, so that the elongated rachis resembles a harpoon.

Climbing palms may be oecologically considered as the highest stage of the class of *scramblers* (Fig. 150), to which many other lianes in the rain-forest belong, Bambuseae among others. Many species of Bambuseae climb high up the tree; but more frequently they remain within reach of the underwood, and fix themselves to the branches of the smaller trees and shrubs by means of their recurved, long and thorn-like vegetative buds. Special climbing organs are not therefore present in this case, but some peculiarities of the buds, in particular their curvature, may have arisen as adaptations for climbing.

FIG. 150. Edge of forest in Amboina with a palm-liane. From a photograph by G. Karsten.

Cyclanthaceae and Pandanaceae, which are allied to palms, also possess lianoid representatives. Of Cyclanthaceae we find lianes in species of the genera Carludovica and Sarcinanthus (tropical America); of Pandanaceae, numerous species of Freycinetia in the Malay Archipelago and Polynesia are lianes. All three genera consist entirely or partially of root-climbers,

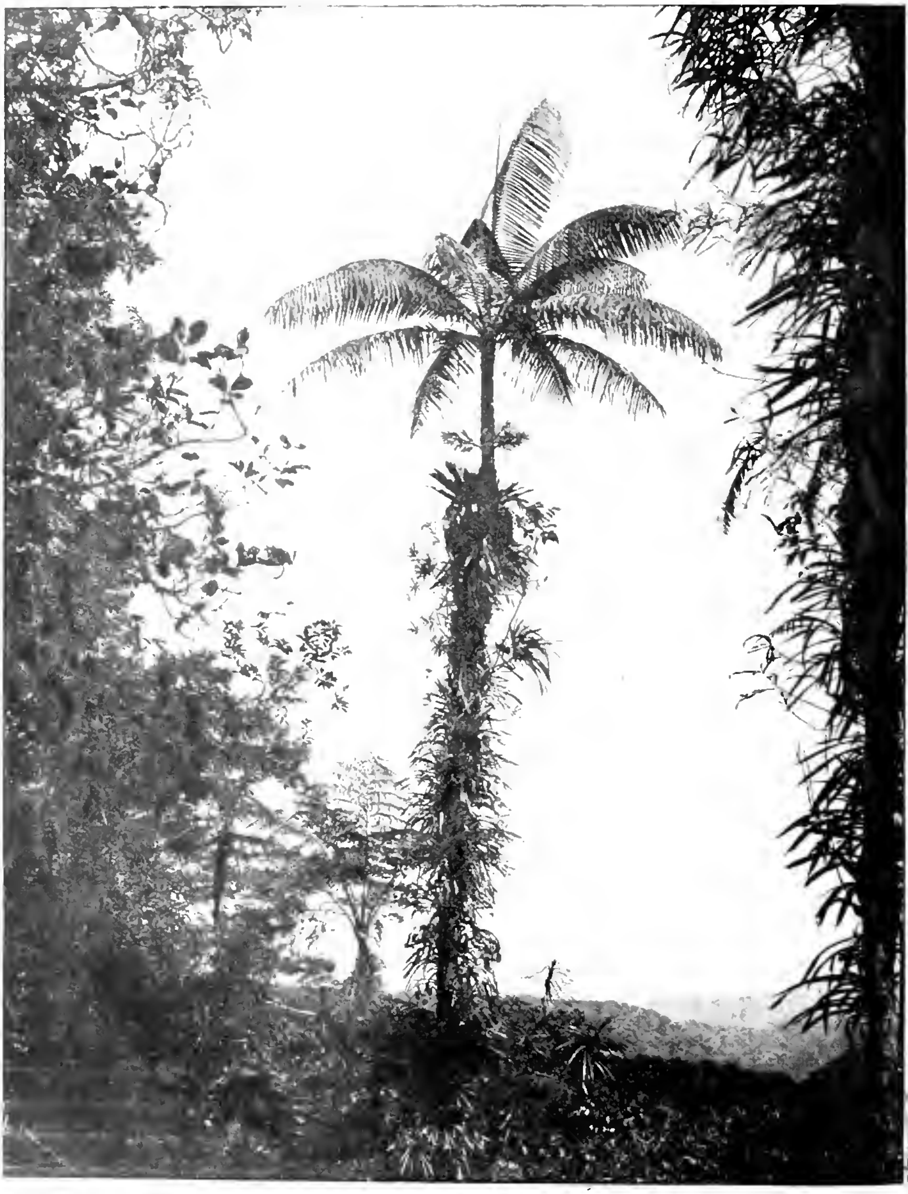


FIG. 151. A palm, the lower part of whose stem is encircled by a root-climbing fern, and its upper part by Freycinetia sp. Samoa. Altitude 300 meters. From a photograph taken under the direction of Kuppen-Loosen.

and within their own areas form common and striking constituents of the rain-forest. The Freycineticae (Fig. 151) are tall climbers, which reach

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Fig. 192. Root-climbing lianes on a tree-stem in the South Mexican rain-forest (Province [illegible]. Below: [illegible] with bipartite leaves. Further up: Araceae. Highest [illegible] are visible [illegible] leaves of Araceae. Around the stem, the cord-like [illegible] Araceae on the branches of the tree. From a photograph by G. Karsten.

the crowns of the highest trees and clothe their stems most luxuriantly with long-leaved shoots. The species of Carludovica are less lofty and less vigorous climbers. Yet I saw Carludovica Plumieri play an imposing part in the forests of the Lesser Antilles, where as a pronounced shade-plant it enveloped all the stems in the gloomy forests with its palm-like leaves, between which projected its extremely peculiar creamy-white spadices decked with long filiform staminodes. Sarcinanthus with one species, S. utilis, is limited to the forests of Central America and Southern Mexico. It is easily recognizable in our Figs. 129, 152, and 153, by its bipartite leaves.

FIG. 153. Sarcinanthus utilis (Cyclanthaceae) climbing on tree-stems of the South Mexican rain-forest. Province of Chiapas. From a photograph by G. Karsten.

Among other monocotyledonous lianes, besides those mentioned, the Araceae are in the first rank. The large genera Philodendron, Monstera, Pothos, and some smaller ones, contain a number of tall large-leaved root-climbers, that form one of the most striking features of the tropical rain-forest, particularly in America (Figs. 129, 152).

The stems of these lianes, like those of Carludovica, produce along their whole length numerous adventitious roots of quite dissimilar anatomical and physiological natures (Figs. 154, 155). Some are developed as *anchoring-roots* and are relatively short (often 2–3 decimeters, or even less); they are markedly negatively heliotropic, so that they press themselves directly against the support; they grow nearly horizontally, whether it be owing to diageotropism or to rectipetality. In the histological structure of the anchoring-roots the mechanical elements are prominent, particularly in the form of tough fibres, whilst the conducting elements are very poorly developed (Fig. 155, *b*).

The *absorbing-roots* are markedly positively geotropic and grow downwards without branching until they reach the ground; once there, apical growth usually ceases soon, while numerous lateral roots spring from the apical region and descend vertically into the soil. The same thing happens if the roots reach water. In many species, the absorbing-roots creep over the surface of the bark, alongside of their own stem; but in others, particularly in those that climb high up among the branches, the absorbing-roots descend freely through the air, and, after emitting terrestrial roots,

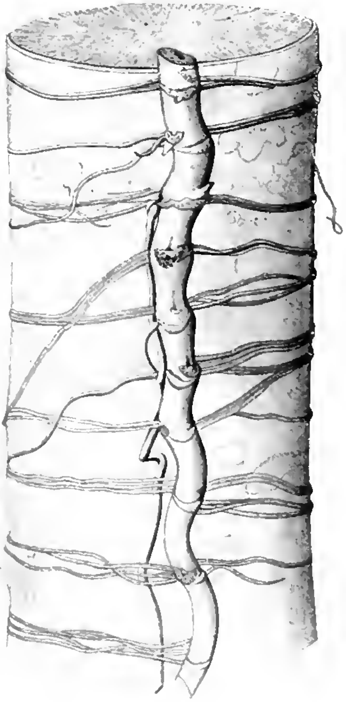

Fig. 154. Stem of Philodendron melanochrysum with vertical absorbing-roots and horizontal anchoring-roots. One-sixth natural size. After Went.

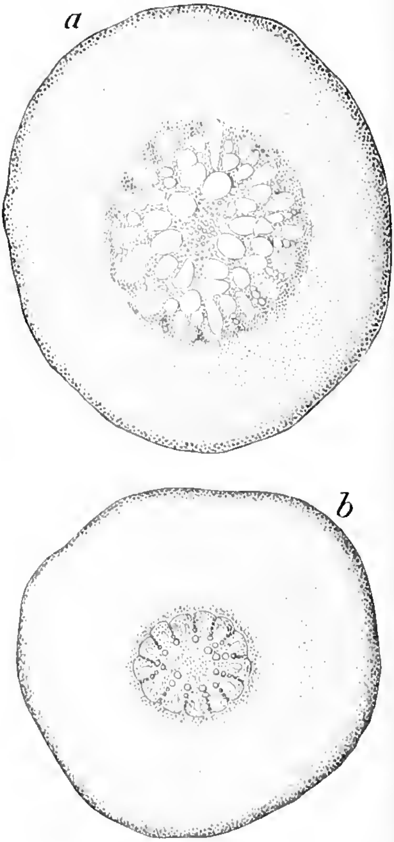

Fig. 155. Anthurium sp., from Trinidad. Epiphytic liane. Transverse sections of roots. *a* absorbing-root; *b* anchoring-root. Magnified 10.

form tightly stretched cords (Figs. 152, 159), which are often exceedingly long but only about as thick as a lead-pencil, and are extensively used as rope ('cipo' of the Brazilians) in their native country; this latter type I observed in America alone, where however it was very common. In the absorbing-roots in contrast with the anchoring-roots, the conducting elements are strongly developed and the mechanical elements weakly (Fig. 155, *a*).

Besides the root-climbers mentioned, there are in the rain-forest many others—of woody kinds, for instance, species of Piper and of Ficus; of herbaceous kinds, species of Vanilla and of Begonia. In tropical America the species of Marcgravia, which also climb by means of anchoring-roots, are widespread, and they are striking by reason of the strongly marked dimorphism exhibited by the leaves, those on the branches adpressed to the supporting trunk differing from those borne by the branches spreading freely from it; their peculiar inflorescences are also a remarkable feature.

Here and there tree-trunks of the rain-forest, but only those of moderate diameter, are entwined by lianes (Fig. 147). But this feature is not exactly common. Most *twiners* stand up quite free, often as straight as an arrow, between the stems of the trees, whether it be that they have raised themselves to the light on a thin stem that has since died, or at first have grown up without support. Of the lofty twiners of the tropical rain-forest may be particularly mentioned, Menispermaceae, Magnoliaceae (Schizandra, Kadsura), Malpighiaceae, Euphorbiaceae (Tragia, Dalechampia), Combretaceae (Combretum, Quisqualis), Asclepiadaceae, Compositae (Mikania).

The majority of large kinds of woody lianes of the tropical rain-forest, in particular those with stems as thick as one's leg and lobed or cleft in cross-section, belong to the highest type of climbing plants, the *tendril-climbers*. As a rule one can recognize this character only on obtaining a view of the upper portion of the climber, and this lies concealed in the branches of the leafy canopy of the forest. Standing on the ground at the bottom of the rope-like stem of the climber the method of attachment of its upper parts is as little recognizable as is that of a ship's backstay to the mast when looked at from the deck.

Many of the most widely distributed, most striking, and largest tendril-climbers both in the Old and New Worlds belong to the large genus Bauhinia, the species of which—many of them hitherto undescribed owing to lack of flowers—have axes with a flattened band-like form and exhibiting more or less strongly marked wavy curvatures (Fig. 156). In tropical America they are very common. I have seen them abundant in Brazil and in the Antilles, but most of all in Trinidad, where the zigzag loops of the relatively younger branches hang down from the leaf-canopy in all parts of the forest. The undulations do not occur on young axes, and they disappear again at an earlier or later time of life, because straight layers of wood are

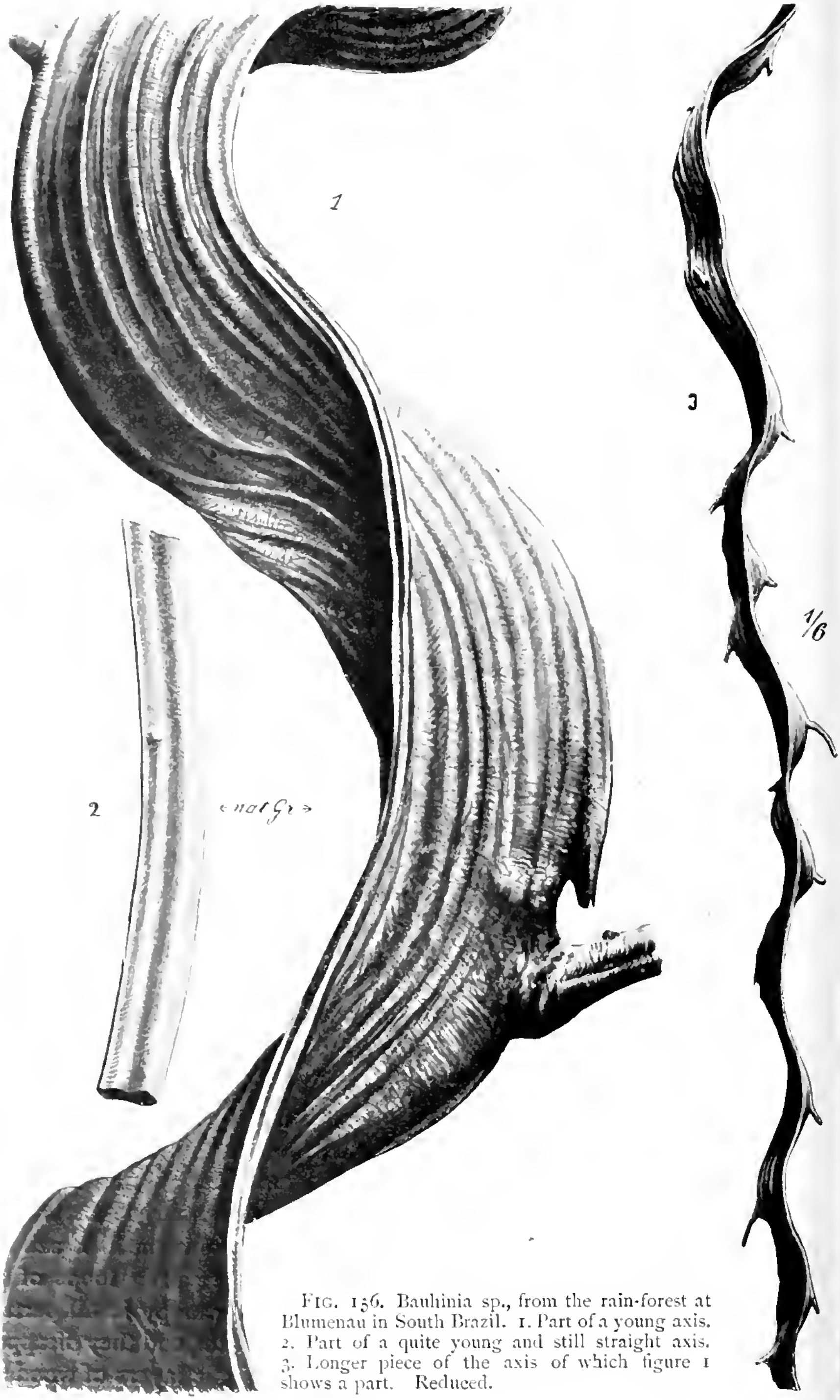

FIG. 156. Bauhinia sp., from the rain-forest at Blumenau in South Brazil. 1. Part of a young axis. 2. Part of a quite young and still straight axis. 3. Longer piece of the axis of which figure 1 shows a part. Reduced.

deposited on the curved ones (Fig. 157). The original wavy part of the axis then represents a narrow ladder between two massive ladder-standards.

The oecological significance of the undulations is apparent so soon as an attempt is made to pull down the liane. The branches of the supporting tree are so firmly caught into the concavities, which are aided by the downwardly directed hook-like stumps of the lateral branches, that such attempts, if they succeed at all, do so only by the breakage of many twigs. On the other hand, when once the stem has become straight, no further hindrance occurs, and its weight causes it to slip gradually to the ground. That even wavy axes may slip down owing to the death of supporting branches and to their own considerable weight is shown by their frequently hanging down from the leaf-canopy.

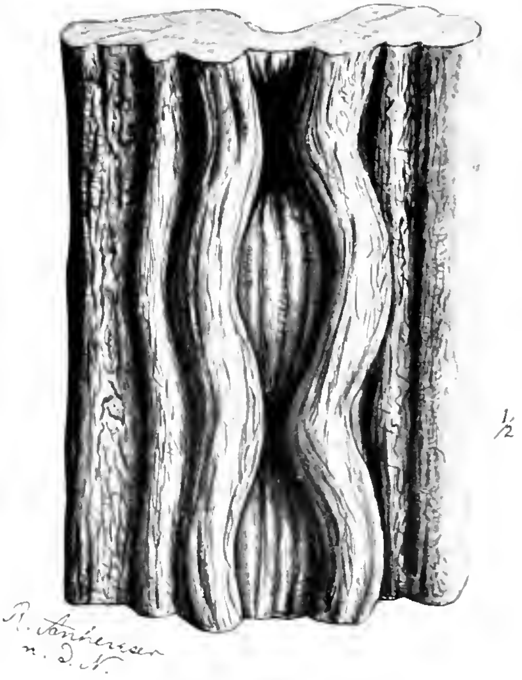

FIG. 157. Bauhinia sp., Pernambuco. The wavy young axis is placed between two straight layers of growth.

Of other lofty tendril-climbers in the tropical rain-forest we have of branch-climbers many Sapindaceae (*watch-spring climbers*) with remarkable cable-like stems composed of strands, species of Securidaca (Polygalaceae) (Fig. 103), species of Hippocratea in both the Old and New Worlds, species of Dalbergia (Fig. 104) and Machaerium in Brazil, many Anonaceae (*hook-climbers*) in tropical Asia, and species of Cissus (*stem-tendril climbers*); of *leaf-tendril climbers* the Bignoniaceae have a wood that is cruciform in transverse section.

iv. *EPIPHYTES OF THE RAIN-FOREST*[1].

To a still greater degree than lianes, epiphytes contribute to the characteristic physiognomy of the tropical virgin forest. Resting on the trunks of the trees and on the twigs right up to their extreme tips is a wealth of phanerogams and ferns, not only herbs, but also shrubs and even trees

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[1] Schimper, I and II.

(Figs. 158, 159); whereas in Europe only mosses, lichens, and small Algae can grow in such situations. In the rain-forest such small forms as are the epiphytic vegetation in Europe are usually driven out on to the leaves, which they frequently densely coat, and are then termed *epiphyllous plants*.

The sites occupied by epiphytes generally appear little suited for the nutrition of large plants. Epiphytes are, however, frequently found on very rough bark, in the forks of branches where hûmus has collected, in the persistent pocket-like leaf-bases of palms, and in similar positions. Many of them occur chiefly on quite smooth surfaces, such as the mast-like stems of many palms, the still smoother as it were polished stems of bamboos, and also on glossy leaves. The wisps of Tillandsia usneoides,

Fig. 158. Obliquely growing tree-stem with epiphytes. From right to left: above, Philodendron cannaefolium; below, pendent, Codonanthe Devosiana; above, Ficus sp. (arborescent), Vriesea; below, Anthurium sp., Rhipsalis two species. From a photograph by H. Schenck.

FIG. 150. Tree-trunk with epiphytes. Blumenau, Brazil. Below: [illegible] Rhipsalis sp. To the right: cord-like aerial roots (absorbing roots) of [illegible] sp. To the left: an obliquely ascending liane-stem. From a photograph by H. [illegible]

To face p. [illegible]]

several meters in length, lie rootless and without any attachment, thrown down, as it were, on to the ends of branches (Fig. 48); and Asplenium Nidus frequently supports its funnels that are more than a meter in height, in rows along thin liane-stems.

According to their mode of life, epiphytes may be classified in four groups :—

1. PROTO-EPIPHYTES. This is a very slightly homogeneous group, and includes species that are *compelled to acquire nourishment from the surface of the supporting structure and from direct supplies from atmospheric sources.*

2. HEMI-EPIPHYTES. These are epiphytes that *germinate and pass through their earliest development on trees, but subsequently become connected with the ground by their roots,* so that as regards their nutrition they are subject to the same conditions as terrestrial plants, particularly root-climbing lianes.

3. NEST-EPIPHYTES. This group is composed of species that *by appropriate devices collect large quantities of humus and water.*

4. TANK-EPIPHYTES. In these *the root-system is developed only as an anchoring-apparatus, or is entirely suppressed, so that the whole process of nutrition is carried on by the activity of the leaves.* The epiphytic Bromeliaceae, at least in the tropics, are the sole representatives of this group; the New Zealand genus Astelia, consisting of lianes, appears to follow them.

Proto-epiphytes are frequently devoid of definite adaptive features. Thus, for instance, small ferns that grow on moist fissured bark differ in no way from those on the ground. In general, however, even the ferns of this group are distinguished from the allied terrestrial plants of the evergreen rain-forest by their decided xerophilous character, which the irregular and scanty supply of water from their substratum sufficiently explains. The epiphytes of the humid forest show protective devices against the loss of water by transpiration, similar to those usual among plants that inhabit physiologically dry stations. Such protection in this case is very rarely afforded by hairs, much more frequently by a very thick cuticle and by a sinking of the stomata into funnel-shaped depressions, most frequently, however, by devices for the storage of the water, which at one time is in excess on account of the rain, at another time is very scanty. Such water-reservoirs may be developed in the form of a massive aqueous tissue in the leaves, which then appear to be remarkably thick and juicy, as in Peperomia, species of Aeschynanthus and other Gesneraceae (Fig. 16 a), many Asclepiadaceae, or numerous water-tracheids are present, as in the leaves of many orchids (Fig. 16), or special plant-members are converted into water-reservoirs. Thus, the tuber-like structures possessed by so many epiphytes—for instance numerous orchids, though not all of them—many

Ericaceae, Utriculariae, the young fig-tree (Fig. 160), also the spindle-shaped swollen petioles of Philodendron cannaefolium, and the older, yellowish, greatly thickened leaves of species of Peperomia and of Gesneraceae, supply the plants to which they belong with water, so that, as has been proved experimentally, they thrive without receiving any water from outside so long as this supply is available, but rapidly wither whenever it is exhausted.

Whilst the roots of many proto-epiphytes do not differ essentially from those of terrestrial plants, others are provided with a mechanism by which every drop of falling water is at once absorbed. This takes place by means of the *velamen*, a tissue that covers the roots of nearly all epiphytic orchids (Fig. 161) and of certain epiphytic Araceae. The cells of this tissue, which is usually composed of several layers, resemble tracheids, are provided with spiral bands, and in dry weather contain air. They are bounded within by an endodermis (exodermis), some of whose cells are differentiated as passage-cells. If water reaches the root it is sucked up by the velamen as if by blotting-paper, and fills the cell-cavities. Thence it passes more slowly through the passage-cells into the interior of the root.

FIG. 160. Ficus sp. Epiphyte. Young plant with tuber. Natural size. After Went.

The roots of the epiphytes of this group are for the most part exposed to light and consequently often contain chlorophyll. This circumstance has caused one of the most peculiar adaptive features among epiphytes, namely the differentiation of the root-system as the sole organ of assimilation, with at the same time an atrophy of the leaves. Such assimilating roots either creep along the bark or hang freely down through the air; they are, in many cases, dorsiventral (Fig. 114), and, to permit the interchange of gases, they are always provided with permeable places which are absent from the weakly assimilating roots of other orchids.

To the *hemi-epiphytes* belong chiefly very large, partly arborescent forms, such as the epiphytic fig-trees, species of Clusia and Carludovica, and large Araceae belonging to the genera Philodendron and Anthurium. At first the hemi-epiphyte behaves like one of the proto-epiphytes and develops similar water-reservoirs. Its roots are of one kind, and all serve as anchoring and absorbing organs. Later on, as in the root-climbing Araceae[1], there sets in a sharp differentiation of short anchoring-roots and long absorbing-roots, and the absorbing-roots descend to the ground,

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[1] See p. 313.

so that the epiphyte, though placed high up on a tree, yet resembles a terrestrial plant in regard to its absorption of nutriment. Many epiphytes of this class, like Carludovica Plumieri, which has already been described, and several Araceae are at the same time lianes; on the other hand, there are also lianes that germinate in the soil, but their stems gradually die from below upwards, so that in their later stages they subsist just like hemi-epiphytes. They have been termed *pseudo-epiphytes*.

The largest of the hemi-epiphytes in the tropics of both hemispheres are species of the genus Ficus. The gigantic banyan-tree, Ficus bengalensis

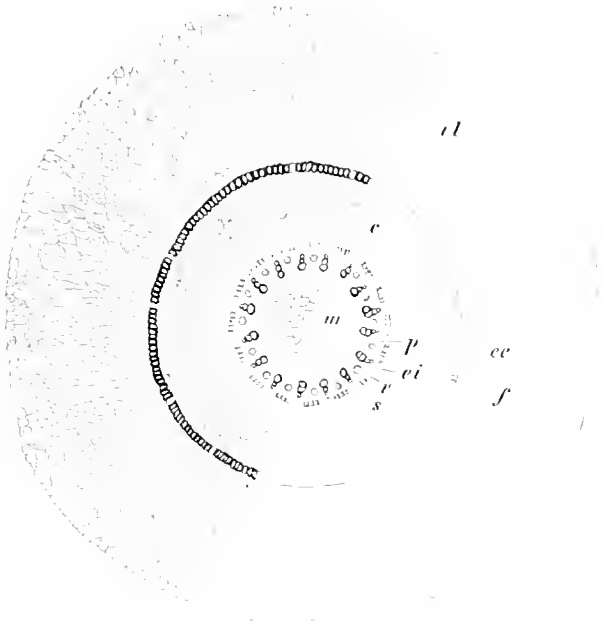

FIG. 161. Dendrobium nobile. Transverse section through the aerial root. *vl* velamen; exodermis; *f* passage-cells in the exodermis; *c* cortex; *ei* endodermis; *p* pericycle; *s* xylem; phloem; *m* pith. Magnified 28. After Strasburger.

ig. 162), of the East Indies is universally known as an immense living lumned hall, consisting of a flat expanded canopy of leaves and numerous em-like prop-roots growing down from the boughs. Like all hemi-iphytes. the banyan germinates on the bough of a tree, and at first s only such nutritive substances available as occur on the bark of the pporting branch. When once, however, its absorbing-roots are de-loped[1], the supporting tree soon perishes under the shade of its rapidly owing guest, so that but for the knowledge of the development of the nyan the former presence of its host would never be conjectured.

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[1] See p. 314.

Like many other arborescent forms of this group, the banyan is an epiphyte proper in its youth only. When once it has developed its absorbing-roots, which

Fig. 162. Ficus bengalensis, in the botanic garden at Buitenzorg. In the centre Asplenium Nidus as an epiphyte. From a photograph.

[illegible] resemble columns and become very thick, and when the original hos [illegible] ed, the banyan becomes quite an independent plant. New absorbing-root which in this case are also supporting-roots, are constantly being formed by the horizontally spreading crown, and thus its columned hall is built up. In most hemi-epiphytes, if the absorbing-roots have no mechanical functions to fulfil they remain soft and flexible.

The collecting of humus that forms the characteristic of the *nest-epiphytes* takes place in various ways. It is sometimes the roots that become interwoven into a large sponge-like frame, which detains falling leaves and the like, even after their decomposition, as in many orchids (Fig. 163); sometimes the leaves of the epiphyte, arranged in a rosette, incline together below to form a funnel, as in Asplenium Nidus (Fig. 139)—the plant

Fig. 163. Grammatophyllum speciosum (Orchidaceae). A nest-epiphyte with negatively geotropic roots, in the botanic garden at Buitenzorg. From a photograph by G. Karsten.

gured had attained very large dimensions—and many other ferns, and n the common Anthurium Hügelii of the West Indies, an aroid greatly esembling ferns in habit. Even in these cases, particularly in Anthurium ügelii and in the orchids, there is usually a differentiation in the root-ystem, as some of the roots which are not geotropic and are very strongly onstructed essentially contribute to form a framework, or act as anchoring-oots, whilst numerous thin, lateral roots grow vertically upwards, so that e lining of the root-nest appears to be bristling with countless needles ig. 163). In contrast with nearly all other forms of roots, these thin roots re negatively geotropic, and this is oecologically connected with the fact that tritive material, especially water, comes from above and not from below.

In other cases, either all the leaves or some of them go to form *pockets*, as they assume such a position against the stem as to make with it a receptacle in which humus can accumulate. Either each leaf by itself forms a pocket, or several leaves take part in the formation of a general pocket. In many species, there has arisen a differentiation between pocket-leaves, which fulfil the function of assimilation only to a subordinate extent and for a short time, and assimilating leaves endowed with quite other characters.

FIG. 164. Platycerium grande. Nest-epiphyte with pocket-leaves. Pasoeroean, East Java. From a photograph by J. Kobus.

The most remarkable examples of pocket-leaves appear in the fern-genus Platycerium (Fig. 164), in which they are sessile and broad, are closely applied below to the bark of the tree, and form a pocket above, whereas the stalked, narrow, dichotomous foliage-leaves hang loosely down.

FIG. 165. Nidularium Innocentii. A tank-epiphyte from Brazil. Half the natural size.

Tank-epiphytes. The epiphytic Bromeliaceae, which belong particularly to the genera Tillandsia, Vriesea, Aechmea, and Nidularium, possess, in the majority of cases, rosette-like vegetative shoots, whose stiff leaves are widened out below like spoons, and fit so closely together that, like water-tight *tanks*, they collect rain-water, of which a full liter may descend from one of the larger forms on to a careless collector: besides this, like the less tight leaf-funnels of the nest-epiphytes, they contain all kinds of detritus of mineral, vegetable, and animal origin, and this, as the vigorous growth of the plant shows, affords a fertile nutritive substratum. The rosettes of leaves spring from a short, gnarled system of axes fixed to the substratum by short thin roots, which are, however, as strong as wire (Fig. 165).

The roots consist almost exclusively of thick-walled fibres and take no part in the nutrition, as has been proved experimentally. The absorption of nutriment takes place entirely through the leaves, by means of peltate scale-hairs (Fig. 166), which are situated in particular on the dilated bas of the leaf that is usually under water. If there should be no water o the surface of the leaf, these hairs contain air alone; every drop of wate however, is at once absorbed by them, just as by the velamen of orchids and it reaches the interior of the leaf owing to the activity of passage-cell that are rich in protoplasm (Fig. 167).


Fig. 166. Vriesea. Scale-hair. Magnified 340.

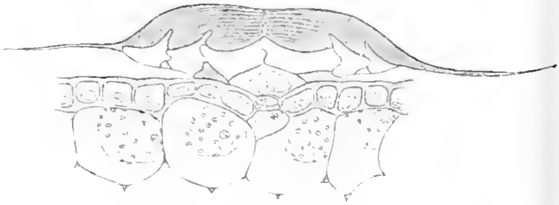
Fig. 167. Tillandsia usneoides. Scale-hair. Magnified 375.

From this type, which is exhibited in a pure form in particular b species of Vriesea, Aechmea, and Nidularium, not inconsiderable deviation occur in many species of Tillandsia, especially Tillandsia usneoides (Fig 168, 169). This most remarkable of all epiphytes, often completel covering the trees in tropical and subtropical America, consists of shoot often far more than a meter in length, thin as thread and with narrow grass like leaves, and only in early youth fixed to the surface of the supportin plant by weak roots that soon dry up. The plants of Tillandsia ow their attachment to the fact that the basal parts of their axes twine roun the twigs of the host. The shoots are covered all over with scale-hair which in structure and behaviour resemble those of other Bromeliacea The dispersal of the plant takes place less by seed than by vegetati means, through the transport of severed shoots by the agency of t wind or of birds, which readily utilize the fragments in the constructi of nests.

Wiesner[1] made a number of determinations of the amount of light in the orchid quarter of the botanic garden at Buitenzorg. The orchids are cultivated there on stems of species of Plumiera, in the shade of lofty trees of Evia acida, Bl.

The brightness in the orchid quarter was on the average 1/10·8 of the full daylight, and the diffuse front light on the stems of the Plumiera trees was on the average 1/60–1/65 of the total daylight (I maximum = 0·025-0·023). When the sun shone, the intensity of the light from above rose to 1/4·7–1/7·7 of full daylight (I maximum = 0·319-0·194).

FIG. 169. Tillandsia usneoides. Fragment of a shoot. Natural size.

The following orchids were growing well: Agrostophyllum javanicum, Bl., Eria ornata, Lindl., Spathoglottis plicata, Bl., Thelasis carinata, Bl. Others, on the contrary, appeared to feel the want of sufficiently intense light: for instance, Thelasis elongata, Bl., Dendrobium acuminatissimum, Lindl., Coelogyne Rochusseni, De Vriese, C. Lowii, Pont., C. macrophylla, Teijsm. et Binn., Vanda tricolor, Hook., Oncidium ampliatum, Lindl.

FIG. 168. Tillandsia usneoides. Sprig. One-fifth natural size.

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[1] See p. 55.

These orchids, owing to the mode of spreading their organs, are principally adapted to light from above. The same holds good for many epiphytic ferns. The widespread and very common Asplenium Nidus occurs under very various degrees of illumination. Wiesner observed for it: L = 1/4 up to 1/38 (I maximum = 0·4-0·042).

Epiphytes whose vegetative organs lie flat against the bark are adapted to light from the front. Hence in the Buitenzorg garden, the otherwise common Taeniophyllum Zollingeri, Reichb. f., a small leafless orchid with assimilating roots pressed close to the bark, does not grow in the orchid quarter, because the light from the front is too weak. Wiesner has communicated the following, as a result of numerous observations made by himself, regarding the degree of light demanded by this plant:—

LIGHT-REQUIREMENTS OF TAENIOPHYLLUM ZOLLINGERI, REICHB. F. (after Wiesner).

	L.	*I maximum.*	*I mean.*
Limits of development	1/3–1/32	0·533-0·050	0·166-0·015
Most vigorous development	1/7–1/9	0·228–0·177	0·071–0·055
Arrest resulting from insufficient intensity of light .	1/32	0·050	0·015
Arrest resulting from too intense light . . .	1/2–1/3	0·811–0·533	0·251–0·166
Flowers were observed with	1/5–1/8	0·320–0·205	0·101–0·062

Besides the epiphytes belonging to the Phanerogamae and the Pteridophyta which alone have been dealt with so far, the tropical virgin forest also possesses others among Algae, Fungi, Lichenes, and Bryophyta, and many of these plants, in particular some Hepaticae, also show a high degree of adaptation to the substratum. Whilst the occurrence of such lower cryptogams on the bark of trees is also exhibited in temperate forests, and actually to a far greater extent than in tropical forests, their appearance as *epiphyllous forms*, that is epiphytic on leaves (Fig. 170), is apparently confined to the tropics. Epiphyllous forms are quite common features particularly on ageing leaves, in very humid rain-forests.

The epiphytic plants on a tree in a virgin forest are not the same from its base to its topmost branches, but exhibit a well-marked differentiation. Low down on the trunk are many plants that are also terrestrial, such a species of Hymenophyllaceae, Carludovica, climbing Araceae; ascending higher, these indifferent forms disappear, and the xerophilous character otherwise foreign to the rain-forest, increases with the increasing adaptation to an epiphytic habit (Fig. 171), so that the epiphytic species met with which occasionally also occur on the ground, appear to be plants of very dry stations, and, to some extent, of stations with strong illumination. Th epiphytes on the highest branches and consequently those that are mos insolated are identical with those that form the aërial flora of well-lighte woodland and of the savannah of dry open districts. Hence after the partia clearance of the forest, the epiphytes on the lower portions of the trees tha are left standing die, whilst those on the crowns gradually spread down wards and cover the whole tree.

Different species of trees frequently show distinctions in their epiphytic flora. Thus tree-ferns and the calabash-tree (Crescentia Cujete), which is so common in tropical America, are most markedly preferred; even certain epiphytic species, such as Trichomanes sinuosum in tropical America, occur apparently on tree-ferns only.

v. *BUDS IN THE RAIN-FOREST.*

The *vegetative buds* of woody plants in the rain-forest do not exhibit any marked difference in relation to a condition of activity or of repose. The type of winter-bud with its large dry covering of scales and considerable differentiation, is foreign to the constantly humid rain-forest, whereas it reappears in dry forest and savannah.

Dormant buds are as a rule very small in the rain-forest, frequently without any covering of scales and without protection by other plant-parts: they are then, however, frequently coated with a dense brown tomentum or with a kind of varnish. Their change into active buds, as far as one can see, consists simply in this, that their parts begin to grow.

FIG. 170. Kibessia azurea. Leaf studded with numerous epiphyllous lichens. Natural size. After Stahl.

In other cases both active and dormant buds have envelopes. The envelope is almost always soft and juicy, and is formed either of stipules or of the petioles of the nearest older leaves.

I have observed small hairy, but otherwise uncovered buds, in the botanic garden at Buitenzorg, on the following woody plants: Calophyllum tomentosum, Viburnum sundaicum, Rottlera tinctoria, Chrysophyllum Cainito, Sideroxylon firmum, Ardisia fuliginosa, Diospyros subtruncata, Mabe Ebenus, Pterospermum Heyneanum, species of Sterculia, Schima Noronhae, Thea cochinchinensis, Flacourtia Ramontchi, Capparis Heyneana, Nothopegia Colebrookiana, Bl., Cinnamomum sericeum, Ryparia caesia, Cluytia oblongifolia, Coelodepas bantamensis, Tetranthera chrysantha, Tectona Hamiltoniana (Fig. 172, 2). Many of these plants in the mature condition have glabrous leaves. Uncovered buds with a coating of varnish are much less common. I found them in the Buitenzorg garden in Tabernaemontana pentasticta and Achras Sapota. I also noticed protection by stipules in Artocarpaceae, Urticaceae, Piperaceae, and Rubiaceae also in Wormia ochreata (Fig. 172, 4), species of Tabernaemontana, and Phyllanthus zeylanicus. Treub and Potter have described several simila cases; the latter has also furnished figures. According to Potter, remova of the protective slender trumpet-shaped stipules, in Artocarpus incisa occasions the arrest of the enclosed leaves. In Canarium zeylanicum, Bl.

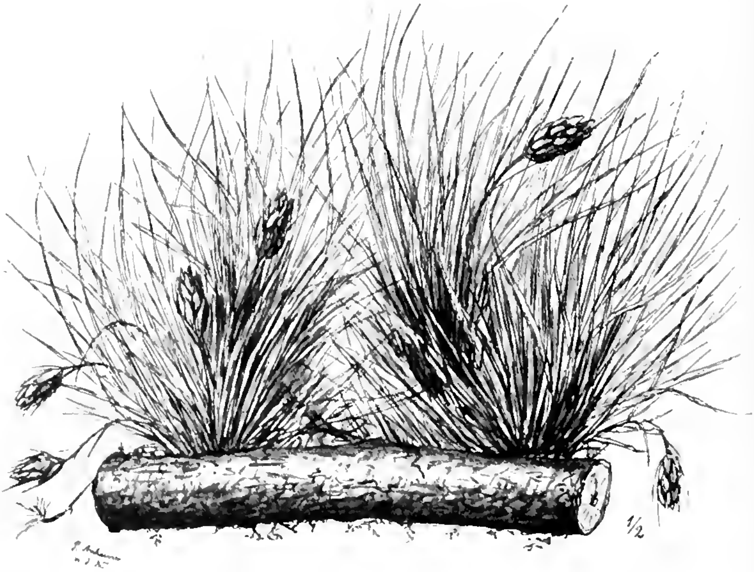

Fig. 171. Tillandsia stricta, var. Schlumbergeri. A markedly xerophilous light-demanding epiphyte of South Brazil. Half the natural size.

the scale-like stipules develop more quickly than the blade and enclose the bud. In several species of Wormia the bud is enclosed by wing-like outgrowths of the petiole (Figs. 172, 5, and 174).

Very peculiar are the chambers occurring, in some woody plants, between the petioles of next older leaves, which in such cases always stand in whorls of two or more. The chambers are formed by the adhesion of the lower edges of the petioles and above are provided with a slit, out of which in time the completely concealed terminal shoot protrudes. P. Groom has described and figured such structures (Fig. 173). I have observed in the Buitenzorg garden a similar method of bud-protection in Calpicarpum Roxburghii, Alstonia verticillosa (Fig. 172, 1), Garcinia Livingstonii, and G. ferrea (Fig. 172, 3). The phenomenon is most striking in Alstonia, in which the chamber is formed by the bases of the petioles of the four leaves of the whorl and its opening is occluded by a spherical drop of resin. The stipular and petiolar chambers contain resinous or mucilaginous

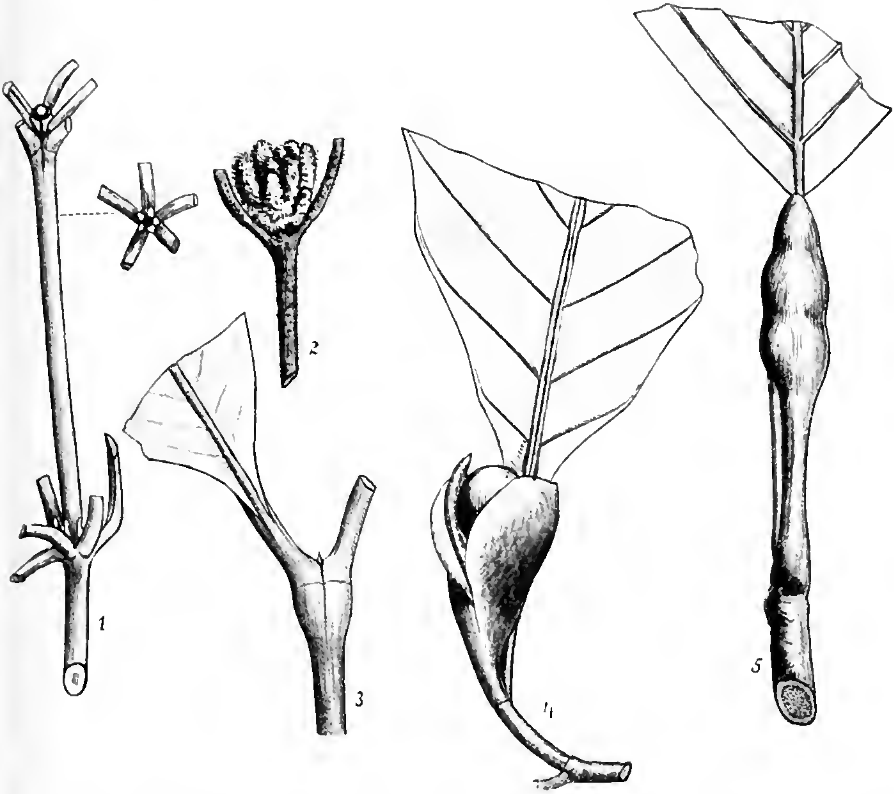

FIG. 172. Foliage buds of tropical woody plants from the botanic garden at Buitenzorg. 1. Alstonia verticillosa. 2. Tectona Hamiltoniana. 3. Garcinia ferrea. 4. Wormia ochreata. 5. Wormia triquetra. Natural size. Drawn by R. Anheisser.

substance, or a mixture of both, which is excreted by colleters, and is regarded as protective in function. Groom has published further details in regard to this matter.

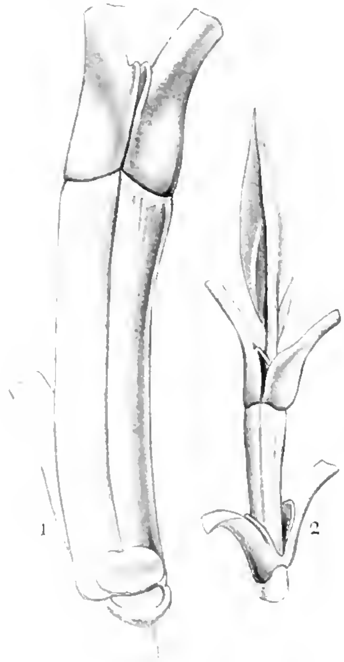

FIG. 173. 1. Tabernaemontana dichotoma; terminal bud. 2. Clusia grandiflora ?; young shoot. After P. Groom.

More remarkable even than the structure of foliage-buds is, in many cases, their manner of opening. Treub has very justly remarked: 'Trees shoot out their leaves.' One of the most astonishing phenomena of tropical vegetation is that in many trees the young leaves, as in Theobroma Cacao and Mangifera indica (Fig. 177), or quite young shoots, as in Brownea hybrida (Fig. 175), Amherstia nobilis (Fig. 176) and other Caesalpiniaceae, after *having attained their full size, hang down limply like tassels and are usually also devoid of chlorophyll*, so that, by their white or rosy red colour, they contrast with the green foliage. The vertical position in the pendent shoots is solely due to the want of turgescence; in pendent leaves it is caused by the active curvature of the pulvinus as well.

The pendent leaves are completely differentiated only after having concluded their superficial growth. Then it is that chlorophyll appears in their hitherto colourless and small chromatophores, whilst the originally homogeneous mesophyll differentiates into palisade-tissue and spongy parenchyma, and thickens its delicate walls. These processes are accompanied by a gradual assumption of a condition of turgescence and of tension in the tissues.

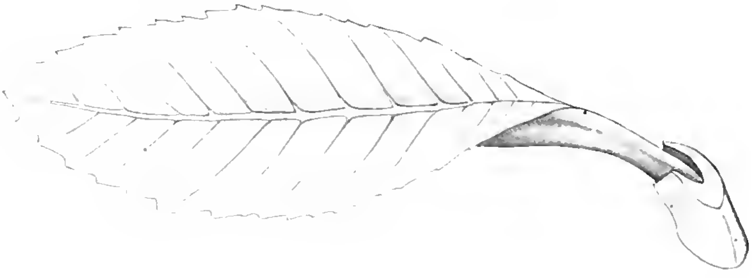

FIG. 174. Wormia Burbidgei. Leaf with bud concealed in the sheath. After P. Groom.

All authors who have described the above phenomenon have, possibly with justice, included it among the protective devices. Opinions however differ as to the nature of the danger to be guarded against. Wiesner considers the danger to be too strong illumination; Potter, too great heat; Stahl, mechanical damage by heavy rain; Haberlandt, several factors acting simultaneously. Decisive experiments have not yet been made.

FIG. 175. Brownea hybrida with pendent young twigs. Botanic garden at Buitenzorg. From a photograph by M. Treub.

Stahl, who has closely studied pendent leaves and pendent shoots, mentions the occurrence of pendent leaves in Monstera deliciosa, Mangifera indica, Theobroma Cacao, Durio zibethinus, Quercus glaberrima, Acer laurifolium, in fact in trees of very diverse affinities. On the other hand, to both Stahl and myself pendent twigs are known in connexion with the Caesalpiniaceae alone—in Amherstia nobilis, species of Brownea, Jonesia, Maniltoa, Humboldtia, Cynometra.

Fig. 176. Amherstia nobilis. Twig with pendent young lateral twigs. Botanic garden at Buitenzorg. From a photograph by Treub.

Pendent leaves and pendent twigs by no means occur in the majority o woody plants of the virgin forest, but only in a minority of species, to whic however a number of economic and ornamental trees belong, so that th phenomenon is generally striking.

In many cases the mode of development of shoots does not diffe essentially from that of woody plants of temperate zones. But the pro tection of young members is possibly more frequently observable than i temperate zones, whether it consists of a rich coating of hairs, a vertical li of the leaves, or of their production under cover of the older foliage. Man statements regarding this subject occur in the works of Potter, Stahl, and Wiesner already referred to.

The admirable researches of Raciborski regarding the *structure of flower-buds* were conducted partly on tropical plants. Characteristic distinctions depending on climate between the flower-buds of tropical plants and plants of other zones were mentioned by him in a few cases only. Yet the peculiar phenomenon, that *flower-buds are immersed in water, or contain water in their calyx until shortly before their anthesis*, appears to be limited to humid tropical districts. For instance, in the West Indies I found the boat-shaped bracts in the inflorescence of Heliconia Bihai (Fig. 178) and Heliconia caribaea always full of rain-water; the flower-buds were below water-level, but shortly before opening they raised themselves above it by curving sharply. In like manner, in Nidularium (Fig. 165) I saw the short inflorescence nestling between the bracts always submerged in a cistern supplied with rain and dew, out of which the open flowers protruded singly. The boat-like bracts of the long distichous inflorescence of species of Vriesea, for instance Vriesea incurvata, contain a mucilaginous liquid, which completely surrounds the bud and is probably secreted by the plant. The latter is certainly true of the similar mucilaginous liquid, which accumulates in the sac-like fused pairs of bracts surrounding the flower-buds of certain Acanthaceae (Fig. 179), which are so tensely filled that a puncture causes the liquid to spurt out violently. Flower-buds with a water-holding calyx were first described by Treub in connexion with Spathodea campanulata, and have formed the subject of a comprehensive and conclusive monograph by Koorders which has brought to light a number of interesting details, especially as regards secreting hydathodes. The number of species with water-holding calyces is small—so far as is known only thirteen species, limited to representatives of the families of Bignoniaceae, Solanaceae, Verbenaceae (Fig. 180), Scrophulariaceae, and Zingiberaceae—whereas water-holding bracts are very common.

FIG. 177. Mangifera indica. End of twig. The young leaves flaccidly pendent. Half the natural size. After Stahl.

vi. *CAULIFLORY IN THE RAIN-FOREST.*

In temperate zones flowers appear mostly on the current year's twigs, more rarely on those of the preceding year, but only in a few species, such as Cercis siliquastrum, on older branches or stems; whereas in constantly humid tropical forests *cauliflory*, that is to say the formation of flowers on old wood, is not rare. It is occasioned by the fact that dormant axillary buds become further developed after several or many years, and breaking through the cortex, freely expand their flowers (Figs. 181 and 182).

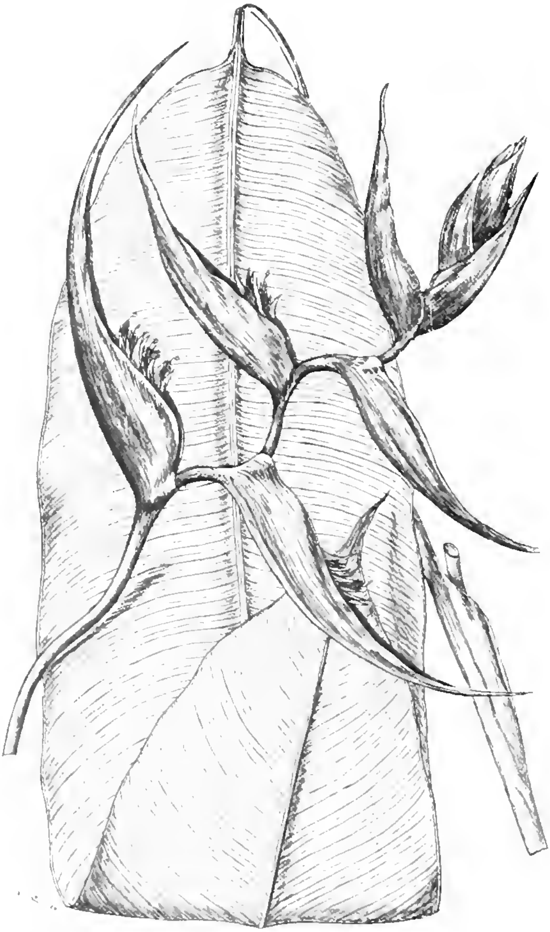

FIG. 178. Heliconia Bihai. Boat-like bracts containing water. Half the natural size. From Flora Brasiliensis.

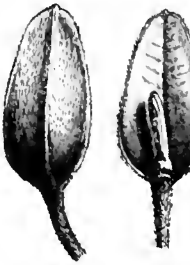

FIG. 179. Mendozia Velloziana. Flower-buds surrounded by a pair of adherent bracts filled with mucilaginous liquid. Blumenau, South Brazil.

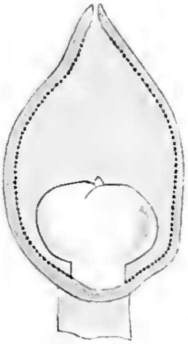

FIG. 180. Clerodendron Minahassae. Water-holding calyx of a fruit. Natural size. After Koorders.

In cauliflory the flowers appear sometimes only on main stems, sometimes only on branches, sometimes, and this is most usual, on both main

Fig. 181. Parmentiera cereifera, a cauliflorous tree in fruit. Cultivated in Ceylon. From a photograph.

tem and branches alike. One and the same species is either always or nly partially cauliflorous.

In Java I observed cauliflory—

(a) *On the main stem exclusively* in Aristolochia barbata, Jacq., Saurauja cauliora[1], Parmentiera cereifera, species of Kadsura, Cynometra cauliflora, Diospyros tricta, and other trees.

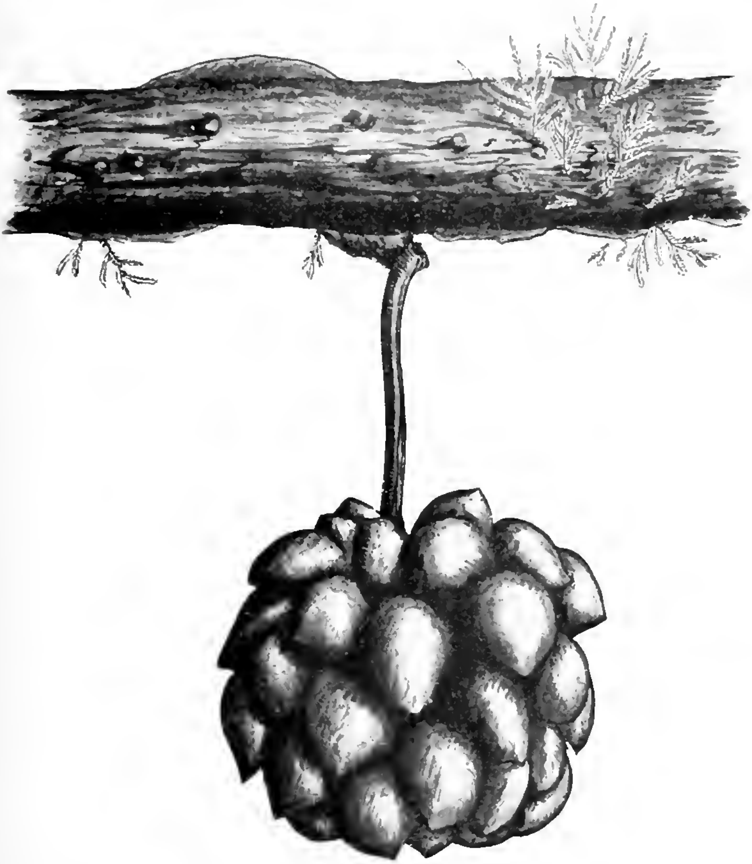

FIG. 182. Kadsura cauliflora. Javanese liane in fruit. Natural size. Drawn by R. Anheisser.

(b) *On the branches only* in Jonesia minor, Epicharis sericea, Flacourtia inermis, vodia Batjan, Actinodaphne sp., Kibara coriacea, Saurauja nudiflora.

It is of course by no means impossible that species in the first list also occasionally roduce flowers on old branches, and vice versa. I consider the habit in question as onstant only in the case of the two species of Saurauja, of which I observed umerous specimens.

(c) *On both stem and branches* in Theobroma Cacao, Crescentia Cujete, Arto-

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[1] Whenever no author's name is mentioned, the names are those on the labels in the otanic garden at Buitenzorg.

carpus integrifolia, Covellia lepicarpa, Sterculia rubiginosa, Oreocnida major, Diospyros sp., Averrhoa Bilimbi, and others. The cauliflory is very peculiar in Stelechocarpus Burakol, a small tree belonging to the Anonaceae, for in it the female flowers spring in tufts out of thick warts on the stem, whilst the smaller male flowers shoot out of the axils of leaves that have just fallen from the twigs. In Taxotrophis javanica, on the other hand, I found the male flowers definitely on the stem, but the female flowers in the axils of leaves on young twigs.

Cauliflory either excludes the formation of flowers on young twigs, as in cases enumerated above, or the flowers may appear on young twigs as wel as on the old cortex. Frequently cauliflory appears to be an occasiona feature only.

Among plants that are not exclusively, but are only occasionally cauliflorous, are for instance, Saurauja pendula, Ficus cuspidata, Capura alata, Medinilla laurifolia Drimyspermum longifolium, Oreocnida major, Sterculia rubiginosa, Browne coccinea.

All possible transitions connect typical cauliflory with the production o flowers on young twigs. Thus a number of species are cauliflorous onl on relatively young branches; for instance Flacourtia inermis, Evodi Batjan. In other cases the flowers appear on the defoliated base o a foliage shoot, the upper part of which bears leaves; for instance specie of Lasianthus, Goniothalamus Tapis, Gonocaryum myrospermum. I a number of herbaceous plants the flowers appear only in the axils o fallen leaves, as in Campelia marginata, Agalmyla staminea, Cyrtandr nemorosa. According to Johow, the flowers of several Sapotaceae occu only on two-year-old defoliated portions of the twigs.

The separation in space of the vegetative and reproductive functions— for this is the subject under discussion—is exhibited more strikingly tha in true cauliflory, *wherever certain leafless or very weakly foliaged twig springing from the main stem or from the thickest branches alone are fertil* whilst the crown remains purely vegetative. Such twigs, for instanc encircle, like lianes, the lofty stem of Couroupita guianensis, and bea spherical fruits as large as one's head.

In Ficus sp. 'Minahassae' (Fig. 183), thin whip-like, scale-leaved twig spring from the main stem and the thickest branches, on which little fig are grouped in small capitula. In Ficus rhizocarpa such twigs spring o close to the ground only[1]. In Anona rhizantha, which has been investigat by Eichler, the fertile twigs are subterranean at their base and only the flowering tips project above the ground.

The question has often been raised why cauliflory is so much common in the tropics than in temperate zones, and the distribution has usual been associated with the conditions of pollination. To me it seems mo probable that it is owing to the weaker development or less degree

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[1] I noticed both species at Buitenzorg.

toughness of the bark. This opinion is supported by the fact that in dry districts, where the bark is considerably developed and is rich in fibres, cauliflory is very rare.

vii. *SAPROPHYTES AND PARASITES IN THE RAIN-FOREST.*

If Alfred Moller's observations in South Brazil be generally applicable, saprophytic fungi appear to be even more abundantly developed in the umus of the tropical rain-forest than in the forests of Central Europe. Never,' says Möller, 'does the action of the fungus kingdom, which stands ntermediate between the animal and vegetable kingdoms, strike us so orcibly as here in the tropical forest, where the persistent humidity and eat constantly bring out the growth of fungi to a degree that is attained ith us [in Central Europe] only exceptionally, after warm rainy days[1].'

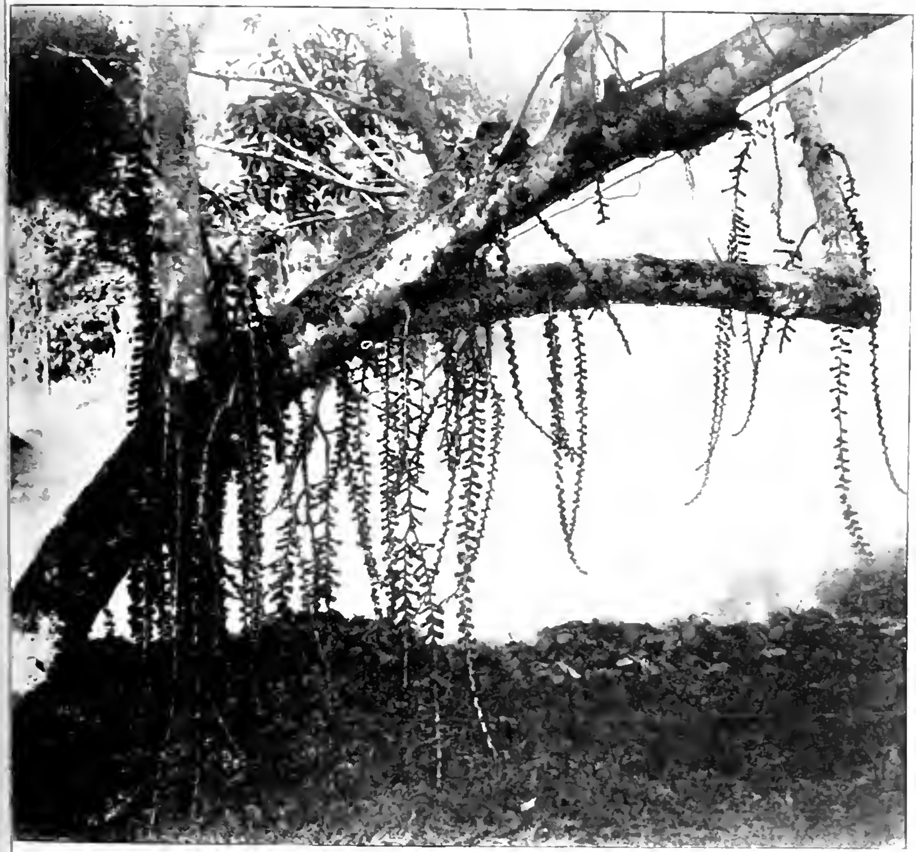

FIG. 183. Ficus sp. 'Minahassae.' Cauliflorous. Botanic garden at Buitenzorg. From a photograph by Treub.

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[1] Alf. Moller, I. p. 3.

Nevertheless, as was stated before[1], saprophytic fungal vegetation in tropical forests is much less striking than it is in the cool forests of higher latitudes, for in the tropics it is chiefly composed of small and even microscopic forms and includes but few large Hymenomycetes. Alfred Moller, in his mycological contributions from South Brazil[2], has, however, proved that very striking and large forms of fungi are not wanting among tropical humus-plants.

Phanerogamic saprophytes are in the number of species much more numerous between the tropics than beyond them, and are largely inhabitants of the dampest and shadiest rain-forest. Yet even there they do not strike the eye, but this is partly due to the fact that the commonest species are for the most part very small and delicate, so that even when very numerous they do not make much show. The few larger forms—those about the size of our Neottia or of Monotropa are to be reckoned amongst them—as far as my observations go, occur only singly, whilst many of the small forms grow socially and occur sporadically in abundance; for instance the orchidaceous Wullschlägelia aphylla and the burmanniaceous Apteria setacea, in Dominica; the gentianaceous Voyria trinitatis in Trinidad; Lecanorchis javanica and Burmannia (Gonyanthes) candida neither of which is quite devoid of chlorophyll, in Java. These, however are isolated productions. I have often roamed for hours through tropica rain-forests in America and Java without seeing a single phanerogami saprophyte[3].

The saprophytes of the tropical rain-forest occur both on firm, mainl mineral, soil which is however permeated with humus-solutions, as wel as on loose, slightly decomposed mould and on still coherent thougl rotting stems and branches. Thus, in Dominica, we found Burmanni capitata on decomposing stems and branches, and the sole habitat o which I found Epipogon nutans in Java was the rotten trunk of a tree which in Germany might have led me to expect Buxbaumia indusiat but not a saprophytic orchid. I found however on this trunk, crowde together as in a nest, twenty specimens of this remarkable Epipogon in a stages of development.

In respect to their occurrence as revealed by the naked eye, holoparasite show relations not very different from those presented by saprophytes, bu large forms are more frequent among them. For instance, I observe far more numerous large parasitic Polyporeae on trees than large sapro phytic fungi. Among phanerogamic parasites, as among saprophyte social species are common. This is, for instance, true to a large exter of the Javanese Balanophora elongata, but I know this plant only in th

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[1] See p. 226.

[2] Alf. Möller, II-V.

[3] Even the sharp eyes of Pa-Idang, the excellent guide to the Javanese forest, could n [illegible] cases discover 'white orchids.'

high mountainous regions above the tropical climate. We saw in the dark rain-forest of the interior of Trinidad the brownish-red inflorescences of Helosis guyanensis, like densely crowded raspberries, springing from the otherwise bare soil.

The most wonderful of all parasites are, as is well known, the Malayan species of Rafflesia, foremost among which is Rafflesia Arnoldi in Sumatra, with solitary flowers measuring one meter in diameter. Personally, I have seen in its native home only the somewhat smaller R. Patma, and that on Noesa Kambangan, a small island of South Java, where it grows socially, if not in an actual virgin forest, at any rate in one that has been abandoned to itself for many years. I wrote the following note on the spot regarding its habitat and occurrence: 'After traversing the narrow belt of littoral forest, one reaches a thin forest of medium height, which uninterruptedly clothes the stony southern slopes. The soil is almost entirely covered by a herbaceous aroid about a meter high. On the trees are hanging the very long cords of a Cissus, the bases of which, as with most lianes, creep along the ground over long stretches. These prostrate parts of the liane, often several meters long, are, as Junghuhn has already correctly stated, the parts that bear the parasite. They bear the buds in rows, and in stages of development up to the size of one's head, alternating with rotten black remains of flowers and empty basin-like outgrowths, that served as the matrix of flowers now vanished. The sole perfect flower, that apparently has only just opened, possesses a bright tobacco-brown colour and emits a foetid odour. Insects, however, are not visible, either within or on the flower' (February, 1890).

Not within the rain-forest, but in more open and brighter situations, I met with the most striking examples of tropical parasitic growth. Specially remarkable was a tract of country in the West Indian island of Grenada, which was quite overrun by Cuscuta americana: most of the trees were completely covered by a bright yellow veil, that hung down around them to the ground and covered the shrubs and herbs as far as the nearest trees. At many places, for instance in Java and especially in the neighbouring thousand islands, species of Cassytha appeared in great abundance as a reddish-yellowish green felt-like coating over woody and herbaceous plants.

Cuscuta contains a little chlorophyll, Cassytha considerably more. This sequence leads to the foliaged hemiparasites, which are represented in the tropics by the Loranthaceae alone, although by numerous species of several genera. Mingled with epiphytes, from which they are distinguishable only by their root-system, they contribute to the luxuriance of the vegetation covering the branches of the trees, while many of them develop a magnificent show of blossom.

SELECT LITERATURE.

1. General Character of the Tropical Rain-forest.

Berg, A. Physiognomy of Tropical Vegetation in South America. Fourteen plates London, 1854.

Brandis, D. I. Suggestions regarding Forest Administration in the Madras Presidency. Madras, 1883.

—— II. Der Wald des äusseren nord-westlichen Himalaya. Verhandl. des naturh Vereins der preuss. Rheinlande und Westphalens. Bd. XLII. s. d.

—— III. The Forest-flora of North-West and Central India. With Atlas. London, 1874

Engler, A. Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete. Deutsch-Ost Afrika. Bd. V. Berlin, 1895.

Haberlandt, G. Eine botanische Tropenreise. Leipzig, 1893.

Hooker, J. D. Himalayan Journals. London, 1854.

Hooker, J. D., and Thomson. Introductory essay to the Flora Indica. London, 185

Humboldt, A. v. I. Aspects of Nature. English edition. Longmans and Murray London, 1849. Also as Views of Nature. English edition. Bohn, London, 185

—— II. Voyage aux régions équinoxiales du nouveau continent, fait en 1799–180 Livr. XI. Paris, 1807.

Junghuhn, Fr. Java, deszelfs gedaante, bekleeding en invendige structuur. Germa edition by Hasskarl. Bd. I. 1852.

Kittlitz, F. H. v. Twenty-four Views of the Vegetation of the Coasts and Islands the Pacific. English edition. London, 1861.

Kurz, S. Preliminary Report on the Forest and other Vegetation of Pegu. Calcutt 1875.

Martius, C. F. P. von. I. Die Physiognomie des Pflanzenreiches in Brasilie München, 1824.

—— II. Tabulae physiognomicae. Flora brasiliensis. I–IX. 1840 bis 1847.

Möller, Alf. Aus dem südbrasilianischen Urwalde. Forstliche Blätter. 1891.

Pechuel-Lösche, E. Die Loango-Expedition. Abth. III, Hälfte 1. Leipzig, 1882.

Pöppig, E. F. Reise in Chile, Peru und auf dem Amazonenstrome während de Jahre 1827–1832. Leipzig, 1835–1836.

Saint-Hilaire, A. de. Tableau de la végétation primitive dans la province de Min Geraes. Annales des sciences naturelles. Tom. XXIV. 1831.

Schimper, A. F. W. Die Gebirgswälder Java's. Forstlich-naturwiss. Zeitschrift. 189

Wallace, A. R. Tropical Nature: with other essays. London, 1878.

Warburg, O. Vegetationsschilderungen aus Südost-Asien. Engler's Jahrbüche Bd. XVII. 1893.

Zollinger, H. Ueber Pflanzenphysiognomie im Allgemeinen und diejenige de Insel Java insbesondere. Zürich, 1835.

2. Oecological Characteristics of Plants growing in the Tropical Rain-forest.

Brown, R. An Account of a new Genus of Plants, named Rafflesia. Trans. Lin Society. Vol. XIII. 1820.

Drude, O. I. Palmae. Engler u. Prantl, Die natürlichen Pflanzenfamilien. II. The literature is cited.

—— II. Cyclanthaceae. Ibid.

Eichler, A. W. Anona rhizantha. n. sp. Jahrb. des botan. Gartens zu Berli Bd. II. 1883.

Engler, A. I. Triuridaceae. Engler u. Prantl, Die natürlichen Pflanzenfamilie II. 1. The literature is cited.

Engler, A. II. Araceae. Ibid. II. 3.
—— III. Burmanniaceae. Ibid. II. 6.
—— IV. Loranthaceae. Ibid. III. 1.
—— V. Balanophoraceae. Ibid.
Esser, P. Die Entstehung der Blüthen am alten Holze. Inaug. Diss. Bonn, 1887.
Figdor, W. Ueber Cotylanthera Bl. Ein Beitrag zur Kenntniss tropischer Saprophyten. Annales du Jardin botanique de Buitenzorg. Vol. XIV. 1896.
Giesenhagen, C. Die Hymenophyllaceen. Flora. Jahrg. LXXIII. 1890.
Gilg, E. Vitaceae. Engler u. Prantl, Die natürlichen Pflanzenfamilien. III. 5.
Goebel, K. I. Ueber epiphytische Farne und Muscineen. Annales du Jardin botanique de Buitenzorg. Vol. VII. 1889.
—— II. Pflanzenbiologische Schilderungen. Die Epiphyten. Bd. II. 1893.
Groom, P. I. On Bud-protection in Dicotyledons. Trans. Linn. Society. Series 2. Vol. III. 1892.
—— II. Contribution to the Knowledge of Monocotyledonous Saprophytes. Journ. Linn. Society. Botany. Vol. XXXI. 1895.
Haberlandt, G. I. Anatomisch-physiologische Untersuchungen über das tropische Laubblatt. Drei Theile. Sitzungsberichte der Wiener Akademie. Bd. CI. 1892. Bd. CIII. 1894. Bd. CIV. 1894.
—— II. Eine botanische Tropenreise. 1893.
Hieronymus, G. Santalaceae. Engler u. Prantl, Die natürlichen Pflanzenfamilien. III. 1. The literature is cited.
Huth, E. Ueber stammfrüchtige Pflanzen. Berlin, 1888. Contains many references to the older literature.
Johow, Fr. I. Zur Biologie der floralen und extrafloralen Schauapparate. Jahrb. des k. botan. Gartens zu Berlin. Bd. III. 1884.
—— II. Die chlorophyllfreien Humusbewohner West-Indiens. Pringsheim's Jahrbücher. Bd. XVI. 1885.
—— III. Die phanerogamen Schmarotzerpflanzen. Santiago, 1890.
Jungner, J. R. Anpassungen der Pflanzen an das Klima in den Gegenden der regenreichen Kamerungebirge. Botanisches Centralblatt. Bd. XLVII. 1891.
Karsten, G. I. Untersuchungen über die Familie der Chroolepideen. Annales du Jardin botanique de Buitenzorg. Vol. X. 1892.
—— II. Morphologische und biologische Untersuchungen über einige Epiphytenformen der Molukken. Ibid. Vol. XII. 1894.
Koorders, S. H. Ueber die Blüthenknospen-Hydathoden einiger tropischen Pflanzen. Annales du Jardin botanique de Buitenzorg. Vol. XIV. 1897.
Koorders, S. H., en Valeton, Th. Bijdrage tot de kennis der boomsoorten van Java. I–IV. Batavia, 1894–1897.
Krasser, Fr. Melastomataceae. Engler u. Prantl, Die natürlichen Pflanzenfamilien. III. 7. The literature is cited.
Lindau, G. Acanthaceae. Ibid. IV. 3 b.
Martius, Ph. v. Ueber die Vegetation der unechten und der echten Parasiten. Münchener Gel. Anzeigen. 1842.
Mettenius, G. H. Ueber die Hymenophyllaceen. Abh. d. math.-phys. Klasse der kgl. sächs. Gesellsch. d. Wissensch. Bd. VII.
Möller, Alf. I. Aus dem südbrasilianischen Urwalde. Forstliche Blätter. 1891.
—— II. Die Pilzgärten einiger südbrasilianischen Ameisen. Botan. Mittheil. aus den Tropen. Heft VI. Jena, 1893.
—— III. Brasilische Pilzblumen. Ibid. Heft VII. Jena, 1895.
—— IV. Protobasidiomyceten. Ibid. Heft VIII. Jena, 1895.
—— V. Ueber einige besonders auffallende Pilze Brasiliens. Botanisches Centralblatt. Bd. LXXII. 1897.

Müller, Fr. I. Notes on some of the Climbing Plants near Desterro in South Brazil. Journ. Linnean Soc. Botany. Vol. IX. 1867.

—— II. Zweigklimmer. Kosmos. Bd. VI. 1887.

—— III. Die Keimung einiger Bromeliaceen. Berichte der deutschen botanischen Gesellschaft. Bd. XIII. 1895.

Niedenzu, F. Malpighiaceae. Engler u. Prantl, Die natürlichen Pflanzenfamilien. III. 4.

Petersen, O. G. Musaceae, Zingiberaceae, Cannaceae, Marantaceae. Ibid. II. 6.

Pfitzer, E. Orchidaceae. Ibid. II. 6. The literature is cited.

Potter, M. C. Observations on the Protection of Buds in the Tropics. Journ. Linnean Soc. Botany. Vol. XXVIII.

Prantl, K. Morphologie der Gefässkryptogamen. Heft I. Leipzig, 1875.

Raciborski, M. Die Schutzvorrichtungen der Blüthenknospen. Flora. LXXXI. Ergänzungsband zu Jahrgang 1895. p. 178.

Radlkofer, L. Sapindaceae. Engler u. Prantl, Die natürlichen Pflanzenfamilien. III. 5.

Schenck, H. Beiträge zur Biologie und Anatomie der Lianen, im Besonderen der in Brasilien einheimischen Arten. Theil I. Beiträge zur Biologie der Lianen. Theil II. Beiträge zur Anatomie der Lianen. Botan. Mittheil. aus den Tropen. Heft IV. Jena, 1892. Heft V. Jena, 1893.

Schimper, A. F. W. I. Ueber Bau und Lebensweise der Epiphyten Westindiens. Botanisches Centralblatt. Bd. XVII. 1884.

—— II. Die epiphytische Vegetation Amerikas. Botan. Mittheil. aus den Tropen. Heft II. Jena, 1888.

—— III. Ueber Schutzmittel des Laubs gegen Transpiration, vornehmlich in der Flora Java's. Monatsberichte der Berliner Akademie. Bd. VII. 1890.

Schumann, K. Cactaceae. Engler u. Prantl, Die natürlichen Pflanzenfamilien. III. 6. The literature is cited.

—— II. Bignoniaceae. Ibid. IV. 3.

—— III. Rubiaceae. Ibid. IV. 4.

Solms, H. G. zu. Rafflesiaceae. Ibid. III. 1. The literature is cited.

—— II. Pandanaceae. Ibid. II. 1.

Stahl, E. I. Regenfall und Blattgestalt. Annales du Jardin botanique de Buitenzorg. Vol. XI. 1893.

—— II. Ueber bunte Laubblätter. Ein Beitrag zur Pflanzenbiologie. II. Ibid. Vol. XIV. 1896.

Szyszylowicz, J. v. Marcgraviaceae. Engler u. Prantl, Die natürlichen Pflanzenfamilien. III. 6. The literature is cited.

Treub, M. I. Iets over Knopbedekking in de Tropen. Handelingen van het eerste Nederlandsch. Natuur- en Geneeskundig Congres, Amsterdam, 1887. (Reference in Botanisches Centralblatt. Bd. XXXV. 1888. p. 328.)

—— II. Sur une nouvelle catégorie de plantes grimpantes. Annales du Jardin botanique de Buitenzorg. Vol. III. 1882.

—— III. Observations sur les plantes grimpantes du Jardin botanique de Buitenzorg. Ibid. Vol. IV. 1883.

—— IV. Les bourgeons floraux du Spathodea campanulata Beauv. Ibid. Vol. VII. 1889.

Warburg, O. Begoniaceae. Engler u. Prantl, Die natürlichen Pflanzenfamilien. III. 6. The literature is cited.

Went, F. A. F. C. Ueber Haft- und Nährwurzeln bei Kletterpflanzen und Epiphyten. Annales du Jardin botanique de Buitenzorg. Vol. XII. 1893.

Wiesner, J. Zur Physiologie von Taeniophyllum Zollingeri. Sitzungsberichte der Wiener Akademie. Bd. CVI, Abth. I. 1897.

Wittmack, L. Bromeliaceae. Engler u. Prantl, Die natürlichen Pflanzenfamilien. II. 3. The literature is cited.

CHAPTER V

TROPICAL DISTRICTS WITH PRONOUNCED DRY SEASONS

1. General Characteristics of the Vegetation in Periodically Dry Tropical Districts. Formations. Xerophilous trees. Xerophilous shrubs. Lianes. Epiphytes. **2. Woodland Formations in Periodically Dry Tropical Districts.** i. *General Remarks.* Transformation in woodland vegetation by gradual transition from constantly humid to periodically dry districts. Chief types of woodland: monsoon-forest, savannah-forest, thorn-forest. ii. *Tropophilous and Xerophilous Woodland in India.* Forest vegetation in Pegu according to Kurz. Forests of Tectona grandis in East Java. iii. *Woodland in Tropical East Africa.* Engler's description of the formations. iv. *Tropophilous and Xerophilous Woodland in Tropical America.* Savannah-forest in Venezuela. Thorn-bushland (caatinga) of Brazil. Thorn-bushland on the limestone hills in Minas Geraes. **3. Tropical Grassland Formations.** i. *General Character of Savannah.* ii. *Savannah in Africa.* Savannah on the Loango coast according to Pechuel-Lösche. The baobab. East African savannah according to H. Meyer and Engler. iii. *Savannah in America.* The llanos. The campos of Brazil according to Warming.

1. GENERAL CHARACTERISTICS OF THE VEGETATION IN PERIODICALLY DRY TROPICAL DISTRICTS.

Tropical districts with either one or two pronounced dry seasons, several months long, particularly occupy the interior of continents, and include much greater areas than do those with a constantly humid climate. Their vegetation never attains the luxuriance of the rain-forest, and above all bears the impress of a less favourable environment. The dry periods bring the vegetation of the tropics oecologically nearer to that of the zones that are cold in winter, because physiological dryness of soil is caused by a scarcity of atmospheric precipitations, as well as by cold.

Whilst the constantly humid districts are uniformly clad with evergreen rain-forest, the periodically dry districts present a much more varied appearance as regards vegetation, inasmuch as slight differences in the climate cause a rapid change in the type of formation, and edaphic influences are much more effective than where the soil is always moist.

Districts with very abundant rainfall during the wet season, if they have pronounced dry seasons accompanied by great heat, are clad with luxuriant forests the trees of which lose their hygrophilous foliage during the dry season and renew it at or immediately before the commencement of the monsoon-rains; apart from this they have only xerophilous organs well protected against drought. Such tropophilous forests, whose alternating hygrophilous and xerophilous character is regulated by the monsoon, have been termed *monsoon-forests*[1]. Regions with less abundant rainfall are, according to the character of their climate, occupied by xerophilous woodland (savannah-forest, thorn-forest, thorn-bushland) or by grassland, usually of the savannah type. Still greater drought induces the desert character. Tropical desert will be discussed in connexion with temperate desert[2].

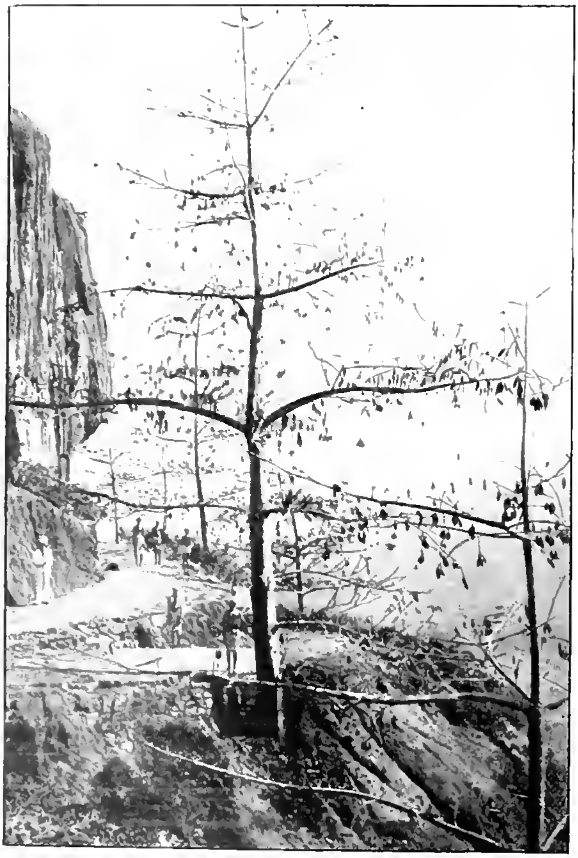

FIG. 184. Bombax malabaricum in the dry season bearing fruit. Ceylon. From a photograph.

The oecological physiognomy of vegetation in periodically dry districts is quite different from that in constantly humid ones especially if we contrast with humid districts those districts which, above all, have a scanty rainfall and show xerophilous vegetation at all seasons o the year. Here the danger of desiccation especially threatening to tall plants, has led to the evolution o highly *xerophilous trees* forming an extremely peculiar tree-type which, in particular, shows it characteristic features in savannah and thorn-forest.

Investigations are greatly needed in regard to the structure and conditions of existence of tropical xerophilous trees, which find no analogue in Central Europe and first appear, in a feebly defined form, in th Mediterranean region.

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[1] See p. 260.

[2] See p. 616.

Pechuel-Lösche gives the following vivid picture of the West African savannah :—

'Many of these characteristic plants are developed only as gnarled and deformed shrubs or dwarf-trees, but many also as lofty trees, some species even ranking among the giants of the vegetable kingdom. They all, however, have this in common, that they thrive only in the open country, in the sunny, well-aired, and dry grassland : it is true, that in places they may combine to form light groves and resemble the thin oakwoods of our pasture-lands, but they never appear in the form of forests. On the contrary, they perish beyond recall in the cover of a well-grown forest, and therefore inhabit neither fringing-forest nor rain-forest. Yet they occur, not infrequently, on the borders of the savannah, where grassland begins.'

The majority of the trees of xerophilous woodland and savannah are of low stature, with a relatively thick stem, which is usually invested with an extremely fissured thick bark; the crown is frequently arranged in tiers (Fig. 184), more often however it is umbrella-shaped, and may even be flattened almost like a disk (Fig. 185). *Umbrella-trees figure in all descriptions of the savannah and of the open forest-formations of the tropics.* I have seen them determining the physiognomy of the vegetation in the savannah of Venezuela, and also occurring in the alpine savannah of Java, which will be subsequently described. Warming portrays them, although in less regular form, in connexion with the campos of Brazil. Hans Meyer says of the East African savannah: 'Whether a tree have a single stem, or like a shrub ramifies from close to the ground, in either case it strives first to grow as high as possible and then to expand horizontally, like a mushroom or an umbrella. It is always flat above as if it were clipped. Thousands and thousands of these usually greyish-brown umbrella-trees, scattered over the grass, through which the red soil gleams and which is brown during the greater part of the year, impart a peculiar physiognomy to the landscape[1].' Brandis mentions as characteristic of the open, dry bush-formations of Southern India, Acacia planifrons (Fig. 126), called umbrella-thorn because its crown, consisting of a mass of twisted knotty branches, thorns, and finely pinnate leaves, spreads out at the top of the stem like an umbrella. That the umbrella-form is an adaptation to the climate appears from the fact that it occurs under similar external conditions in representatives of very different families, for instance the Mimosaceae, Caesalpiniaceae (Cassia), Burseraceae, Myrtaceae. As a protective device against excessive transpiration, such as might be expected in an open xerophilous formation, this spreading out of the foliage appears to be highly unsuitable. As a protection against the mechanical and desiccating action of the wind, it is, on the contrary, proper to the end in view, as it offers a narrow edge to the force of the wind. It is evident

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[1] Engler, op. cit., p. 58.

that such protection is required in the open savannah country as well as on high mountains. The same is true of the trees with their branches in tiers, such as Terminalia Catappa, Bombax malabaricum, which I have seen likewise only in open situations and in well-lighted bush. Much is to be said for the view, which Reiche has already put forward, that the umbrella-

FIG. 185. Acacia of umbrella-form. From the East African savannah. After Engler.

forms have arisen as a means of protection against the wind, but experiments alone can decide the question.

Xerophilous trees of the tropics are mostly bare during dry weather their foliage, although present only during the rainy season, is usually firm and provided with elaborate protective devices against transpiration Pinnate leaves are specially frequent, and by their mobility, which permits them to assume the best position for the time being, they are thoroughly in harmony with the climatic conditions. Evergreen trees, on the other hand, usually have simple, often very hairy, leaves, which in many cases contain so much silica that they assume a consistency resembling sheet-metal, and, in the wind, rattle with a metallic sound, as in the proteaceous Rhopala complicata, a characteristic tree of the llanos. The foliage-buds are provided with a coating of protective scales as thick as, or even thicker than, that of trees of the temperate zones (Fig. 186). Only the flowers apparently dispense with a corresponding protection, and even frequently possess large delicate corollas, although they often open at the height of the dry season, and therefore demand large quantities of water for transpiration.

FIG. 186. Xerophilous foliage-buds. From the Brazilian campos. Left hand: Myrcia longipes. Centre: Eugenia Jaboticaba. Right hand: Eugenia dysenterica. After Warming.

The volume of the wood in comparison with that of the foliage is greater than in hygrophilous trees, and the cortex is frequently covered by a massive scaly bark (Fig. 187).

FIG. 187. Sweetia dasycarpa. From the Brazilian campos. Transverse section through the stem. After Warming.

Besides the protective devices against drought that have been mentioned, and which occur and are similarly differentiated in xerophytes of higher latitudes, there are among the tropical woody plants cases of special and very peculiar adaptation. Thus many tropical trees owe the faculty not only of growing in very dry regions, but also of attaining large and even gigantic dimensions, to the fact that they *store up large supplies of water for the dry season.* Amongst these trees is the mighty baobab (Adansonia digitata) of the African savannah, which will be dealt with subsequently; in addition the wonderful bottle-trees (Cavanillesia arborea (Willd.). K. Schum., and other Bombaceae) of the open thorn-bush of Central Brazil, the trunks of which, swollen like a cask up to a thickness of five meters (Fig. 193), serve as water-reservoirs; also, in the same forests, Spondias tuberosa (Anacardiaceae), the tuberous swellings of whose roots become filled with water. Finally, in contrast with rain-forest and monsoon-forest, xerophilous woodland, especially in the thorn-forest, contains arborescent succulents, particularly species of Cereus in tropical America (Fig. 128), and of Euphorbia (Fig. 198) in Africa.

The *shrubs of the savannah* are not less xerophilous than the trees. Their hypogeous parts are very strongly developed as compared with their epigeous parts, and often form such a massive system of thick lignified axes that, following Lund and Liais, we may describe some of them, such as those of Andira laurifolia and Anacardium humile of the campos, as hypogeous trees. In Andira, for instance (Fig. 188), the system of rhizomes, consisting of branches as thick as one's arm, frequently covers an area ten meters in diameter, whereas the epigeous foliage-shoots are thin and never more than a meter in height. Such hypogeous axes appear to serve as water-reservoirs, as also do the tuberous woody rhizomes that occur on numerous small shrubs and bushes in the campos (Figs. 203, 204).

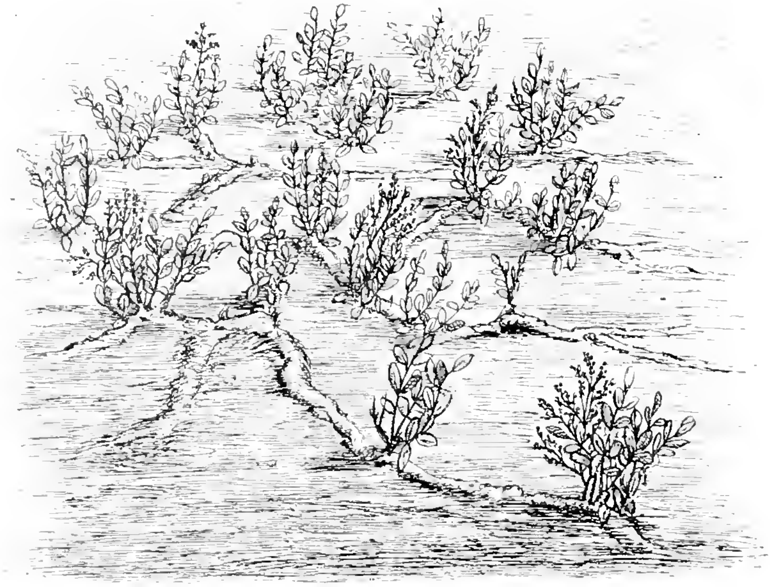

Fig. 188. Andira laurifolia. From the Brazilian campos. After Warming.

Thin woody lianes occur in xerophilous woodland, in particular in thorn-forest, but disappear in the savannah; but in the savannah, for instance in the Brazilian campos, there are found erect shrubs belonging to families and genera that with these exceptions include only climbing forms. Schenck considers it probable that many of these shrubs have been derived from lianes and are to be considered as cases of reversion to an erect mode of growth[1]. Lianes also disappear in the low shrub-formations of Northern Brazil. In savannah-forest and thorn-forest, into which savannah and shrublands pass when the humidity increases, they are sometimes found in small numbers and poorly developed.

Epiphytes belonging to the Phanerogamia and Pteridophyta are very scantily represented on the trees in well-lighted xerophilous savannah-woodland, or are entirely absent. They become more abundant as soon as the trees grow closer together, and many a savannah-forest is by no means poorly decked with Bromeliaceae, Orchidaceae, Cactaceae, and ferns. Even epiphytic species of Ficus, and perhaps of Clusia, occur in savannah, where they appear to be confined to palms, the persistent petiole-bases of which serve as receptacles for the young plants (Fig. 200). In all the epiphytes of such dry formations the xerophilous character is most pronounced; all protective measures against the loss of water, and all devices for the collection and retention of rain-water, with which we are already acquainted, are specially well developed in them. Yet, with the exception of the figs, they are only small forms.

Eminently characteristic as is this epiphytic flora of the xerophilous tropical district, and perfectly as it is adapted to the climatic conditions prevailing in the district, yet it is composed exclusively of species from the rain-forest. The highest branches of the virgin-forest trees, those in fact that receive sunlight almost without hindrance, are the homes of the savannah epiphytes. It is from the virgin forest that they have colonized the dry tracts of country[2].

2. WOODLAND FORMATIONS IN PERIODICALLY DRY TROPICAL DISTRICTS.

i. *GENERAL REMARKS.*

The change in the vegetation on passing from a constantly humid tropical district into one with abundant rainfall but periodically dry, appears only slight during the wet season, but is manifested in the dry season, particularly by the great number of defoliated trees.

Trees that are at times bare of foliage are very scantily represented in the rain-forest and are usually not noticed at all, the less so that their defoliation and foliation have frequently no connexion with the seasons of the year. If however one proceeds during the dry season, for instance, from the constantly humid West Java to East Java, where there is very little rain during the east monsoon, the foliage becomes very thin, as it has been completely shed by many trees and partially so by others. In addition to this, slight influences exerted by the soil suffice to call into being the teak-forest, which is almost completely leafless in the dry

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[1] Schenck, I, p. 60.

[2] See p. 199.

season. The appearance is quite different from that presented during the so-called dry season in West Java, where the difference in the vegetation during the west and east monsoons respectively is indeed visible, but much less marked in the lowlands, for example at Buitenzorg, and hardly visible at all in the mountains.

To the north of the Cordilleras on the coast of Venezuela, as well as among them in the moist valley of Caripe, during the dry season (February) I found myself surrounded by dense evergreen rain-forest, whereas south of the Cordilleras on the side of the llanos the open savannah-forest, composed almost exclusively of leafless trees, would have presented a wintry aspect had not many trees and epiphytes been in full flower.

The periodically deciduous tropical forests and the low xerophilous woodlands of the tropics have hitherto been much less investigated than has the rain-forest. It is however certain that they display much variety. Like rain-forest they form chiefly mixed wood, in which hardly a single species of tree can be described as dominant; occasionally however one species gets the upper hand and may even form nearly pure woods, as for instance Tectona grandis in East Java. As regards the height and mode of growth of the trees, as well as of the underwood and herbaceous vegetation covering the soil, there are numerous modifications, which, from the point of view of the Indian forester, have been utilized to constitute numerous types and subtypes. But, without straining a point, they can all be deduced from the chief types that we have established, *monsoon-forest, savannah-forest, and thorn-forest*, or from intermediate forms of these[1].

ii. *TROPOPHILOUS AND XEROPHILOUS WOODLAND IN INDIA.*

Kurz has given a detailed description of the periodically deciduous forests in Pegu, where however they owe their varied characteristics not only to the climate, but also in a high degree to the soil. Coming nearest in physiognomy to the evergreen rain-forests, are those deciduous woods termed by Kurz 'mixed forests,' which according to our terminology belong to the monsoon-forests and form in Burma the true home of the valuable teak-tree (Fig. 190). Here the trees average in height 70–80 feet, but in many parts of the country are even 120 feet high ('upper mixed forests'). They grow straight and are often accompanied by lianes. Their epiphytes are practically confined to the tops of the trees. The intervals between the trees are frequently filled with a tall bamboo thicket; but shrubby and herbaceous vegetation, particularly grass, is very scanty (Figs. 125 and 189).

Other forests of Pegu, especially those that Kurz names 'open forest,' perhaps also his 'dry forest,' are xerophilous forests of low or middle height (30–60 feet high) which belong to our type of savannah-forest. Here

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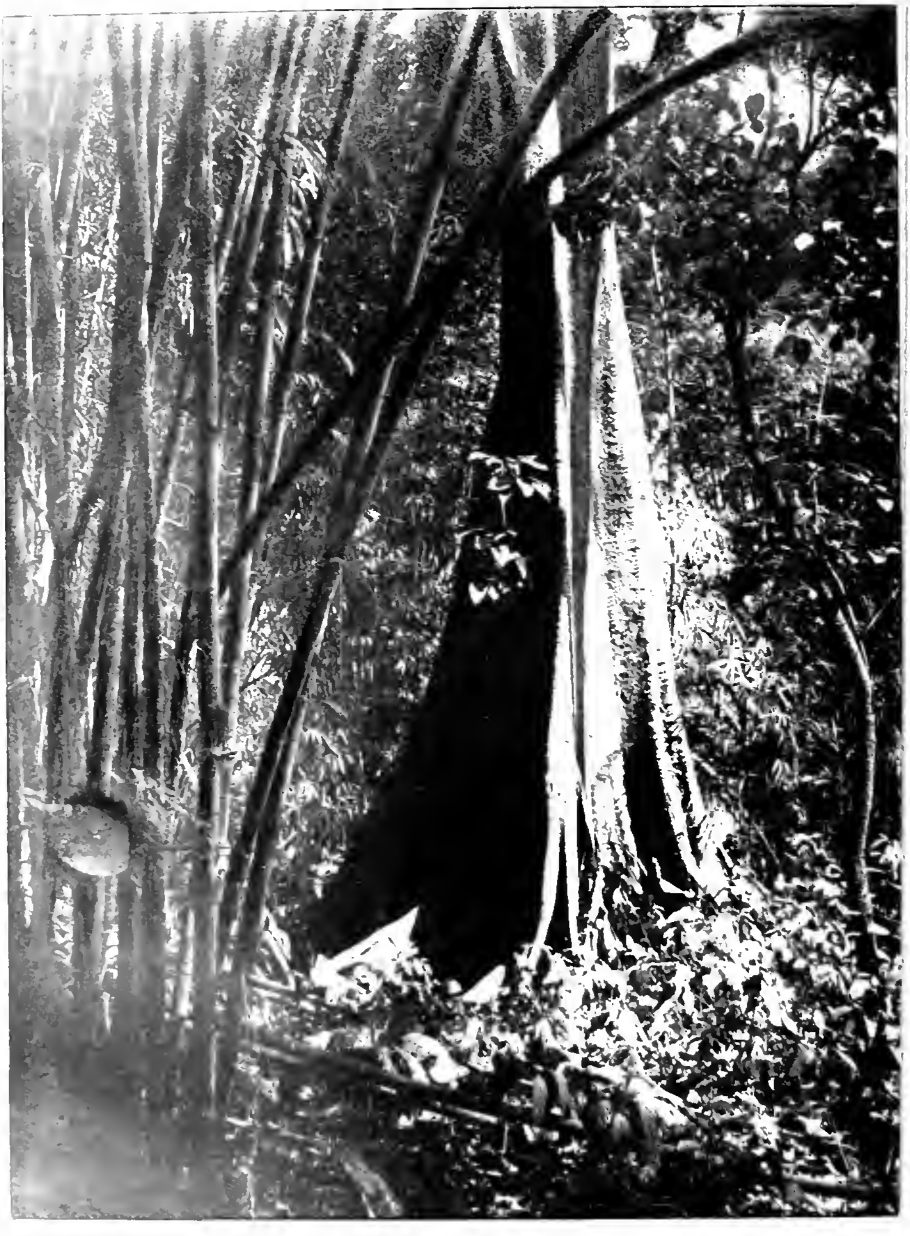
[1] See p. 260.



[illegible] Forest, Pegu. [illegible] Reserve. Tharawadi. *a* Cephalostachyum [illegible] sp. From a photograph by J. W. Oliver.

he forest is thin ; trunks and branches are thick and gnarled, covered with rich epiphytic flora. Lianes and shrubs are poorly represented, whereas he soil is covered with a turf composed either of grass and perennial erbs, or of grass alone.

Kurz distinguishes two forms of his 'mixed forest'—'upper mixed forest' and 'lower ixed forest.' In the 'upper' the trees are taller than in the 'lower,' but less varied.

Large bamboos play an important part in the '*upper mixed forest*' (Fig. 189) ; eak is as a rule present ; Sterculia villosa and S. urens, Milletia Brandi-iana, Grewia elastica, Duabanga grandiflora, Erythrina stricta and E. suberosa re the characteristic trees, but many other species are represented. Shrubs are cantily and badly developed, but we have Helicteres plebeja, Thespesia Lampas, rewia hirsuta, and others. Lianes are also few in number, represented amongst thers by Combretum, Calycopteris, Abrus precatorius. Accordingly the interior f the forests is very easy of access. A grassy covering to the ground is quite xceptional, and then consists of the so-called teak-grass, a species of Pollinia. erns are scanty on the ground, and only those species are present that withstand reat drought. Numerous herbaceous plants spring from the soil, but without overing it. Bryophyta are very scarce and confined to moist sandstone rocks Hypnum, Fissidens, Marchantia). Epiphytes are not numerous, and occur only n the tops of the trees.

The '*lower mixed forest*' averages 70 to 80 feet in height, sometimes attaining oo feet ; it is richer in lianes and also in shrubs, and therefore denser than the upper mixed forest.' Kurz mentions about fifty species of trees as the leading onstituents of this forest, and about as many more as rather of local occurrence. Ve find among the former the most diverse families represented :—Sterculiaceae, Ialvaceae, Bombaceae, Dilleniaceae, Sapindaceae (Schleichera), Anacardiaceae dina, Mangifera, Spondias), Combretaceae (various species of Terminalia, Ano-eissus), Lythraceae (various species of Lagerstroemia), Samydaceae (Homalium), iospyraceae, Bignoniaceae (Spathodea, Heterophragma, Stereospermum, Calo-anthes), Euphorbiaceae (Antidesma, Emblica), Mimosaceae (Albizzia), Rubiaceae arious species of Nauclea, Gardenia, Randia), Artocarpaceae (various species of icus), Myrtaceae (Barringtonia, Careya), Loganiaceae (Strychnos Nux-vomica).

Among the shrubs are in particular Thespesia Lampas (Malvaceae), Grewia irsuta (Tiliaceae), Premna, Clerodendron (Verbenaceae), Ceratogynum, Phyllan-hus, Baliospermum (Euphorbiaceae), Desmodium, Flemmingia (Papilionaceae), two pecies of Calamus.

The lianes are extremely diversified. Kurz specially mentions more than fifty pecies, among them numerous Leguminosae (Butea, Spatholobus, Entada, Caes-lpinia of various species, Acacia, Dalbergia, Phaseolus, Pueraria, Mucuna, Dolichos, lezoneurum, Abrus precatorius), Menispermaceae (Stephania), Rhamnaceae (Zizi-hus, Gouania, Colubrina), Celastraceae (Celastrus), Sapindaceae (Stephania), itaceae (Vitis, many species), Rubiaceae (Paederia), Euphorbiaceae (Rottlera, ridelia), Verbenaceae (Symphorema, Congea), Combretaceae (Combretum of various pecies, Calycopteris), Cucurbitaceae (Zehneria, Luffa), Convolvulaceae (Argyreia f various species, Ipomoea), and others ; of Monocotyledones, Smilax and Scin-apsus ; also Gnetum scandens (Fig. 147) and Lygodium.

Among the herbs, which never cover the ground, the Scitamineae are prominent. Besides, there are numbers of grasses, Araceae, Compositae, Malvaceae, and so forth.

The trees bear as epiphytes, mosses (Neckera, Metirium), various common orchids, ferns and asclepiads, besides remarkably numerous and diversified parasitic Loranthaceae.

The savannah-forest in Pegu appears under various forms, which Kurz describes as 'eng-forest,' or 'laterite-forest,' 'low forest' and 'savannah-forest.' 'Eng' is the native name for Dipterocarpus tuberculatus, which is characteristic of the first form of forest.

'*Eng-forest*' occurs chiefly on laterite, but also, although in a less developed form, on various diluvial soils. The height of the leaf-canopy on pure laterite soil is about 30 to 40 feet, on more clayey or loamy soil about 70 to 80 feet. Most of the trunks have fissured thick scaly bark and remarkably thick knotty and crooked stems. Dipterocarpus tuberculatus predominates on purely laterite soils; on other kinds of soil it is scanty, or absent. More than forty other species of trees besides are usually abundant. There are Dipterocarpaceae (Shorea, Pentacme), Meliaceae (Walsura), Dilleniaceae (Dillenia), Celastraceae (Lophopetalum), Rhamnaceae (Zizyphus), Anacardiaceae (Buchanania, Melanorrhoea), Styracaceae (Symplocos), Diospyraceae (Diospyros), Myrsinaceae (Myrsine), Euphorbiaceae (Phyllanthus, Aporosa), Papilionaceae (Dalbergia, Xylia), Rubiaceae (Wendlandia, Nauclea, Randia, Gardenia), Combretaceae (Terminalia), Myrtaceae (Careya, Eugenia), Lythraceae (Lagerstroemia), Loganiaceae (Strychnos Nux-vomica), and many others intermingled in the greatest confusion. Growing between the trees there are bamboos (B. Tulda and B. stricta), an acaulous palm (Phoenix acaulis), low very sparse shrubs, among which the author, strangely enough, also includes large herbaceous plants, even annuals, and a few lianes that scarcely climb. The grass on the ground is usually very richly developed (Andropogoneae, Paniceae, Cyperaceae), and is intermingled with numerous small herbaceous plants (Malvaceae, Acanthaceae, Rubiaceae, Campanulaceae, Gentianaceae, Scrophulariaceae, Labiatae, Papilionaceae, Compositae, Scitamineae, Amaryllidaceae, Orchidaceae, Commelinaceae, Eriocaulaceae, and so forth.

A crowd of epiphytic orchids, species of Hoya, ferns (Platycerium for instance), grow in great numbers on the branches of the trees.

The '*low forest*' resembles the eng-forest in its growth, and is to be considered as systematically intermediate between the eng-forest and the 'lower mixed forest.' Its soil is richly overgrown with Andropogoneae or with Imperata cylindrica.

Kurz's '*savannah-forest*' has the same height as the eng-forest. It grows on deep alluvial soil, especially near rivers. The trunks of the trees are very short, often hardly taller than the so-called elephant-grass (species of Andropogon, Coix, Saccharum, Phragmites) that covers the ground; the crowns are very strongly developed and often flattened above. The species of trees are partly identical with those in the 'lower mixed forest.' It is a typical savannah-forest.

The greatest part of the forest in *East Java* may be described as a transition form between rain-forest and monsoon-forest, but edaphic influences there, as generally in climatic transitional districts, are very

Fig. 190. Monsoon-forest, Burma. Bwet Reserve, Tharawadi. Tectona grandis: *a* mature tree. *b* young tree. *c* dodm. *d* Acacia Catechu. *e* Bambusa in flower. From a photograph by J. W. Oliver.

effective, and occasion a richer differentiation in the kind of vegetation covering the soil than in West Java, where the vegetation appears to be practically dependent on climate only. Particularly in East Java there occurs on soil that easily dries up or that is comparatively impervious, the djati-forest formation, a typical tropophilous deciduous forest.

The *djati-forest* owes its name to the economically valuable djati-tree, Tectona grandis—the teak-tree (Fig. 190), which has a wide distribution over ontinental India, yet only in Java forms pure forests in which other trees ccur merely as subsidiary species. The teak-tree is by no means a giant, ither in height or in thickness of stem. It is at most 25 meters high. Its cordate leaves, reminding one of those of Catalpa, are very large, and he violet flowers, that open in the middle of the rainy season, are arranged n pyramidal panicles. The trunk possesses a light coloured bark and is levoid of epiphytes; on the other hand, figs (species of Urostigma) requently colonize the branches. During the dry season (June until ctober) the teak is quite leafless and displays its new leaves in November ith the advent of the west monsoon.

Cordes has given a detailed description of the oecology and the flora of he natural djati-forest of East Java—artificial teak-forest occurs in West ava, as well as in British India.

In contrast with the rain-forest of West Java the appearance of the djati- rest is very different at different seasons of the year. In August and eptember, at the height of the dry season, the picture the forest presents almost wintry. The vast majority of the trees, among them especially e teak-tree, are quite leafless, and the ground is covered by a rustling yer of their dry leaves, which do not decay until the rainy season. The ees accompanying the teak are more recognizable in the dry season than uring the rains. Acacia leucophloea is known by its umbrella-shaped rown; Albizzia procera by its bark resembling that of birch. Some ees remain green, among them the commonest companion of the teak, utea frondosa, which in contrast with the teak adorns itself at the height the dry season with its large fiery papilionaceous flowers. Evergreen so are the sapindaceous Schleichera trijuga, the mimosaceous Albizzia ipulata, with a regular umbrella-shaped crown, and the fig-trees perched n the branches of other trees.

Between the tall trees numerous smaller ones grow, especially Emblica ficinalis, Gaertn., a euphorbiad, also Dillenia aurea, and other plants. alms are very rare, bamboos occur here and there. Shrubby vegetation richly developed and varied. The Leguminosae are specially numerous, r instance Acacia tomentosa, Willd., species of Cassia, Papilionaceae; but ibiscus Lampas also frequently shows its large yellow flowers. The nes are all thin-stemmed and chiefly Papilionaceae, such as Abrus pre- torius, species of Mucuna, and the like. The herbs vary greatly according to the nature of the soil. If it be moist and rich in humus, thickets of tall Zingiberaceae appear (species of Curcuma, Kaempferia, Elettaria), which open their beautiful flowers in the second half of the dry season (September—October). Specially dry soils are chiefly overgrown by tall grasses, such as the alang-alang (Imperata arundinacea) and glagah (Saccharum spontaneum, Linn.). Among the numerous, mostly inconspicuous, herbaceous perennials should be mentioned — Malvaceae (Urena, Sida), Compositae (Conyza lacera, Burm., Wollastonia, Adenostemma viscosum) some Araceae, very small Acanthaceae, Commelinaceae; finally, variou Amaryllidaceae that flower in the dry season (Eurycles amboinensis Pancratium zeylanicum, Crinum asiaticum).

Except the figs already referred to, epiphytes are very scanty in the djati-forest and are limited to a few small orchids, Asclepiadaceae an Aeschynanthus. The presence of epiphytic ferns is a sign that there ar hollows in the branches: and mosses occur only exceptionally on soun trees. On the other hand parasitic Loranthaceae are very common.

Most of the herbs mentioned are greatly reduced in size during the dry season, or, if annuals, are entirely absent. In July and August the Ama ryllidaceae flower, with the Butea; later on, in September and October many other plants join in, such as the already mentioned Zingiberacea but in particular most of the trees except the teak. Still greater is th show of blossom at the very commencement of the monsoon-rain, i November: then it is that most of the shrubs blossom, whereas the herb the development of whose flowers is closely dependent on metabolic activit usually blossom in the rainy season. On the whole, the show of blosso in the djati-forest, in accordance with the greater dryness and stronge light, is far greater than in the rain-forest.

November is the time when the leaf-canopy is renewed. The tea clothes itself with leaves, at first red, that soon form dense masses foliage. April, May, and June are the months that are poorest i flower.

iii. *WOODLAND IN TROPICAL EAST AFRICA.*

It is not yet possible to give a satisfactory account of the condition the vegetation in tropical East Africa south of the equator. There a very few meteorological data, which moreover embrace a short period onl and few botanists have yet travelled through the region. From th accounts given by collectors, and by other travellers devoid of scientif training, the coast country up to the Zambesi river presents the appea ance of a richly differentiated vegetation with various formations of woo land, grassland, and desert. What share in this differentiation is due climate and what to edaphic influences, how far its character is origin and how far modified by man, cannot be decided at present.

The woodland of the coast of East Africa is mainly xerophilous and assumes the form sometimes of savannah-forest, at other times of thorn-forest and thorn-bush, naturally with several transitional forms. The less extensive tracts of tall-stemmed forest (Figs. 191 and 192) may possibly be classified as monsoon-forest, in harmony with the sharp division of the

FIG. 191. Part of a forest in the coast region of German East Africa. From a photograph.

ear into rainy and dry seasons, but accurate accounts are wanting, as ar lso data regarding the condition of the foliage at different seasons of the ear.

'No type of formation,' says Engler, 'is so richly developed in Africa as that f the "*bush-woodland*."' According to his account, this formation belongs to hat I have designated thorn-forest, with shrubs frequently predominating, and with a gradual transition to desert as the moisture decreases. To the African thorn-forest in particular belongs Engler's 'dense bush' of the lower bushland, and his 'steppe-bush thicket' of the inland.

Engler emphasizes the systematic uniformity of the 'bush-forest' of tropical Africa, its systematic resemblance to that of Cis-gangetic India, and its physiognomic resemblance to that of Central and South America (Mexico, Argentina, and Chili). Systematically, the abundance of various species of Acacia is characteristic of this forest, and the genera Dichrostachys and Albizzia, which also have bipinnate leaves, are represented by numerous individuals. Woody plants with pinnate leaves are seldom as plentiful (Bignoniaceae, Odina belonging to the Anacardiaceae, Harrisonia one of the Simarubiaceae, some Rutaceae, Burseraceae, Connaraceae, Caesalpiniaceae). Plants with digitate leaves are common, for example Commiphora, Rhus, Jasminum, Vitex. Most plants of the thorn-forest have simple leaves, which are persistent in most of the species and have a very thick cuticle; for example, species of Euphorbiaceae, Celastraceae, Rhamnaceae, Rubiaceae, Sterculiaceae, Verbenaceae, Compositae; and inconspicuous whitish flowers are common. In the dense woods there are very few herbs, but these are plentiful in the clearings. Twining and climbing plants, possibly only thin-stemmed forms, are rich in species: Peperomia and Angraecum appear as epiphytes.

Fig. 192. Forest tract in the coast region of German East Africa. From a photograph.

The second type of the xerophilous low forest, the *savannah-forest*, is apparently far less developed in Africa than is the thorn-forest. A typical savannah-forest in the sense in which I use the word, is Engler's 'steppe-forest,' which occurs particular in Unyamwezi. 'Erect trees, 7–12 meters high with stems 3–4 centimeters thick, form the prevailing type; Leguminosae with pinnate leaves, which are termed 'myombo,' are dominant and sometimes pure: thus in Unyamwezi Berlinia Eminii occurs, but species of Acacia, Sterculia, Terminalia, and Kigelia also occur. There is little underwood, the shrubs and small trees of Anona, Combretum, and others are so scattered that travelling through the myombo-forests is in no way impeded. Succulent plants are rare, only here and there is an Aloe or a candelabra-like Euphorbia; but numerous herbs cover the ground[1].'

iv. *TROPOPHILOUS AND XEROPHILOUS WOODLAND IN TROPICAL AMERICA.*

The high forest of the interior of South America, especially of Brazil south of the Amazon, is in part tropophilous and should be classed as monsoon-forest. The forests of Minas Geraes described by Warming shed their foliage periodically, but without ever becoming leafless, as the defoliation of most of the trees immediately precedes their acquisition of new foliage.

The marked xerophilous types of savannah-forest and thorn-forest (including thorn-bush) are richly represented throughout the whole of tropical America, and frequently alternate with savannah. Wherever the humidity increases the savannah first passes over into savannah-forest. So at least I have observed in Venezuela, where on climbing the coast Cordilleras from the south the hitherto scattered trees closed in to form an almost close forest, the soil retaining its grassy growth. The low forest, comparable with a dense orchard, consisted chiefly of Leguminosae with umbrella-shaped crowns, especially of species of Cassia, whose completely defoliated twigs were decked with yellow flowers. Scattered among the leafless trees appeared two evergreen, very thick-leaved species of trees, Rhopala complicata (Proteaceae) and the cajú, Anacardium occidentale. All the branches, especially those of the leafless trees, bore small hard-leaved or densely hairy species of Tillandsia, among which T. recurvata was very abundant, and also a few markedly xerophilous orchids, in particular a beautiful flowered species of Jonopsis. Amongst the trees a columnar species of Cereus, equal to them in height, was frequently noticed. The soil was covered with rich and tall but completely dried-up grass.

Savannah-forest certainly occurs also in other parts of tropical America. Thus, apparently belonging to this type, there are 'capoes,' forest-tracts replacing the vegetation of the savannah (campos) on moister ground in Central Brazil (see Fig. 127).

Thorn-woodland, as forest, bush, or shrub, is extensively developed in tropical America. It forms an essential part of the coast vegetation in East Central Mexico (Fig. 128). Under the well-known and dreaded name of 'caatinga,' in particular it covers extensive tracts of country with a small rainfall in Brazil, between the savannahs (campos) of the south

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[1] Engler, op. cit., p. 62.

and the rain-forests of the Amazon and its tributaries. It alternates frequently with the savannah, and in this case, as in all dry districts, edaphic influences are in the first place responsible for the change in the character of the vegetation, since savannah prevails on a stiffer soil that is superficially wetted by the rain, whereas woodland occupies a sandy soil that is very permeable to water. The caatingas exhibit thorny bushes, chiefly formed of Mimoseae, among which there rise more or less numerous trees, including the strange 'barrigudos[1]' and columnar Cactaceae. Thin lianes climb among the bushes; epiphytes are absent or are extremely scarce. The herbaceous vegetation is limited to prickly Bromeliaceae (Fig. 193).

The caatingas of Brazil have frequently been described, especially by Martius, Saint-Hilaire, Liais, and recently by Detmer. Martius[2] gives the following vivid account of them:—

'It is quite different (i.e. compared with the rain-forest) with the forests termed by the Brazilians *caatingas*, or *light-forests*, which lose their leaves during the dry season and break out into leaf again only after persistent rain has set in with the wet season. They consist of trees of considerably more stunted growth, and, when leafless, remind the European traveller of the appearance of his native broad-leaved forests at the commencement of winter. They belong chiefly to the northern provinces of Ceara, Rio Grande do Norte, Pernambuco, Piauhy, Goyaz, and Bahia, where they occupy the sandy, primary granite, or jurassic limestone soils, over immense tracts. Dry districts, poor in springs and whose rivers dry up in summer, hills or plains, are the native country of these remarkable forests. The traveller journeys across them only with fear and trembling during the dry months. Surrounding him, as far as he can see, stand the bare leafless stems, motionless, unfanned by the slightest breeze; not a green leaf, not a juicy fruit, not a verdant blade of grass, on the burning, bare soil; alone appearing to retain still a fleeting trace of life, are the strangely shapen stems of Cereus, which here like huge candelabra, and there crowded together in serried ranks, stand threatening with their poisonous spines. . . . If, however, a sudden shower of rain should loosen the bonds of the vegetable kingdom . . . then, as if by magic, a new world springs into existence. From the richly branched stems, leaves of soft green colour shoot forth, countless rarest forms of flowers expand, the bare limbs of formidable thorny hedges and of climbing plants clothe themselves anew with fresh foliage. . . .'

As characteristic plants of the caatingas, Martius mentions Spondias tuberosa, Arr., Anona obtusifolia, DC., Caesalpinia pubescens, C. glandulosa, Bert., Capparis lineata, Pers., C. longifolia, Gw., C. laevigata, Mart., Pourretia tuberculata, Mart., and Chorisia ventricosa, Nees et Mart., Thryallis brasiliensis, several small species of Bombax, several species of Acacia, of Mimosa, and of Jatropha, 'an angular forked Euphorbia, the single species of this African form that occurs in Brazil.'

The account by Liais does not add any essential points to that of Martius. Yet he mentions the occurrence of many forms of Cactus and a great number of prickly Bromeliaceae, as terrestrial herbs.

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[1] With reference to these barrel-trees, see p. 349.

[2] Martius, op. cit., pp. 16, 17.

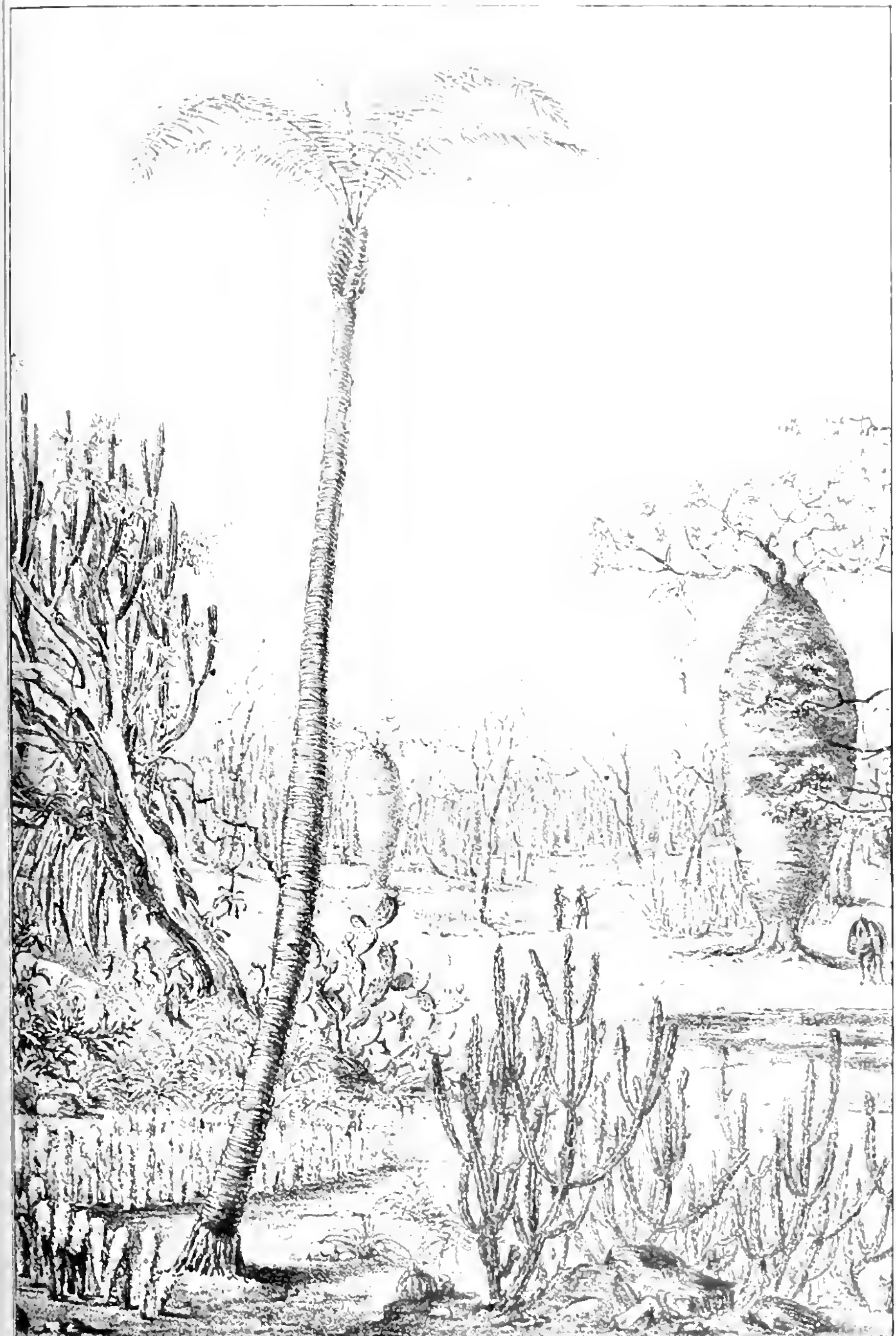

FIG. 193. Tropical thorn-woodland: caatinga-forest, when leafless. The palm to the left is Cocos coronata. Province of Bahia, Brazil. After Martius.

Detmer, who saw the caatingas of the province of Bahia in September (the month of passage from the dry to the rainy season), makes the following remarks:—

'The dry soil consists of greyish-white loose sand. On it are growing everywhere thorny shrubs, for the most part quite leafless, and forming a dense undergrowth, which is impenetrable in places and here and there is slightly overtopped by isolated trees. Between the shrubs often grow a great number of "mandacarus," trees of Cereus, 20 feet high, the massive stems of which, woody at the base, give place above to a few thick 4-5 angled ramified branches, which are studded with long thorns. The soil between the shrubs is covered by very large "gravattas"—terrestrial Bromeliaceae, with half-parched, sharp-edged leaves, grouped in rosettes, above which their dried inflorescences project; in addition there are only a few other plants, some of which bear greyish-green, extremely hairy leaves. Short palms with palmate or pinnate leaves are also plentiful.'

FIG. 194. Thorn-bush on calcareous soil in Minas Geraes. Uvaria macrocarpa, Cereus coerulescens. After Warming.

Thorn-bush similar to that of the caatingas also appears in South Brazil at Minas Geraes (Fig. 194). According to Liais and Warming, it is there confined to rocky limestone hills, and differs from the neighbouring forests by the much more complete defoliation, by the greater abundance of shrubs between the trees, which are further apart, also by its more marked xerophilous character, and consequently by the greater abundance of thorny and succulent plants.

Thorn-woodland is also richly developed in the *Antilles*. It is very extensive, for instance, on the east coast of Jamaica, where it consists in particular of Mimosaceae and species of Cereus, and, as in Minas Geraes, it appears to be confined to calcareous soil. Several of the smallest islands are almost completely covered by it, for example the Danish islands that have been described by Eggers.

FIG. 195. Landscape at Lagoa Santa in Minas Geraes. On the ridges, savannah (campos); in the valleys, forest. After Warming.

3. TROPICAL GRASSLAND FORMATIONS.

i. *GENERAL CHARACTER OF SAVANNAH.*

Whilst in regions with rain at all seasons of the year grassland plays quite a subordinate part and owes its limited appearance to local influences, in regions with marked dry seasons, especially in Africa and in South America, it covers extensive areas, usually in the form of *savannah*, less frequently in that of *steppe*.

The appearance of a tropical savannah remains always essentially the same, at least in plains (Figs. 127 and 195). Tall grasses, in many districts exceeding the height of a man, spring up in dense tufts, separated by bare intervals of soil, which is very variable, physically as well as chemically, and is frequently coloured red by iron oxide. On high plateaux the grass is shorter, frequently not taller than in our meadows, and more intermingled with herbaceous perennials and under-shrubs At greater or less distances apart trees appear, usually as stunted, gnarled, dwarf trees, resembling our apple-trees, but occasionally as lofty individuals, which as a rule belong to characteristic species not present in the forest. Besides dicotyledonous trees palms also occur in savannah.

When the trees become closer, the savannah passes over into savannah-forest, and when the trees disappear it passes into steppe. Such transitions are frequent, and are sometimes occasioned by climatic causes, but more frequently by changes in the nature of the soil.

ii. *SAVANNAH IN AFRICA.*

Pechuel-Lösche has given a vivid description of the savannah on the Loango coast, which may be considered as generally typical of the physiognomy of savannah in lowlands. However, the baobab (Adansonia digitata) is not in the picture, nor are the thick-leaved dwarf trees which rise singly above the grass and which the author describes elsewhere (Fig. 196). He distinguishes two forms of savannah, the open and closed savannah. *Open savannah* 'consists of less fully packed, and more loosely distributed flexible grasses, less than a man's height, which allow of one's passing through them and of having a sufficient view of the surroundings; the *closed savannah* consists of densely crowded stiff grasses, which shoot vigorously upwards, and which act as a strong barrier to the natives and render any digression from the trodden path either very difficult or impossible. . . . The open grassland occupies the greater area. The main part of it consists of grasses about one meter high. In many districts, scattered all about among these there are, gracefully waving in the breeze, very loose sprays of a charming Andropogon and Cymbopogon, three meters in height, and of a shorter Ctenium. The closed grassland, even when it has become transformed into stunted jungle, is almost entirely formed of Paniceae, the stiff culms of which spring up four and five meters high. The latter height is however already relatively considerable and exceptional, and according to numerous measurements a length of five and a half meters is to be considered as the extreme limit of growth.

'The vegetative activity of all campine[1] grasses occurs during the season when storms are rife; before this season is over, the grasses have matured their seeds and begin to die, like the wheat in our [Central European] fields. Even during their most rapid development they never

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[1] Campine = savannah.

exhibit the verdant, refreshing tints of our meadows, as the growing haulms are always intermingled with others which are dried, either broken down or rod-like erect, and which lend a pale yellow or brownish tint to the otherwise dull green. These dried remains, even in the midst of the rainy season, afford sufficient fuel for a fire, and render it possible for the crop to be partially burnt to the ground, or at any rate singed. Tracts cleared down to the ground by the flames, if seen from a distance, in the first days of their growth, when the countless young shoots and leaf-tips are emerging, often vividly recall the sprouting crops of our own fields.

FIG. 196. Anona senegalensis, grasses and nests of termites. From the West African savannah, Loango. After Pechuel-Losche.

'The rich show of the flowers of the varied perennials that gives beauty to the meadows of other parts of the earth, the transitory splendour of the bulbous plants of many steppe-districts, are both foreign to the campines. Only in the open are some of Flora's children found scattered: dull red or yellow-flowering indigo-plants, a humble Striga lutea, Louret, with fiery red flowers, the decorative Cassia mimosoides, Linn., with golden yellow ones, occasionally a Clerodendron with brilliant scarlet flowers. More seldom, flourishing among the grasses are species of Vernonia, V. cinerea, Less., with violet flowers, and V. senegalensis, Desf., with white or light rose-coloured flowers; the latter being one of the commonest[1].'

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[1] Pechuel-Lösche, op. cit., pp. 130–2.

The African savannah possesses not only dwarf trees, but also large, even gigantic ones. The most renowned of these giants of the savannah is the monkey-bread tree, or baobab, Adansonia digitata, 'a tree that is variously developed, but as a rule well grown and of gigantic proportions; the trunk and crown appear to be of excessive, one might say, of uncouth thickness[1].' The baobab is confined to open country, in particular to savannah, and absolutely reigns over wide tracts of it (Fig. 197):

'In general, the form of the monkey-bread tree resembles that of our huge oaks growing on pasture lands. Like these, it exhibits many individual peculiarities, but as a rule it has its limbs less gnarled and not given to such sharp bends. For the sake of sharply marking off the different kinds of individuals of Adansonia, these may be ranged under three heads according to their habit of growth. The massive unbranched bole is either cylindrical, almost uniformly thick throughout, and like a column bears its crown at a great height; or it is short, remarkably thick-set and swollen, and subdivided not far from the ground into a number of equal-sized boughs; or low down it sends out a huge mass of boughs, but up to at least about two-thirds of its height above the ground it remains distinctly recognizable as the main trunk[2].'

According to Pechuel-Lösche, an Adansonia of the first form, standing at Landana, measured 17 meters up to the first bough, with a girth of 8 meters. The girth of the trunk of a tree of the second form, standing at Ambrizette, was 27 meters.

'The Adansonia is specially important as a true sign of the open country. It demands space, air, and light; if these conditions of its welfare are not fulfilled, it languishes and dies. The open grassland is its home; I have never found it in high-forest. In other respects, however, it is indifferent whether it grows close to water or on dry hill-tops; I have even found some on quite swampy ground. As soon, however, as bushes settle round it and trees begin to encircle it, it shows threatening signs of ruin: it gets crowded out, loses its branches, and finally utterly collapses[3].'

The wood of the baobab is spongy, soft, juicy, and forms a vast water-reservoir, to which the tree owes its existence and vigorous development in the savannah. It is however leafless during the dry season.

More concisely, but likewise very vividly, has the *eastern tropical African savannah* (Fig. 198) been described by Hans Meyer. It consists chiefly of grass and small perennials with but few thorny shrubs; every 100–200 paces rises a tree or bush of the mimosa-form, that is to say with bipinnate leaves. The grass does not form a close sward, but grows in isolated tufts, the intervals between which are occupied by bare, red, laterite soil. The trees are usually so far apart, that one can look between them for miles in all directions; less frequently they close in and give the landscape a park-like appearance.

As an example of the systematic composition of the Central East African grassland, some of Engler's statements are appended, regarding the forma-

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[1] Pechuel-Lösche, op. cit., p. 178.

[2] Id., p. 177.

[3] Id., p. 181.

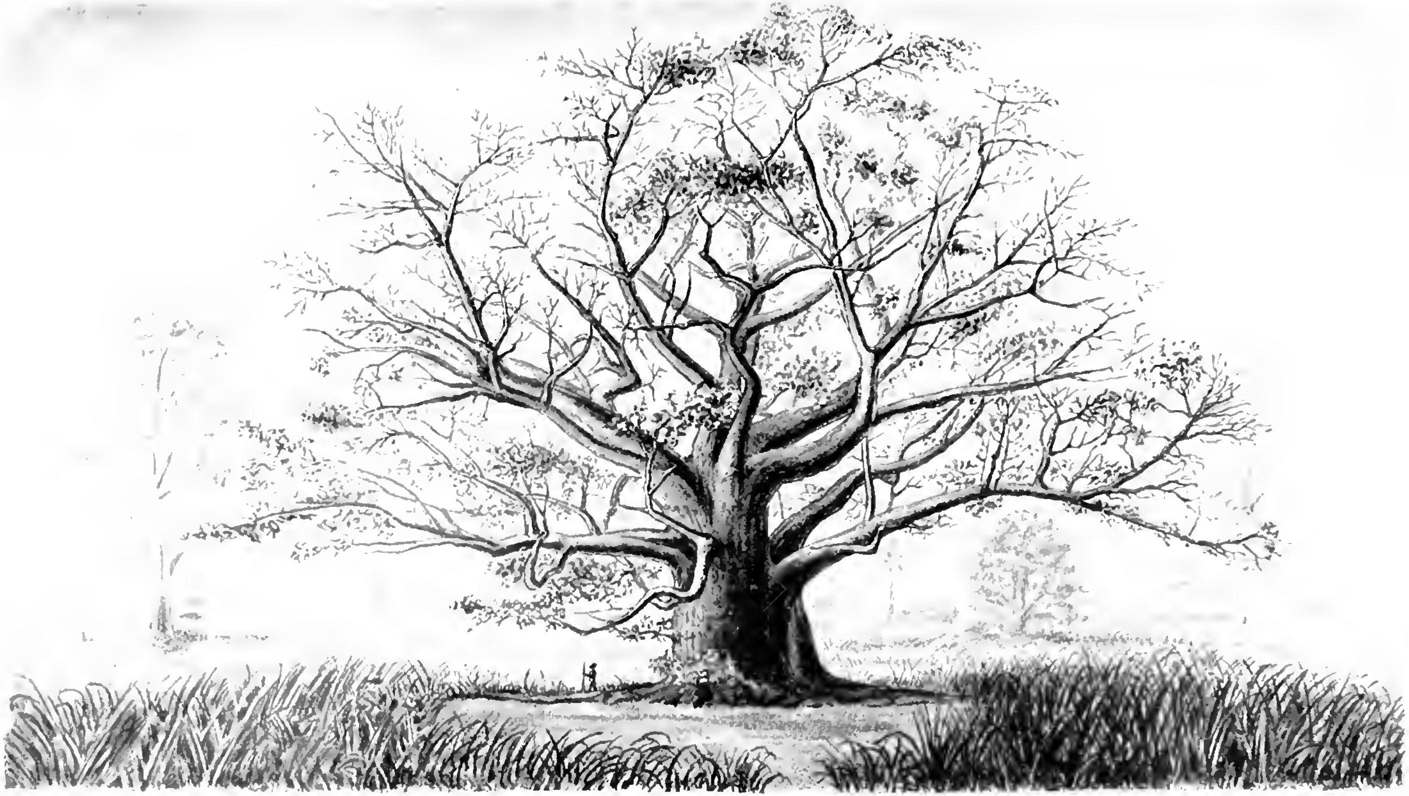

FIG. 197. Adansonia digitata, the baobab. In the background: oil palms, Elaeis guineensis. From the West African savannah, Loango. After Pechuel-Lösche.

tions termed by him, 'high-grass-steppe,' 'bush-grass-steppe,' and 'tree-grass-steppe':—

The *high-grass-steppe* of Engler, which is a steppe according to our terminology

FIG. 198. Arborescent Euphorbia in the savannah. German East Africa. From a photograph.

, consists chiefly of Andropogoneae with tufts of haulms 1–2 meters high; there also, however, numerous other forms of grass, usually lower in stature, Paniceae

FIG. [illegible]. Savannah landscape in German East Africa. In the centre: a termites' nest. To the right: Sterculia appendiculata, a Doom

To face p. 369.]

(Tricholaena, Setaria, Pennisetum), Agrostideae (Sporobolus, Aristida gracillima), Chlorideae (Enteropogon, Chloris, Leptochloa, Lepidopironia), Aveneae (Tristachya, Trichopteryx), Festuceae (Eragrostis). The subordinate herbs growing among the grasses are 'partly bulbous or rhizomatous plants with solitary flowering shoots, partly herbaceous perennials that form a short low stock and send up a tuft of flowering shoots.' Herbaceous Monocotyledones are not numerous. Engler specially mentions Aneilema Johnstonii, Commelina bracteosa, Chlorophytum macrophyllum and C. tuberosum, Gloriosa virescens, also some species of Scilla, Asparagus, some Amaryllidaceae (Haemanthus, Hypoxis), Iridaceae (Acidanthera), Orchidaceae (Lissochilus, Habenaria). Among Dicotyledones, greyish-green Amaranthaceae, not unfrequently 1-2 meters high, take a prominent place: they belong chiefly to Celosia, Digera, Sericocomopsis, Pupalia, Aerva, Achyranthes, Nothosaerva. The Nyctaginaceae are represented by the common weed Boer-haavia diffusa, the Aizoaceae rather weakly by Trianthema pentandrum and Glinus otoides, the Phytolaccaceae by two annual succulent herbs, Limeum viscosum and Giesekia pharnaceoides. Talinum patens, a succulent weed belonging to the Portu-acaceae, is common. The Cruciferae are very scanty (two species of Farsetia). A strong contingent comes from the Papilionaceae, especially species of Indigofera and Tephrosia, besides several Hedysareae (Zornia, Stylosanthes, Desmodium, Pseudar-hria), Phaseoleae (Rhynchosia, Eriosema), and many others. The Caesalpiniaceae are oorly represented by a few Cassieae. Species of Polygala, Malvaceae, and Sterculia-ceae are fairly numerous. The Euphorbiaceae are few, and there are no Umbelliferae. Among the Gamopetalae, Asclepiadaceae (Gomphocarpus, Stathmostelma, Schizo-lossum) and Convolvulaceae (Convolvulus, Ipomoea, especially Astrochlaena) play prominent part by their abundance and by their large flowers. Labiatae are also umerous (especially species of Leucas), but the most numerous of all Dicotyledones re Acanthaceae (especially species of Justicia, Barleria, Blepharis capensis, Neur-canthus scaber). The family of Compositae, which is so richly developed in the South American prairie, is poor in forms in the South African, and is limited to pecies belonging to Vernonieae and Inuleae. The following families also upply representatives of subordinate import: Gentianaceae (Enicostemma verti-illatum), Boraginaceae (species of Heliotropium), Verbenaceae (Leptostachys), Scrophulariaceae (Striga, Scoparia), Solanaceae (Solanum), Cucurbitaceae Corallocarpus, Cucumis), Passifloraceae (Tryphostemma, Adenia), and Rubiaceae Oldenlandia).

Engler's *bush-grass-steppe*, a shrub-savannah according to our terminology, ontains singly, or in small groups, various kinds of shrubs. The following are epresented: Anonaceae (Anona senegalensis), Capparidaceae (Capparis, Courbonia, adaba, Maerua, Thylachium), Leguminosae (Acacia, Diphaca), Malpighiaceae (Di-spis albida, Triaspis auriculata), Euphorbiaceae (species of Phyllanthus, Bridelia, calypha, Flueggea), Anacardiaceae (Rhus villosa, R. glaucescens), Celastraceae Gymnosporia senegalensis), Sapindaceae (Deinbollia borbonica), Rhamnaceae Zizyphus Jujuba), Thymelaeaceae (Gnidia), Verbenaceae (Bouchea pterygocarpa), canthaceae (Blechum hamatum, Hygrophila Volkensii), Rubiaceae (Crossopteryx fricana, Gardenia Thunbergii).

The trees in Engler's *tree-grass-steppe*, a real savannah according to our rminology, are chiefly species of Acacia (A. subulata, A. Seyal, A. spirocarpa,

A. Senegal, and others). Prominent components are, moreover, Adansonia digitata and Kigelia aethiopica, a tree up to 25 meters high and with a trunk 8 meters in girth. Doom palms (species of Hyphaene) also appear in great numbers in many savannahs (Fig. 199). Other trees of the East African savannah are: Dalbergia melanoxylon (Papilionaceae-Dalbergieae), Poinciana elata (Caesalpiniaceae), Zizyphus mucronata and Berchemia discolor (Rhamnaceae), species of Sterculia, Odina tomentosa and Heeria insignis (Anacardiaceae), Combretum and Terminalia (Combretaceae), Spathodea nilotica (Bignoniaceae), species of Strychnos.

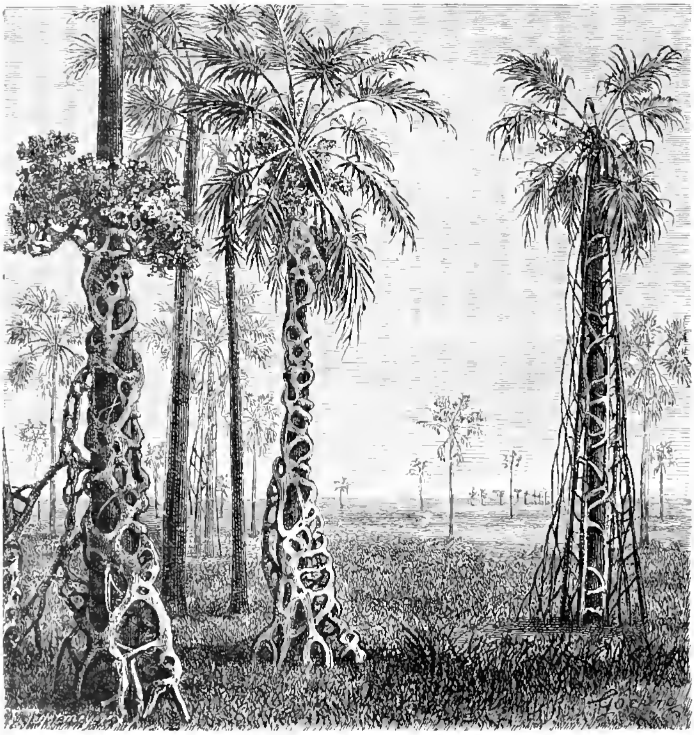

FIG. 200. Landscape in the llano with Capernicia tectorum, the latter in some cases infested by an epiphytic Ficus. Venezuela. After Carl Sachs.

iii. *SAVANNAH IN AMERICA.*

Humboldt, who gave the first description[1] of tropical grassland in connexion with the 'llanos' of Venezuela, regarded the latter as immeasurable treeless plains of grassland. Not only I myself, who have seen only a small part of the llanos, but also Carl Sachs, who traversed them in several directions and frequently travelled over the same country as

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[1] Humboldt, op. cit.

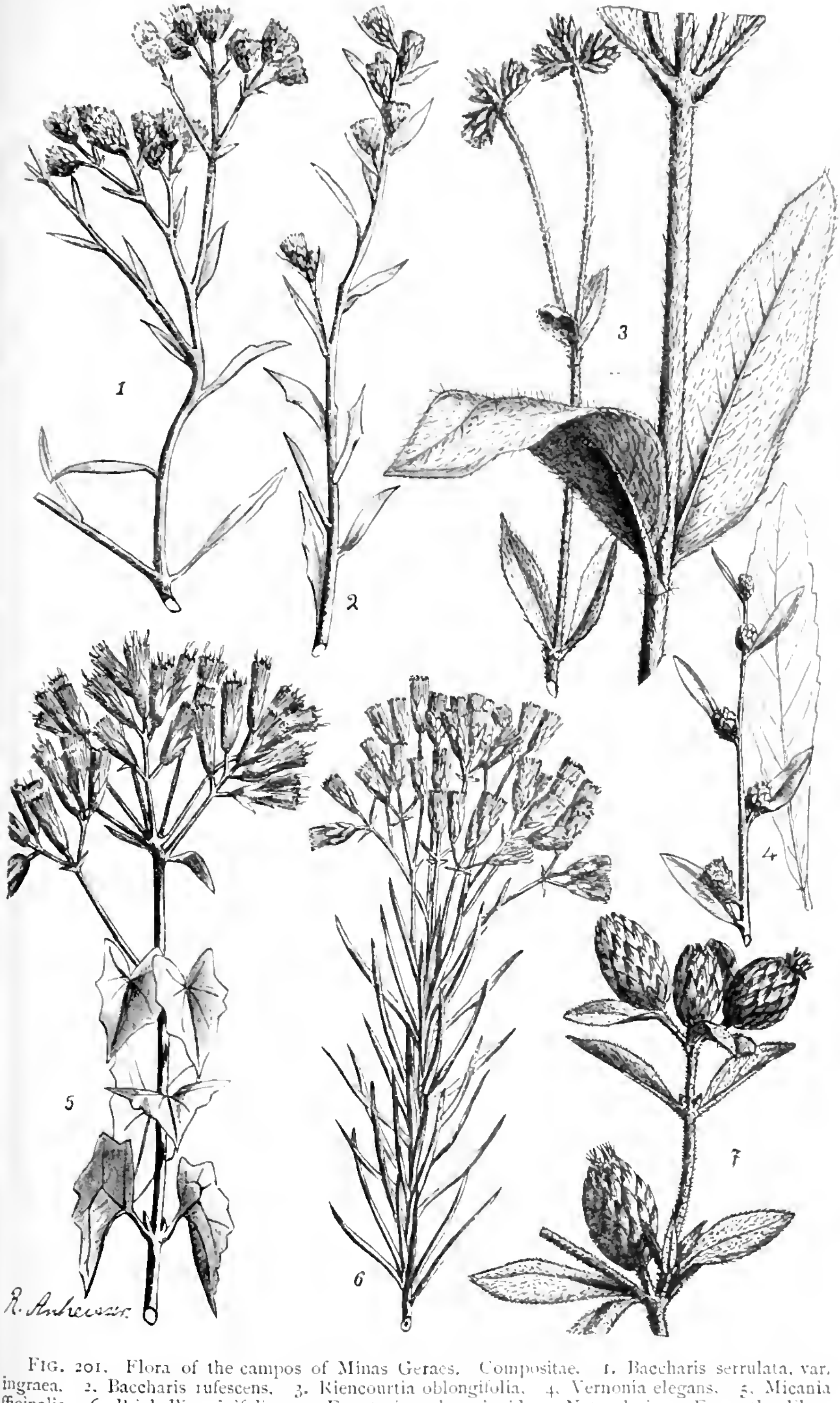

FIG. 201. Flora of the campos of Minas Geraes. Compositae. 1. Baccharis serrulata, var. ingraea. 2. Baccharis rufescens. 3. Riencourtia oblongifolia. 4. Vernonia elegans. 5. Micania fficinalis. 6. Brickellia pinifolia. 7. Eupatorium horminoides. Natural size. From the Flora asiliensis.

Humboldt, have received other impressions of the llanos. The boundless grassland that Humboldt described was not revealed to our eyes, but, on the other hand, a park-like country, in which woodland forms oases and strips in the grassland, and the grassland usually occurs in the guise, not of treeless steppes, but of savannah scantily dotted with solitary trees (Fig. 200).

A similar park-like appearance, a similar differentiation of the grassland as savannah, according to Schomburgk's description[1], belongs to the savannah-districts of Guiana:—

'Forests—I have termed them oases—sometimes miles across, sometimes of less extent, most frequently with a circular outline, rise out of the savannah, like islands from the sea. . . . Fringing the rivers of the savannah for a width of usually 100 to 200 feet, but often more, is a band of vegetation, not luxuriant indeed, but consisting of closely crowded trees and shrubs. . . . The "grass" of the savannah consists for the most part of Cyperaceae with yellow, rough-haired, straggling stems, and they are intermixed with a number of prickly, woody, and herbaceous plants belonging to the families Malpighiaceae, Leguminosae, Rubiaceae, Myrtaceae Malvaceae, Convolvulaceae, Menispermaceae, Apocynaceae, and others. Stunted habit characterizes the growth of the trees, such as Curatella, Bowdichia, Psidium

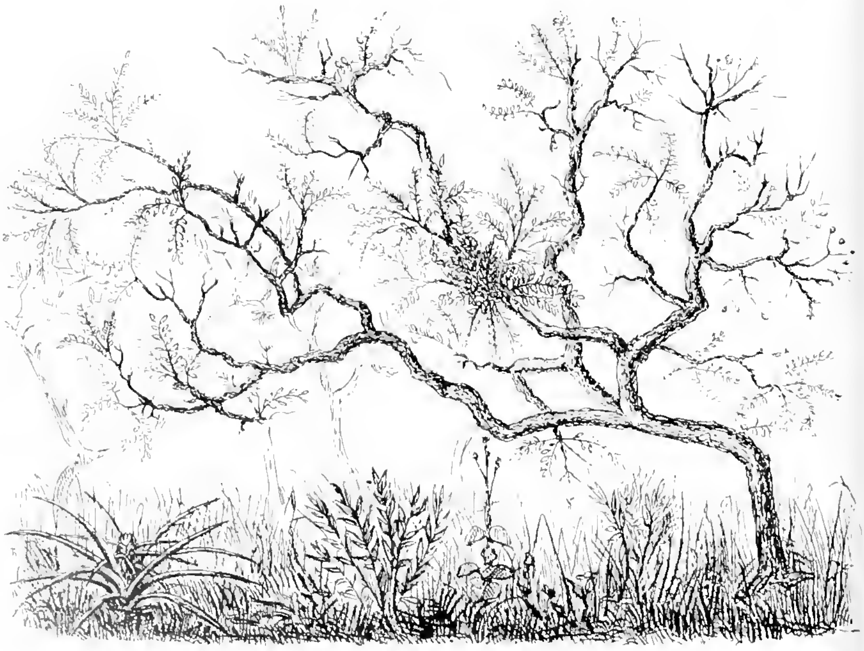

Fig. 202. From the Brazilian campos of Minas Geraes. The small tree: Andira inermis (?). Left hand: Bromelia bracteata. Also Eremanthus sphaerocephalus and Ipomoea sp. After Warming.

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[1] Schomburgk, I, p. 798.

Rhopala, that stand isolated here and there, and especially occur on eminences; these trees are never found in forests. The swampy depressions of the savannah are for the most part occupied by Mauritia flexuosa, sometimes isolated, sometimes forming actual forests.'

The campos of Brazil, like the llanos and the savannahs of Guiana, do not consist of a uniform formation spread over a wide area, but of a richly differentiated, undulating park-like country, in which different forms of woodland and grassland partake, although the latter preponderates.

Saint-Hilaire also describes the campos of Minas Geraes as a hilly tract, the depressions in which form true savannah with stunted trees, whilst the heights are covered with pure steppe. Yet the campo-district is by no means without forest. 'Wherever a damp and deep valley appears in the midst of the free and merely undulating surface of this immense district, wherever a depression occurs on the slope of a hill, one may be certain of finding a group of trees[1]'.

The *herbaceous vegetation* of the savannah has most probably everywhere a xerophilous structure; but only a few observations of the vegetation of the campos, those of Warming, are available. According to him, many herbs, both Dicotyledones and Monocotyledones, have tubers, which function either primarily or secondarily as water-reservoirs (Figs. 203 and 204). The leaves of the grasses are narrow and stiff, the leaves of Dicotyledones are usually small and hard, and frequently the plants are reduced to a completely aphyllous condition.

FIG. 203. Vernonia desertorum. From the Brazilian campos of Minas Geraes. Natural size. After Warming.

Warming has thoroughly studied the systematic composition of the campo of Lagoa Santa in Minas Geraes (Figs. 201–205). He found 554 herbaceous species. The majority of individual plants are grasses, of which about 60 species in particular

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[1] Saint-Hilaire, op. cit., p. 9.

belong to the Paniceae (Paspalum, Panicum) and Andropogoneae (Andropogon, and so forth). According to the number of species, Compositae preponderate, especially Vernonieae (Vernonia) and Eupatorieae (Eupatorium), also Asteroideae, Inuloideae, Helianthoideae, Helenioideae, Mutisieae. The Ligulatae are represented only by a Hieracium. The Papilionaceae (60–70 species) are very numerous, whilst the Caesalpiniaceae and Mimosaceae can show only a few species. Among strongly represented families are Orchidaceae with 35–40 species, and Cyperaceae, Labiatae, Asclepiadaceae, Convolvulaceae, Euphorbiaceae, Rubiaceae with 20–25 species. The Polygalaceae have 10–15 representatives; the Iridaceae, Apocynaceae, Melastomaceae, Verbenaceae, Acanthaceae, Gentianaceae, Scrophulariaceae, Caesalpiniaceae, Mimosaceae, Amarantaceae, Malvaceae have 5–10; the Malpighiaceae, Cucurbitaceae, Ampelidaceae, Umbelliferae, Polypodiaceae, Sterculiaceae have 3–4 species; the Oxalidaceae, Gesneraceae, Turneraceae, Passifloraceae, Bromeliaceae, Menispermaceae, Commelinaceae, Lobeliaceae, Anonaceae, Aristolochiaceae, Rhamnaceae,

Fig. 204. Gomphrena jubata. Flora of the Brazilian campos. Natural size. From the Flora Brasiliensis.

FIG. 205. Flora of the Brazilian campos of Minas Geraes. 1. Sida linifolia. 2. Lippia rotundifolia. 3. Eryngium ebracteatum. 4. Tibouchina frigidula. 5. Croton antisiphyliticus. 6. Crumenaria erecta. 7. Hyptis virgata. 8. Borreria eryngioides. Natural size. From the Flora Brasiliensis.

Boraginaceae, Hypoxidaceae, Eriocaulaceae, Cordiaceae, Moraceae, Lauraceae, Droseraceae have only 1–2 species.

The author found 170 180 species of shrubs. Specially numerous among them are Myrtaceae and Malpighiaceae; then come the Melastomaceae and Compositae. 5–10 species are exhibited by the Euphorbiaceae, Lythraceae, Rubiaceae, Anonaceae, Papilionaceae, Caesalpiniaceae, Mimosaceae. By 3–4 species are represented the Apocynaceae, Bixaceae, Ternstroemiaceae, Loranthaceae. By one, or at most two, species the Erythroxylaceae, Connaraceae, Sapindaceae, Dilleniaceae, Myrsinaceae, Solanaceae, Loganiaceae, Bombaceae, Cordiaceae, Artocarpeae, Bignoniaceae, Simarubaceae, Ochnaceae, Anacardiaceae, Symplocaceae.

Warming estimates the number of tree-species at 76, or including doubtful species, 80. Of families with more than one species there are Vochysiaceae with 8; Papilionaceae, Myrtaceae, and Compositae, with 5 each; Bombaceae, Malpighiaceae, Nyctaginiaceae, with 4 each; Caesalpiniaceae, Mimosaceae, Bignoniaceae, Proteaceae, Myrsinaceae, Rubiaceae, Melastomaceae, with 3 each; Sapotaceae, Combretaceae, Apocynaceae, Erythroxylaceae, Sapindaceae, Palmae, with 2 each. Families with only one species are the Anonaceae, Araliaceae, Connaraceae, Rhizobolaceae, Ternstroemiaceae, Loganiaceae, Chrysobalanaceae, Solanaceae, Verbenaceae, Lythraceae, Euphorbiaceae, Labiatae, Bixaceae, Styraceae, Ebenaceae, Celastraceae, Olacaceae, Dilleniaceae.

SELECT LITERATURE.

1. General Characteristics of the Vegetation in periodically dry Districts.

The literature of this subject is included in that cited under the following headings.

2. Woodland Formations in periodically dry Tropical Districts.

Berg, A. Physiognomy of Tropical Vegetation in South America. Fourteen plates. London, 1854.

Börgesen, F., og Paulsen, O. Om vegetationen paa de dansk-vestindiske öer. Kjobenhavn, 1898.

Brandis, J. I. Forest Flora of North-West and Central India. London, 1874.

—— II. Report on the Attaran Forests for the year 1860. Selection from the Records of the Government of India. Calcutta, 1861.

Cordes, J. W. H. De Djati-Bosschen op Java; hunne natuur, verspreiding, geschiedenis en exploitatie. Batavia, 1881.

Detmer, W. Botanische Wanderungen in Brasilien. Leipzig, 1897.

Engler, A. Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete. Deutsch Ost-Afrika. Bd. V. Berlin, 1895.

Falconer, H. Reports on the Teak Forests of the Tenasserim Provinces. With other papers on the Teak Forests of India. Selections from the Records of the Bengal Government. Calcutta, 1852.

Hooker, T. D., and Thomson, T. Flora Indica. Vol. I. 1854.

Kurz, S. Preliminary Report on the Forest and other Vegetation of Pegu. Calcutta, 1875.

Liais, E. Climats, géologie, faune et géographie botanique du Brésil. Paris, 1872.

Martius, C. F. P. von. I. Die Physiognomie des Pflanzenreichs in Brasilien. München, 1824.

—— II. Tabulae physiognomicae. Flora brasiliensis. Fasc. I–IX. 1840–1847.

Saint-Hilaire, Aug. de. Tableau de la végétation primitive dans la province de Minas Geraes. Annales des sciences naturelles. Tome XXIV. 1831.

Schenck, H. Beiträge zur Biologie und Anatomie der Lianen, im Besonderen der in Brasilien einheimischen Arten. Botan. Mittheil. aus den Tropen. Heft IV. Jena, 1892.

Schimper, A. F. W. Die epiphytische Vegetation Amerikas. Ibid. Heft II. Jena, 1888.

Volkens, Z. Der Kilimandscharo. Berlin, 1897.

Warming, E. I. Une excursion aux montagnes du Brésil. La Belgique horticole. 1883.

—— II. Lagoa Santa. Skrifter a. d. kgl. danske Videnskabernes Selskab. 1892.

3. Tropical Grassland Formations.

Works of Engler, Liais, Martius, Saint-Hilaire, Schenck, Schimper, Volkens, Warming, quoted under 2, may also be consulted.

Humboldt, A. v. Aspects of Nature. English edition. Longmans and Murray, London, 1849; also as Views of Nature. English edition. Bohn, London, 1850.

Jenman, G. S. Aspect and Flora of the Kaieteur Savannah. Demerara, 1882.

Johow, Fr. Vegetationsbilder aus West-Indien und Venezuela. III. Ein Ausflug nach der Höhle del Guacharo. Kosmos. 1885.

Pechuel-Lösche, E. Die Loango-Expedition. Abth. III. Hälfte 1. Leipzig, 1882.

Sachs, Carl. Aus den Llanos. Leipzig, 1879.

Schomburgk, R. H. I. Reise in Britisch-Guiana. Theil III. 1848.

—— II. Versuch einer Fauna und Flora von Britisch-Guiana. Leipzig, 1848.

—— III. A Description of British Guiana. London, 1840.

CHAPTER VI

EDAPHIC INFLUENCES IN THE TROPICS

1. Edaphic Influences in Tropical Inland Country. i. *Laterite.* Physical and chemical properties. Effects on vegetation. Eng-forest in Burma. ii. *Lime.* Unfavourable influence on vegetation in the tropics. Occurrence of thorn-forest on calcareous soil. iii. *Humus.* Its relatively slight development in the tropics. Regur in South India. Absence of peat-formation. iv. *Siliceous Soil.* Sâl-forest of India. Bamboo-forest. v. *Swampy Ground.* Palm-woods. Swamp-forest in Burma. Swamps without forest. vi. *Fumaroles in Java.* Xerophilous vegetation. **2. Formations of the Tropical Sea-shore.** i. *Classification of Tropical Littoral Formations.* ii. *Open Formations of the Sandy Shore.* Pes-caprae formation. Littoral shrubs. Pandanus. iii. *Littoral Woodland above High-tide Mark.* Its occurrence in the Malay Archipelago, in Pegu, in East Africa. Oecological characters. Casuarina-forest. iv. *Woodland Formations below High-tide Mark.* Mangrove or tidal woodland. The Eastern mangrove. Characteristic plants. Oecological characters. Rhizophora mucronata. Vivipary and germination in Rhizophoraceae, Aegiceras, and Avicennia. Habit of mangrove-plants. Stilt-roots. Pneumatophores. Physiognomy of the mangrove-forest in South Java. Nipa-formation. Transition to the inland formations. The Western mangrove. v. *Distribution of Littoral Formations in the Tropics.*

1. EDAPHIC INFLUENCES IN TROPICAL INLAND COUNTRY.

THE differentiation in the flora and in the oecological features of the vegetation, arising from differences in the constitution of the soil, is much more pronounced in the periodically dry districts than in the constantly humid ones, where the rain-forest, without apparently exhibiting any essential difference, extends over the most varied kinds of soil and shows a different physiognomy only in those stations that are swampy or very rich in salts.

Owing to the lack of proper observations, it is not at present possible to distinguish between the physical and chemical influences of the soil in the tropics, and the whole subject of edaphic influence is still very little studied, except in regard to littoral formations, so that we must be satisfied by considering individual kinds of soil and the vegetation peculiar to each, without inquiring closely into causes.

i. *LATERITE*[1].

Tropical zones possess a widespread and characteristic kind of soil, termed *laterite*, a red or dark yellow loam impregnated with ferric oxide or ferric hydrate, and resulting from the weathering of all rocks that contain alumina and iron. Laterite exhibits, in consequence of its varied origin, much variety both in its chemical and physical properties. From true laterite, which contains hard, vitreous or cellular concretions composed of ferric oxide or hydrate, and is limited to the tropics, Wohltmann separates *red-earth*, which is devoid of such concretions, and plays an important part, in particular in extra-tropical South America and even in Mediterranean countries.

With all their chemical differences the laterites possess certain negative characters in common that are important in relation to vegetation, namely great poverty in alkalis and lime or their complete absence, and poverty in phosphorus, magnesia, and sulphur. The chief constituents are silica, alumina, and ferric oxide, in very variable proportions.

The following table gives an idea of the great variability in the chemical composition of laterite:—

COMPOSITION OF LATERITE (after Wohltmann).

	Malanzhe (Central Africa).	Table Mountain.	Gabun.	Rangoon (about).
SiO_2	80·5 %	53·5 %	10·4 %	37·0 %
Al_2O_3	11·1 %	26·8 %	17·8 %	6·0 %
Fe_2O_3	4·0 %	9·8 %	58·0 %	47·0 %

Physically, laterite is characterized by very low capacity for retaining water; in particular, old washed-out laterite, rich in coarse fragments, is very permeable. Being a soil poor in nutriment and drying rapidly, especially after its finely grained constituents have been washed out, *laterite affords a very unfavourable substratum for the existence of plants.* It is not yet known how far the large proportion of iron also affects the characteristic peculiarities of the vegetation.

Laterite, especially in its stony porous forms, induces in the forest a physiognomy which is characteristic both as regards its oecological features and its systematic composition, and which has been described by Brandis and Kurz in respect to Burma.

A tree characteristic of the laterite localities in that country is the eng. Dipterocarpus tuberculatus, which dominates the forest through its social habit, and distinguishes itself essentially from the other accompanying trees by the fact that it exhibits a normal growth in height, whereas the other trees are reduced to gnarled, more or less dwarfed, forms. Such forests are termed 'eng-forest' by Brandis and Kurz[2].

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[1] Wohltmann, op. cit., p. 143.

[2] See p. 354.

ii. *LIME.*

In warm climates, lime appears to exercise an action on plant-life quite different from that which it has in temperate and cold climates. Weathered soil of pure limestone affords less favourable conditions for the growth of plants, and the number of plants whose development is favoured by liming the soil is smaller in low than in high latitudes [1].

Nothing quite certain is known regarding the influence of the chemical properties of lime on the constitution of the vegetation in the tropics, although several species appear to be limited to a calcareous soil. The effects of a calcareous soil that have hitherto been demonstrated refer solely to stony situations, poor in humus, in periodically dry regions, and possibly may be traced back to the low water-absorbing power of lime, therefore to a purely physical property.

In the climate of the monsoon-forest, calcareous soil having the low water-absorbing power just mentioned causes the appearance of the most xerophilous of tropical forest-types, namely the thorn-forest, or it may be of thorn-bush and thorn-scrub, which denote a still greater dryness. The occurrence of thorn-forest on calcareous soil in Central Brazil has been already mentioned [2]. In the periodically dry districts in Pegu, Kurz's 'dry forest,' a type corresponding exactly to our thorn-forest, is characteristic of dry, stony, calcareous soil. It is a bush-like forest, green in the rainy season, 'not very inviting on account of the prevalence of thorny trees and shrubs.' The trees are there of moderate height (50–70 feet, exceptionally up to 100 feet); Acacia Catechu (sha) is in such forests frequently the predominant species of tree, hence the name sha-forest. Finally, forests and bush of similar oecological character have been described by Warburg on calcareous soil at Ceram-Laut.

Warburg observed a diversified primary forest vegetation, where there was almost no humus, on calcareous rocks, if the latter were sufficiently fissured; this vegetation consisted chiefly of bushes, some of which were armed with thorns. One or two endemic species were found there alone. The following species predominated: Trema virgata, Bl., Dalbergia densa, Benth., Eugenia Reinwardtiana, DC., Zanthoxylum diversifolium, Warb., Atalantia paniculata, Warb., Breynia cernua, Müll.-Arg., Acalypha grandis, Benth., Flagellaria indica, Linn., Citrus Hystrix, DC. In places, collections of a small bamboo, Schizostachyum Zollingeri, occurred.

iii. *HUMUS* [3].

Soils rich in humus cover smaller areas in the tropics than in temperate zones, and pure deep humus-soils are very rare. The poverty in humus is a consequence of the acceleration in the development of micro-organisms occasioned by the tropical heat, which is at least for a part of the year

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[1] Wohltmann, op. cit., pp. 134-5. [2] See p. 360. [3] Wohltmann, op. cit., p. 173.

combined with great humidity. In addition, in tropical districts with a heavy rainfall, on account of the great abundance and intensity of atmospheric precipitations, the organic products of decomposition are drained away to such an extent that many tropical rivers, especially during the rainy season, assume a coffee-brown colour.

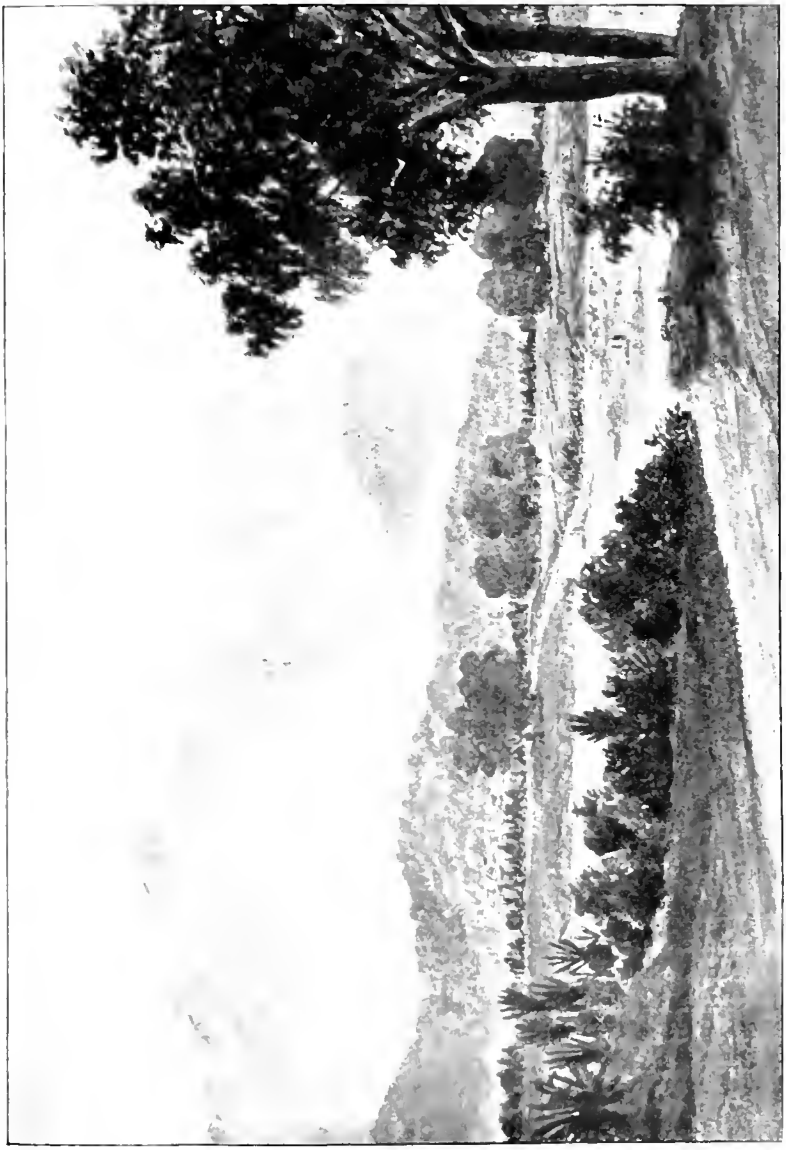

FIG. 206. Landscape in North-West India, at the foot of the Himalaya. In the background: sal-forest. From a water-colour painting by Lady Brandis.

Soil rich in humus, with 8–9 % of organic matter, is found within the tropics, in particular in South India, which is covered to about one-third of its area by the fertile black soil—regur—that also occurs further north; similar soil is found also in flat, densely wooded tracts of country, where the flow of water is slower and shade retards the process of decomposition. *Peat is never produced, except in mountains over* 1,200 *meters in height.*

iv. *SILICEOUS SOIL.*

A very permeable soil rich in silica and gravel is a substratum unfavourable to the growth of trees, and therefore situations with soil of such a nature always exhibit a characteristic form of vegetation. Some species of plants withstand these unfavourable conditions better than others and form more or less pure woods. This is to a great extent the case in India with the sâl-tree (Shorea robusta)[1], which forms forests of great extent in the long valleys (dûns) between the outer chains of the Himalaya Mountains (Fig. 206), then again in a southern very extensive tropical area that is separated from its northern habitat by the Ganges valley. The sâl-forest always occurs on a loose soil that is very permeable to water, and is absent whenever the soil becomes firm. In general it is not the climate, but the soil alone, that determines its presence. Hence the sâl-tree is absent from the western half of the Indian peninsula, where trap is the prevailing rock, whilst it forms extensive forests in the eastern half, which has a very similar climate.

In all probability the occurrence of natural *bamboo-woods* (Fig. 207) is also connected with peculiarities of the soil that are less favourable to other trees, since they usually appear only locally, except in the Burmese mountains, where they sometimes cover extensive tracts. Kurz assigns, as the substratum for bamboo-woods, rocky or shallow alluvial soil in the case of certain species, and deep alluvial soil in the case of others.

Bamboo-woods merit the term 'pure' better than any others, for they consist only of one or two species of bamboo and are devoid of any other plants. According to Kurz, in the very dense forests of certain species of bamboo a few mosses (Hypnum, Fissidens) and lichens appear only here and there on the soil and on the base of the stems.

Bamboo-woods often owe their origin to cultivation. As in such cases they frequently cannot be distinguished with any certainty from others that are produced naturally, it is evidently difficult to shed light upon the obscure problem regarding the conditions determining their appearance.

v. *SWAMPY GROUND.*

According to the still defective observations regarding the oecology of tropical vegetation, a persistent and great amount of water in soil is

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[1] Brandis, op. cit.

extremely important. By the infiltration of water from rivers and lakes, conditions for forest growth are secured in grassland districts and

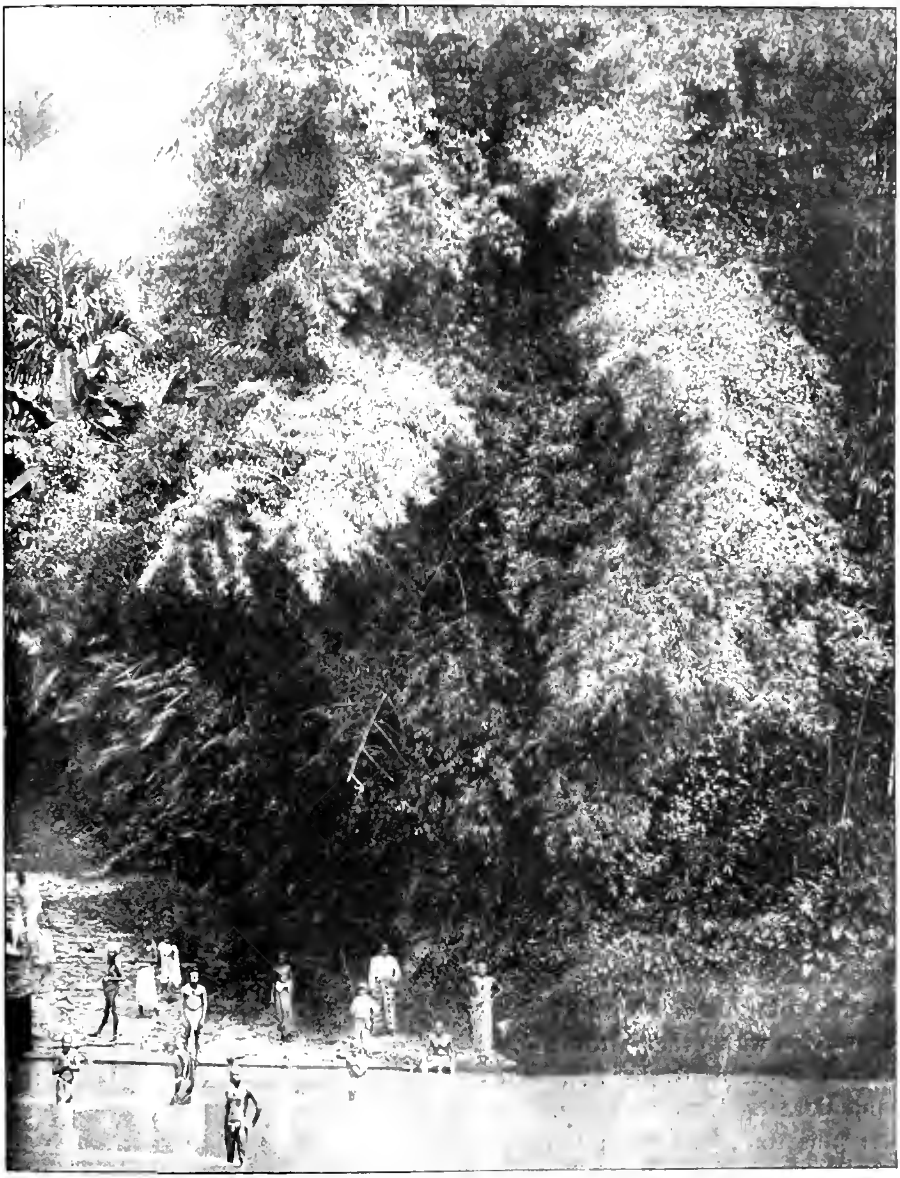

FIG. 207. Exterior of a bamboo-wood. Left hand: Areca Catechu. Java. From a photograph.

tropophilous or xerophilous deciduous forest is transformed into hygrophilous evergreen forest. Stagnant water occasions still more fundamental deviations from the climatic type as regards both the nature of the flora and its oecology. Swampy ground is frequently occupied by pure woods of certain species of palms. Thus, in Trinidad, I observed Mauritia setigera forming the sole vegetation in swampy parts of the savannah of Aripo; in Venezuela and Brazil, other species of Mauritia (M. vinifera, M. flexuosa) similarly congregate to form pure woods; Phoenix paludosa grows socially in the swamps of the Ganges delta, and so on. Certainly mixed forests are not wanting on swampy ground, but they are usually much less rich in species, in particular as regards large trees, than those of less wet soil. The best known among them are the *mangroves* of the tropical shores within reach of tides; they owe their peculiarities partly to the saline nature of the substratum, and will be dealt with later on in connexion with other littoral formations. In contrast with mangrove, the mixed forest of fresh-water swamps in the interior of Burma, Sumatra, and Borneo (Fig. 208), has hitherto been very little studied, although it seems to afford much that is characteristic as regards both flora and oecology.

FIG. 208. Swamp-forest in Borneo. From a photograph by Kukenthal.

Kurz states[1] that *swamp-forest* is 'the most curious forest in Burma, and of great interest to the botanist. In fact, its constituent plants are so dissimilar to

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[1] Kurz, op. cit., p. 29.

those of the surrounding forests, that one must necessarily ask how all these trees come here. The greater part of them do not occur anywhere but in swamps or similar watery places, and, absent from large tracts of country, they reappear in widely separated spots that are adapted for their growth. They might be called the mangrove-forest of the fresh waters, the ground on which they grow being almost as exposed and swampy as that of the mangrove-swamps.' According to a communication by Captain Seaton to Kurz, swamp-forest is completely bare of leaves in the height of the rainy season. Swamp-forest appears in Burma chiefly in the deep alluvial soil of the Irawadi valley, but also along the Sittaung and at the base of the Yoma Hills. It occurs in a typical form in localities which in the rainy season are covered by water up to 4 or 5 feet (sometimes even 7 feet). It consists, like rain-forest, of several tiers: tall trees 60-70 feet high, small trees, shrubs, and plants clothing the ground.

As in most formations with a very peculiar substratum, the tall trees consist of only a few species: Anogeissus acuminatus, Mangifera longipes, and Xanthophyllum glaucum are by far the most prominent. The smaller trees are more diverse; the most commonly seen are Memecylon Helferi, Elaeocarpus photiniaefolia (?), Pavetta parviflora and P. nigricans, Gonocaryum Lobbianum, Symplocos leucantha, Glochidion sp., Hemicylia sumatrana, Flacourtia sp., Cassia Fistula, Randia sp., two species of Eugenia, two species of Aporosa, Garcinia succifolia, Barringtonia acutangula, Dalbergia flexuosa. Among shrubs are in particular Glycosmis pentaphylla, Capparis disticha, Hymenocardia Wallichii, Grewia sinuata, Psilobium sp., Crataeva hygrophila, Combretum trifoliatum, Gardenia sp. The lianes are numerous and many of them very peculiar, as they possess a short stem that reaches only to the surface of the water during the rainy season, and from which there rise disproportionately long and curved shoots, which form an impenetrable thicket; amongst them are Jasminum sp., Gmelina asiatica, Pachygone odorifera, Sphenodesme erysiboides, Tetracera sp., Acacia pennata (?), Ancistrocladus Griffithii, Combretum tetragonocarpum, Roydsia obtusifolia, Derris scandens, D. elegans, D. uliginosa. The terrestrial herbs are scanty and consist chiefly of Carex Wallichii, also Cyperus sp., Fimbristylis sp., species of Polygonum, and Maranta. Orchids abound as epiphytes, especially near small lakes. Accompanying them are large ferns such as Asplenium Nidus, and numerous mosses and liverworts. The water of the pools and swamps is usually very muddy and poor in plants; clear clean water never entertains a very rich flora of common fresh-water plants.

Besides the forest-clad swamps, there are others that resemble oases of grass-land in the midst of the forest. Thus Junghuhn[1] describes swamps in East Java that are covered with water during the rainy season, but dry up more or less completely in the dry season and are overgrown with reed-like grass. Kurz has observed perfectly similar formations in Burma, where they are sometimes free from water during the dry season, and covered with soft juicy species of grass like Hymenachne Myurus and H. interrupta, Panicum Crus-galli and P. antidotale, Isachne sp., Leersia hexandra, with a few herbs, such as species of Jussieua and Xyris, and these plants in the rainy season form floating meadows. Swamps that even in the dry season remain very wet, bear either a flora quite similar to that of the periodically dry ones or are covered with the reeds Phragmites Roxburghii and other species of Phragmites.

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[1] Junghuhn, op. cit., p. 208.

vi. *FUMAROLES IN JAVA.*

Zollinger[1] was the first, and he was followed by Junghuhn[2], to observe in Java the peculiar phenomenon that vegetation close to fumaroles is chiefly composed of alpine species, even when the station is 1,000–1,500 meters below alpine regions. Besides the purely alpine species, there appear in the vegetation around the fumaroles in Java plants which grow in neighbouring forests as epiphytes, but are unknown as terrestrial plants away from the fumaroles.

The fumaroles of Java that I studied consist sometimes of dry crevices encrusted with crystalline sulphur, at other times of crateriform pools, the hot water of which is frequently almost at boiling-point (according to Junghuhn up to 197° F. = 92° C.), and is kept violently bubbling by the gases. Where these pools are collected, usually in large numbers and of different sizes, the soil is a wet white clay, which is said by Junghuhn to arise by the action of sulphuric acid on trachyte; it is usually covered by a yellow efflorescence of sulphur. The ground is frequently so hot that to remain standing on it is impossible. From all the crevices and pools there escape hot vapours of suffocating odour, sometimes of sulphuretted hydrogen, at other times of sulphurous acid. The water has an acid taste and sets the teeth on edge.

Amid these peculiar conditions, frequently close to the bubbling pools, rooted in the hot acid soil, their foliage bathed in hot sulphury vapours, luxuriant bushes flourish, and show no other effects of their environment beyond, in places specially rich in vapour, a white mealy coating on the cortex and leaves.

The bushes of the solfataras are much lower in stature than the surrounding forest and quite sharply marked off from it. None of the small trees and shrubs that form the underwood in the high-forest appear among them; of forest herbs only a few species represented by detached individuals occur; plants that occur elsewhere in the open situations of the same region are entirely absent. In spite of the humidity of the atmosphere and of the soil *the flora of the solfataras is composed of xerophilous species*; in fact, nearly all the xerophytes of the neighbourhood are collected there. There are always numerous plants of Vaccinium varingiaefolium, which otherwise inhabits only the dry alpine region above 2,600 meters, together with Rhododendron javanicum, which thrives on the topmost branches of the neighbouring forest, and Ficus diversifolia, that otherwise occurs only as an epiphyte, and, on the sea-shore near Singapore as a halophyte. In solfataras of lower regions some other species, elsewhere epiphytic, may be added, such as Medinilla javanensis and Rhododendron tubiflorum, whilst as the altitude above sea-level increases, the

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[1] Zollinger, op. cit., p. 43.

[2] Junghuhn, op. cit., p. 453; also Schimper, I.

alpine species in the solfataras steadily increase in numbers (Rhododendron retusum, Gaultheria leucocarpa, Myrsine avenis). Besides these, isolated ferns with leathery leaves, and lycopods, are always present in such spots. It is remarkable, as Junghuhn has already recorded, that the stems of the solfatara-bushes are entirely free from all epiphytic vegetation, even from mosses and lichens; as the above-mentioned author expresses it, a clean sweep is made of the last-named plants—a phenomenon that is also exhibited on the sea-shore.

As has been previously explained[1], the physiological cause of the occurrence of a completely xerophilous vegetation on a wet soil, in a climate with a heavy rainfall, in the midst of a most luxuriant rain-forest, is supplied by the abundance of very soluble salts, especially alum and other sulphates, in the solfataras.

2. FORMATIONS OF THE TROPICAL SEA-SHORE.

i. *CLASSIFICATION OF TROPICAL LITTORAL FORMATIONS.*

Among the edaphic formations of the tropics, only those of the sea-shore have as yet been accurately investigated. They owe their marked characteristics partly to physical and partly to chemical causes, and, as these are very variable, the formations exhibit a physiognomy that frequently varies at short distances.

Tropical littoral formations may be divided into four groups:—

1. *Open formations of the stony and rocky shore.*
2. *Open formations of the sandy shore.*
3. *Littoral woodland above high-tide mark.*
4. *Littoral woodland below high-tide mark.*

The formations on rocky and stony ground of the shore must be left out of consideration, as observations regarding them are wanting. According to my own occasional observations, they appear to afford little that is characteristic.

ii. *OPEN FORMATIONS OF THE SANDY SHORE.*

The flat sandy shore on open coasts, exposed to the wind, is only poorly clad with vegetation. This is also true of the outermost series of dunes, whereas dunes further from the sea, and, still more, the valley-like depressions between them, show a vegetation that increases in density landwards. The most characteristic plants occur where the environment is unfavourable, namely on the loose shifting sand of places exposed to the full violence of the sea-wind. The oecological character of the vegetation on shifting sand by the sea has been already described[2] in a general manner. It was there stated that the first settlers are chiefly creeping

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[1] See p. 91.

[2] See pp. 179–84.

FIG. 210. Pes caprae formation in West Java. Sandy [illegible] shore, with Ipomoea Pes caprae. The shrub in the centre is Scaevola Koenigii. To the [illegible] Croton sp. [illegible]

To face p. [illegible]]

plants, which anchor themselves firmly by means of adventitious roots. The most widely spread of these plants is Ipomoea Pes-caprae (I. biloba),

Fig. 211. Sandy shore with shrubs and Pandanus [illegible] East Africa. [illegible]

which, in both the New and Old Worlds, is rarely absent from sandy shores, and whose rapidly growing shoots, frequently several meters long, generally advance nearest to the sea of all vegetation. Fig. 209 shows the typical Pes-caprae formation. In other areas, other plants of a similar habit prevail, so that, for instance, we can distinguish a Canavalia-formation —named from a papilionaceous genus, several species of which are distributed on the eastern Asiatic shore—or a Spinifex-formation, and so forth. Fig. 210 shows how the Pes-caprae formation develops in more sheltered places. The creeping shoots cover the ground with a network that is only here and there interrupted by larger gaps. Some other plants

Fig. 212. Shrub formation on the sea-shore, close to high-tide mark, near Singapore. In the main Pandanus sp., here and there Scaevola Koenigii and Thespesia populnea. From a photograph by P. Groom.

have taken root on the soil that has become firm, in particular some grasses, and two shrubby species, Scaevola Koenigii and a Croton, are recognizable.

In still more sheltered spots, however, on less shifting, coarse or pebbly sand, shrubs become more numerous, and little trees, in the Old World species of Pandanus, are added (Figs. 211, 212).

In Eastern Asia in such stations, Pemphis acidula very frequently occurs, a bushy lythraceous shrub with small succulent leaves bearing silvery grey scales; Clerodendron inerme, a somewhat thorny shrub, whose long branches covered with dark-green succulent leaves are pendulous, and like brambles and other simple scramblers form tangled thickets, unless they find a support: also the tropical cosmopolitan Scaevola Koenigii (Fig. 210), belonging to the Goodeniaceae, a family otherwise almost confined to Australia, is one of the most remarkable plants of littoral vegetation, thanks to its long and frequently bent shoots which interlace to form a tangled mass, to its large succulent leaves, and to its large panicles of wonderfully white flowers from which white-ribbed stone fruits develop.

In such stations in the Malay Archipelago, and probably elsewhere in Eastern Asia, shrubs and herbs are frequently bound together, and overgrown by a dense tangle of the green and red thread-like stems of Cassytha filiformis.

The shrubs and small trees which, on the side towards the sea, stand apart, become more closely set as their distance above high-tide mark increases—immediately above the latter, indeed, in quiet creeks—so as to form closed woodland that assumes the character of forest, bush, or scrub.

iii. *LITTORAL WOODLAND ABOVE HIGH-TIDE MARK.*

Woodland formations on the sandy and gravelly shore were first described by Junghuhn in connexion with Java, and by Kurz in connexion with Pegu. From the occurrence of many of their characteristic species over a great portion of the Old World the wide distribution of such formations may be surmised; but little is known regarding this. Engler mentions littoral woodland in East Africa, where however it does not appear to cover extensive areas. Nothing is known about its possible occurrence in West Africa, and I cannot remember having seen anything like it in tropical America, although trees like Coccoloba uvifera are not lacking on the shore outside the mangrove. The bush on sandy coasts in Brazil termed 'restinga' appears to be devoid of the halophytic character.

I have met with littoral woodland, in particular on the north coast of Java (Fig. 213), on the small coral islands in the Java Sea and on the island of Singapore, as low or moderately high forest, occasionally interrupted by scrub or by scantily clad stretches of sand. The following description I wrote on the spot, in a forest not far from Priok in Java: but it applies equally well to the other littoral forests that I know:—

'When once we have broken through the dense tangle of branches, that are as it were tied together by the red and green threads of Cassytha, and have entered the interior of the forest (Fig. 214), we meet with a scene radically unlike that of most tropical forests, at least those of humid districts. From the sandy or stony soil, which is bare or covered by only a few scattered dead leaves, there rise up tree-trunks which are either naked, or decked with some few thick-leaved epiphytes, species of Hoya and Dischidia for example, and small crustaceous lichens, and these are often bound together by a confused mass of delicate climbing plants. Should the trees be less dense, the spaces between them are occupied by stubby underwood in which young trees struggle for space with true shrubs and small Pandani, or Crinum asiaticum forms thickets five or six feet high between the tree-trunks.

'The leaves of these plants are frequently quite large, but nevertheless they exhibit in their structure the effects of unfavourable conditions in reference to transpiration, especially in the outer fringe of the formation, where the soil is richest in salts. The foliage of the larger trees is either very dense, or, as with so many denizens of dry districts, is disposed umbrella-like or in tiers; the leaves are thick and leathery (Calophyllum Inophyllum, Terminalia Catappa, Barringtonia speciosa), or succulent and juicy (Scaevola Koenigii, Pemphis acidula, Morinda citrifolia, Clerodendron inerme, Tournefortia argentea, Ximenia americana), frequently in their younger parts densely hairy (Pemphis acidula, Sophora tomentosa, Tournefortia, Thespesia populnea, Heritiera littoralis), rarely provided with a coating of varnish (Dodonaea viscosa). Casuarina equisetifolia reminds one, on a larger scale, of the species of Tamarix in the Mediterranean region; the finely pinnate species of Albizzia and Acacia, the bulbous plants, the narrow and hard-leaved grass, recall dry savannah and steppe.

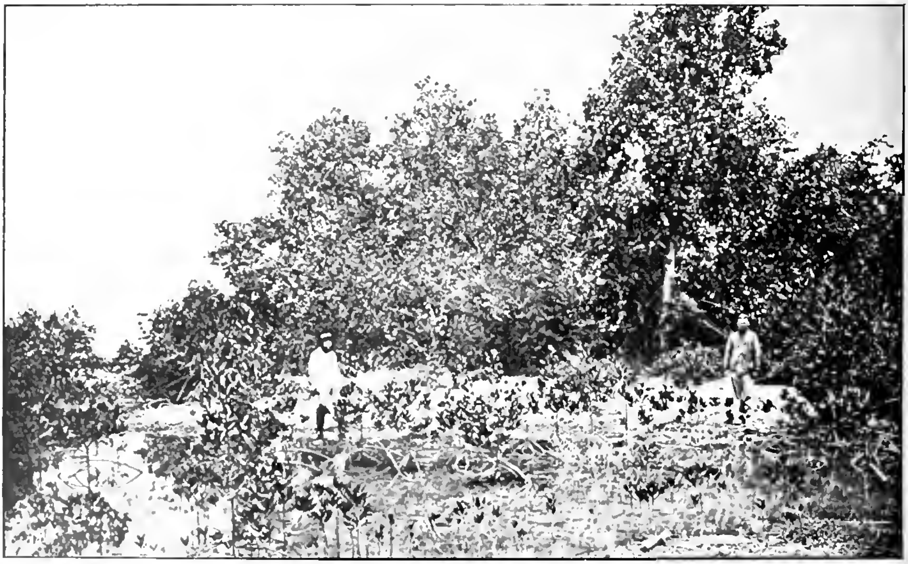

Fig. 213. Littoral formations. In the background, littoral forest of Barringtonia-formation. In the lagoon, young Rhizophora. Java. From a photograph by Warburg.

'As the distance from the sea increases, the protective measures against transpiration become less pronounced; the thick, juicy leaves of Clerodendron inerme, Ximenia americana, Wollastonia, and other plants become like ordinary leaves: many marked halophytic species, such as Barringtonia speciosa, Scaevola, Wollastonia, Tournefortia, gradually become scarcer, whereas inland forms become somewhat more numerous.'

FIG. 214. Interior of a littoral forest. Pandanus as underwood. Island of Singapore. From a photograph by P. Groom.

I have observed in the littoral woodland of Java and of the neighbouring small coral islands the following species of trees: Cycas circinalis, Pandanus (several species), Casuarina equisetifolia, Calophyllum Inophyllum (Guttiferae), Cerbera Odollam (Apocynaceae), Hibiscus tiliaceus and Thespesia populnea (Malvaceae), Terminalia Catappa (Combretaceae), Hernandia peltata (Hernandiaceae), Heritiera littoralis (Sterculiaceae), various Leguminosae (Inocarpus edulis, species of Albizzia, Cynometra, Erythrina, Pongamia glabra, Sophora tomentosa, and others). The number of species of shrubs is far greater; for example, Pandanus (several species), Scaevola Koenigii, Cordia subcordata, Clerodendron inerme, Vitex trifolia, Premna integrifolia, Pemphis acidula, Ximenia americana, Dodonaea viscosa, Allophylus sundanus, Climacandra obovata, Colubrina asiatica, Suriana maritima, Morinda citrifolia, Guettarda speciosa, Excoecaria Agallocha.

The very numerous climbing plants are, with the exception of Entada scandens, all thin-stemmed, and chiefly Leguminosae (such as Guilandina Bonducella, Derris uliginosa, species of Canavalia), also Cassytha filiformis and species of Ipomoea. The small sandy interspaces are chiefly occupied by grasses; other components are various species of Papilionaceae (Vigna, Crotalaria sp.), some inconspicuous Compositae (Conyza indica, Wollastonia glabra and W. biflora), herbaceous Euphorbiaceae (Euphorbia Atoto, Phyllanthus sp., Acalypha indica), Portulaca oleracea and P. quadrifida, and tall, large-flowered bulbous plants (Tacca pinnatifida, Crinum asiaticum, Pancratium zeylanicum).

Kurz mentions as components of littoral woodland in Burma Pongamia glabra, Erythrina indica, Bombax malabaricum, Hibiscus tiliaceus, Cynometra bijuga, Guettarda speciosa, Cycas Rumphii, Thespesia populnea, Scaevola Koenigii, Colubrina asiatica, Derris sinuata, Breynia rhamnoides, Caesalpinia Bonduc, Ipomoea Pes-caprae, Ischaemum muticum. Epiphytes are Polypodium quercifolium, species of Hoya, Dischidia, and some orchids. In Tenasserim, Casuarina equisetifolia may be added.

Various trees and shrubs of the littoral woodland are among the commonest and most frequently cultivated plants, such as Cycas circinalis and C. Rumphii, various large species of Pandanus, Casuarina equisetifolia, Calophyllum Inophyllum, Terminalia Catappa, Morinda citrifolia. Littoral forest is also, without any doubt, the home of the coconut palm.

The littoral forest at other points of the East Asiatic and Australian coasts has probably a physiognomy similar as regards both its systematic composition and its oecology. There are, however, considerable deviations from it. Thus, in Burma, according to Kurz, it belongs to the periodically quite leafless woodland, and on the Bay of Bengal pure woods of Casuarina equisetifolia here and there replace the mixed forest.

In littoral woodland the proximity to the sea is expressed, not merely by marked xerophilous structure — which characterizes it despite the humidity of the climate and the abundance of water in the soil—but also by the fruits or seeds, which are, as a rule, provided with devices to enable them to float. Most of the characteristic fruits and seeds of the sea-drift, that have been already described[1], come from trees and shrubs of the littoral woods. Thus, for instance, Barringtonia speciosa (Fig. 213) is not only characterized by its large leaves and splendid flowers, but, oecologically speaking, much more so by its pyramidal fruits, larger than the fist, which are as light as cork and have a pericarp consisting of a thick layer of floating-tissue. A similar floating-tissue is concealed under a green husk in the large egg-shaped fruit of Cerbera Odollam, in the smaller

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[1] See p. 28.

Figs. 215 and 216. A sea-scape of the mangrove of the Seychelles. Rhizophora mucronata. Above: high tide. Below: low tide. From a photograph by A. Brauer.

almond-like fruit of Terminalia Catappa, under the thick juicy mesocarp of Scaevola Koenigii, in the testa of Cycas circinalis and of Calophyllum Inophyllum. Heritiera littoralis possesses boat-shaped, carinate, hard-shelled nuts, which, thanks to a large internal cavity, are among the best floaters ; and the individual fruits of the huge infructescence of Pandanus, in spite of their beautiful red colour, apparently acquired to attract animals, are hard and almost free from sap, and are chiefly disseminated by marine currents, as is shown by their frequency in drift cast on the shore.

The capacity for floating possessed by the seeds of most plants of littoral woodland, and shared by the partly identical species of the open formations, has occasioned the extremely wide distribution of the plants of these groups of formations. Species from the mangroves, which will be described hereafter, are also provided with floating fruits or floating seeds. But such floating fruits and seeds appear in no formation in such perfection and variety as in littoral woodland above high-tide level.

iv. *WOODLAND FORMATIONS BELOW HIGH-TIDE MARK.*

Within the tropics, as in higher latitudes, the belt of shore within reach of the tide—'the beach'—is quite devoid of vegetation on sandy or clayey coasts exposed to the wind and breakers, and bears only Algae on rocky coasts ; on the other hand, in creeks and lagoons, where the movements of the sea and air are weaker, it is covered by woodland that is sometimes more shrub-like or bush-like, sometimes forest-like, and is termed *mangrove* or *tidal woodland*. It differs from all inland-formations as regards both its flora and its oecology.

Like the littoral woodland above high tide, mangrove consists mainly of species that are very widely distributed. Nevertheless, two extensive areas may be sharply distinguished from one another—an *eastern*, which extends from East Africa over Asia into Australia and Polynesia, and a *western*, which embraces the West African and American coasts.

The Eastern Mangrove.

The eastern mangrove, which shows its greatest wealth of forms in Further India and in the Malay Archipelago and may have originated there, consists, with the exception of a few rare species that doubtfully belong to mangrove, of the following forms:—

Rhizophoraceae: Rhizophora mucronata, Lamk., R. conjugata, Linn., Ceriops Candolleana, Arn., C. Roxburghiana, Arn., Kandelia Rheedii, W. et A., Bruguiera gymnorrhiza, Lamk., B. eriopetala, W. et A., B. caryophylloides, Bl., B. parviflora, W. et A. *Combretaceae*: Lumnitzera racemosa, Willd., L. coccinea, W. et A. *Lythraceae*: Sonneratia apetala, Buch-Ham., S. acida, Linn., S. alba, Smith. *Meliaceae*: Carapa moluccensis, Lamk., C. obovata, Bl. *Myrsinaceae*: Aegiceras majus, Gaertn. *Rubiaceae*: Scyphiphora hydrophyllacea, Gaertn. *Verbenaceae*: Avicennia officinalis, Linn., and var. alba, Bl. (sp.). *Acanthaceae*: Acanthus ilicifolius, Linn. *Palmae*: Nipa fruticans, Thunb.

Many species of woody littoral plants occur at times on dry spots in the mangrove, but very rarely on the mud (Heritiera littoralis in Ceylon, according to Karsten).

At high tide one looks from the sea on to bright green crowns of foliage that rise out of the sea along the shore-line (Fig. 215), sometimes crowded closely together, at other times like isolated outposts. At low tide, as far as the mangrove extends, the ground is no longer covered by the sea, and reveals itself as a bluish-black mud, from which the trees raise themselves on short stems that are, however, supported by tall stilt-like roots (Fig. 216). In the eastern mangrove, the species of tree which forms the advanced line along the sea and which, by its slow forward march, causes a gradual elevation of the coast, is Rhizophora mucronata (Figs. 215–217, and 227). No mangrove-tree is better equipped for resisting the movements of the tide on the soft mud, for propagating itself under these difficult conditions, and for recovering from the frequently quite undiluted salt[1] sea-water the water lost in transpiration. The scaffolding of bow-shaped stilt-roots supporting the stem represents a complete system of anchors, which is strengthened by new roots growing down from the branches to balance the growth of the crown. The leaves possess a marked xerophilous structure (Fig. 17), with a thick cuticle, large mucilage-cells, protected stomata, and especially a large-celled thin-walled aqueous tissue, the dimensions of which increase with the age of the leaf and with the corresponding rise in the amount of salt contained. Old leaves serve essentially as water-reservoirs for the younger leaves.

The mode of propagation is most remarkable in Rhizophora mucronata, which in this respect agrees in the main with the other Rhizophoraceae living in the mangroves (Fig. 218). The fruit, leathery and indehiscent and about the size of a hazel-nut, soon after the completion of its growth is pierced at its summit by the green hypocotyl, as the embryo does not undergo any period of rest, but continues to develop without interruption. The hypocotyl in Rhizophora mucronata is club-shaped and attains a length of sixty centimeters, sometimes even more, before it falls down, leaving behind it the fused cotyledons which served as absorbing-organs. As its lower end is thicker, the seedling falls vertically, with its root-tip downwards into the mud, and within a few hours develops roots that fix

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[1] The statement frequently repeated in literature, that Rhizophora does not occur in pure sea-water, is incorrect. I have seen R. mucronata thriving on the rocky ground of the coral islands of the Java Sea, where there is no fresh water.

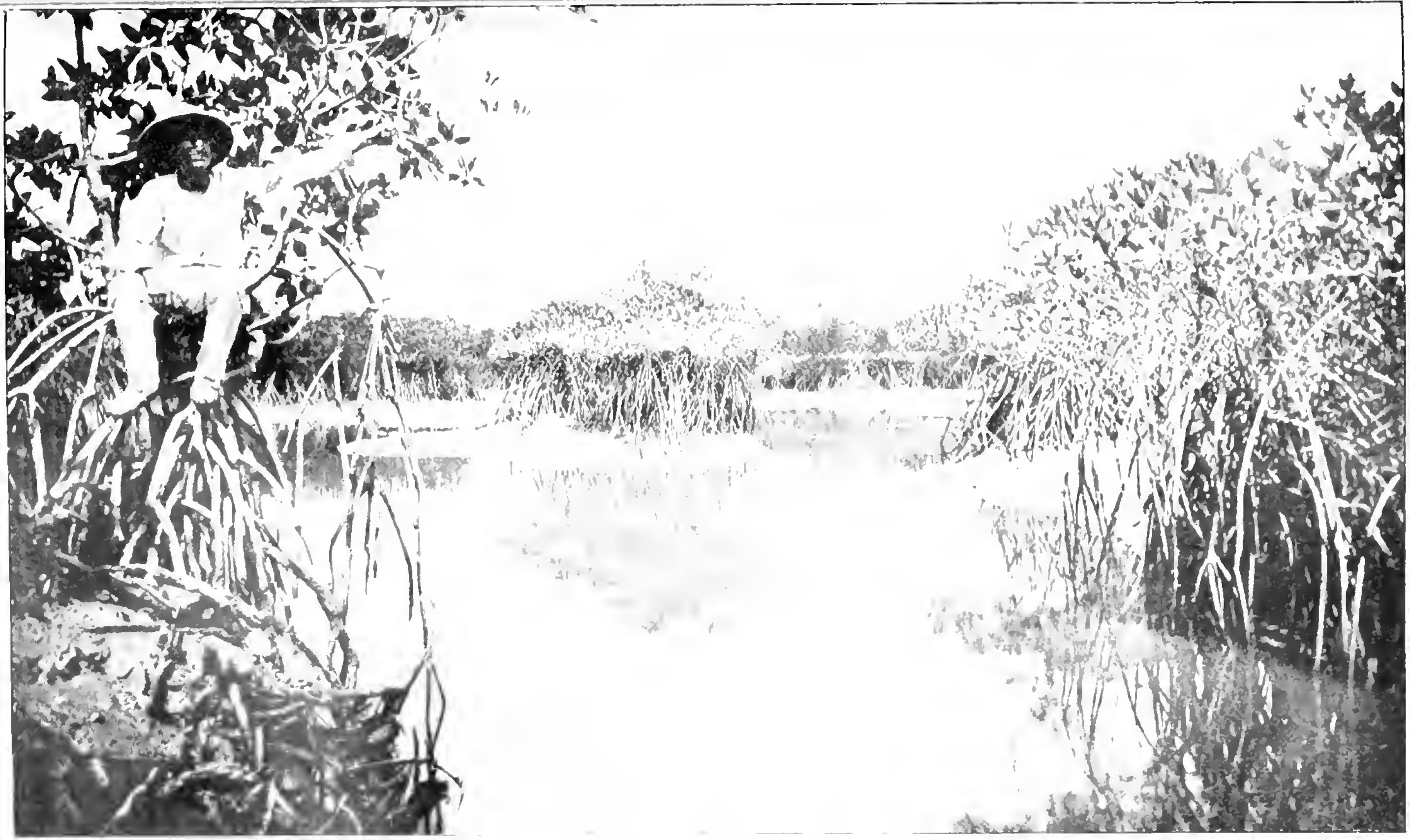

FIG. 217. Mangrove-landscape in Cochin China at low tide. Rhizophora mucronata. From a photo. by O. Warburg.

it firmly; yet, as the occurrence of seedlings in the drift shows, it is often carried away by the falling tide in less sheltered spots. Uprooted

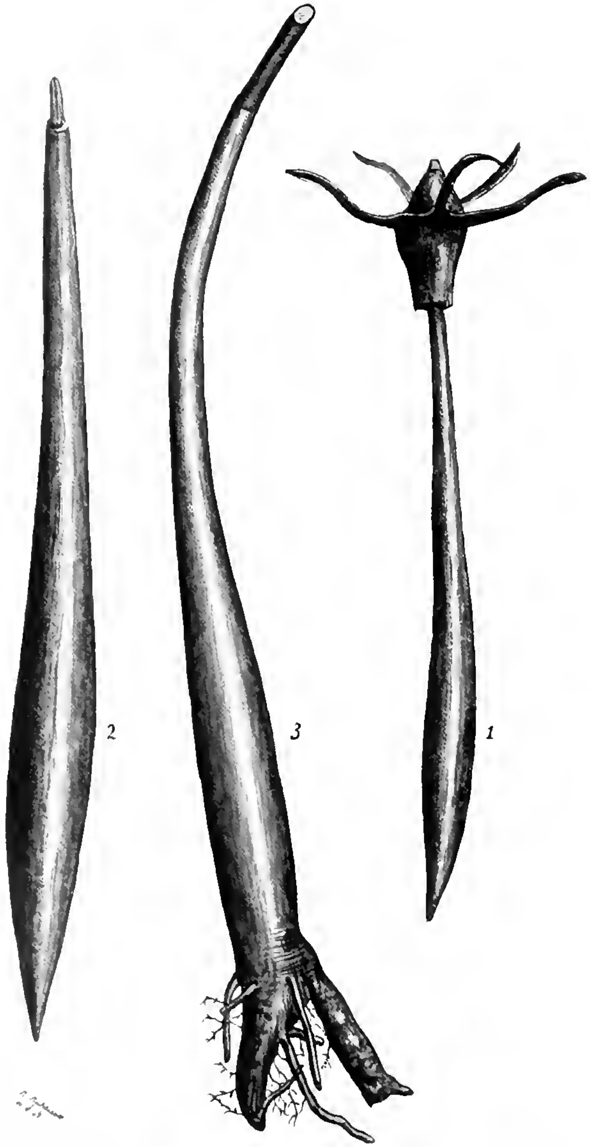

Fig. 218. Kandelia Rheedii. 1. Young seedling still adhering to the fruit. 2. Seedling detached with the plumule upwards. 3. Seedling after taking root; only the base of a shoot bearing several leaves. Three-quarters natural size. Drawn from nature by R. Anheisser.

seedlings can however develop further in suitable situations, because their lower part is positively geotropic and their upper part negatively so. In

FIG. 219. Bruguiera parviflora. Fruits with seedlings in various stages of development, but none quite ready to fall. South Javanese mangrove. Natural size.

Fig. 213 numerous young plants of Rhizophora mucronata, in various stages of development, are visible in a shallow pool, evidently of quite recent origin, on the shore. In other Rhizophoraceae belonging to the mangrove the seedlings are smaller than in R. mucronata and not always markedly club-shaped (Figs. 218 and 219).

Vivipary is also exhibited by Aegiceras majus and Avicennia officinalis. The seedlings of Aegiceras are curved like horns, and are smaller than those of the Rhizophoraceae; they remain enclosed in the thin pericarp of the fruit. Those of Avicennia which fall, sometimes surrounded by the leathery pericarp that dehisces subsequently, and at other times without it, are provided with a bent and densely hairy hypocotyl and with two large cotyledons. The hairs are stiff and curved upwards, and fix the seedling to the mud. In the remaining mangrove-plants vivipary does not occur; but the seedlings of some species, in particular those of Acanthus ilicifolius and, in America, of Laguncularia racemosa, are always further developed than is usual in inland plants.

Fig. 220. Bruguiera gymnorrhiza. Javanese mangrove. From a photograph by G. Karsten.

On proceeding more into the interior of the mangrove we find that other woody species join Rhizophora mucronata and become dominant with increasing distance from the sea. Bruguiera gymnorrhiza surpasses all other mangrove-trees in size (Fig. 220). Other species of Bruguiera, Rhizophora conjugata, Ceriops Candolleana and Kandelia Rheedii, are smaller trees or shrubs. Sonneratia acida (Fig. 221), which often forms pure mangrove, is likewise a small tree; the allied and similar Sonneratia alba prefers stony ground, and frequently grows by itself in open situations, outside the true mangrove. Avicennia officinalis also frequently forms extensive bushy mangrove (Fig. 222), in which the grey foliage, often bedecked with bright yellow inflorescences, extends nearly to the ground. Aegiceras majus is a moderately tall shrub, and Acanthus ilicifolius a thistle-like herb.

The stilt-roots, which give Rhizophora mucronata such a peculiar appearance, occur relatively strongly developed elsewhere only in the herbaceous Acanthus. In Rhizophora conjugata, which does not descend so far towards the sea as does R. mucronata, they are more weakly developed than in R. mucronata. In the other mangrove-trees they are either absent or only slightly developed (Fig. 225); in particular, the anchoring-roots descending from the branches are wanting.

On the other hand, the roots of most mangrove-trees are characterized by the possession of highly peculiar pneumatophores (Figs. 223, 224, 225). These are displayed in their implest form by Carapa obovata Fig. 223, 3), where the serpenine creeping roots project above he mud with their upper edge, ike the blade of a thick knife, but studded with lenticels. In Carapa moluccensis the secondary growth in thickness in the upper part is irregular, so that he root terminates in finger-like outgrowths. In the species of Bruguiera (Figs. 223, 1 and 2; 225), the horizontal roots here and there bend out of the mud into knee-like structures, which in Bruguiera gymnorrhiza bear large lenticels, but in Bruguiera caryophyl-

FIG. 221. Sonneratia acida. Javanese mangrove. From a photograph by G. Karsten.

FIG. 222. Avicennia officinalis at low tide. Javanese mangrove. From a photograph by G. Karsten.

Fig. 223. Pneumatophores of mangrove-trees. Java. 1. Bruguiera caryophyllaeoides. 2. Br
a gymnorrhiza. 3. Carapa obovata: young branch of root. 4. Avicennia officinalis: negative
[illegible] All reduced.

laeoides gradually shed their cortex. Avicennia officinalis (Figs. 223, 4; 224), together with the two American species, Sonneratia acida and S. alba, Ceriops Candolleana, and the American combretaceous Laguncularia racemosa, all have negatively geotropic lateral roots protruding from the ground like asparagus; these are as long as one's finger, or, in Sonneratia, one's arm. The species of Rhizophora do not possess special pneumatophores, yet the upper parts of their stilt-roots that are above the mud perform the same function.

FIG. 224. Avicennia officinalis. Pneumatophores. Mangrove, Java. Half natural size.

That pneumatophores supply subterranean parts of the trees upon which they occur with oxygen was proved by G. Karsten and Greshoff, as has been already explained[1]. All these structures are accordingly provided with devices for absorbing oxygen (lenticels, stomata, thin cork) and for transporting it (intercellular passages in the primary cortex or bast).

By means of a sketch written on the spot, I have attempted in the following paragraphs to give a description of the physiognomy of the mangrove in Java:—

'The lagoon-like bay in South Java known as the "Kindersee" is separated on the south from the Indian Ocean

FIG. 225. Bruguiera gymnorrhiza with knee-roots. Mangrove, low tide, South Liu-kiu. From a photograph by O. Warburg.

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[1] See p. 73.

by the [illegible] island of Noesa-Kambangan, but otherwise enclosed by the shores of the main island, here quite flat. Several rivers pour their sluggish waters into it, and, as they lie low, they feel the influence of the tides even at a great distance from their mouths. Most of them subdivide into several arms. The deltas they enclose are under water at high tide, but a little above water-level at low tide. A better substratum for the development of mangrove could hardly exist, and it is accordingly developed with rare luxuriance.

‘When travelling in a canoe along the banks of the creek, or along one of the numerous arms of the rivers, one does not always observe the same landscape. On exposed shelving coasts, Rhizophora mucronata is almost alone capable of resisting the violence of the waves or of propagating itself in the troubled water; but here on these flat shores, where breakers are unknown, the conditions of existence are far more nearly equally favourable to the various species of plants, so that sometimes one, at other times another, species gains the victory in the struggle for space. Sometimes the shore is occupied by a dense belt of Rhizophorae; sometimes one passes by a little forest of silver-grey, willow-like Avicennia officinalis, var. alba; at still other points the dull green foliage of Sonneratia acida predominates, or the outposts are held by a narrow hedge of Nipa fruticans. Here and there occurs the remarkable spectacle of a Carapa obovata, whose brownish-yellow fruits, as large as one's head, peep from the small crown of the tree, or one sees a bush of Aegiceras majus covered with snow-white flowers and curved horn-shaped fruits. The two species of Bruguiera (B. gymnorrhiza and B. parvifolia) that grow here are less frequent on the margin of the mangrove in contrast with their abundance in its interior, where the crowns of B. gymnorrhiza tower above the other trees, whilst the much smaller B. parviflora with inconspicuous blossom is less noticeable.

‘At low tide one can see the confused crowd of the stilt-roots of Rhizophora, or the crop of asparagus-like rootlets of Avicennia and Sonneratia, with their population of fishes and crabs. I have nowhere else seen the knee-roots of Bruguiera gymnorrhiza in such numbers and dimensions. At other points the sharply keeled roots of Carapa obovata creep with manifold bends over the surface of the mud.

‘At high tide the whole complex of roots is invisible; even the lowest leaves of Rhizophora and of Sonneratia remain for some time submerged. From my canoe I could see young plants of Rhizophora mucronata in the deep water.

‘Epiphytes are very scarce in the mangrove, and at its outer edge are entirely wanting on Rhizophora mucronata. Apparently the salty surface does not suit them, as it renders the substratum, that is already poor in water, still drier physiologically. Only in long creeks and in the interior of extensive mangroves, where the wind does not blow salt spray on to the branches, do epiphytic species, like Platycerium grande and P. alcicorne, also on the “Kindersee” Hydnophytum montanum, become more numerous. Small lichens however always occur, but no mosses; mosses are very halophobous plants.’

An account of the Algae that cover the roots of the trees will be given in the chapter on aquatic plants (p. 791).

In tropical East Asia and Australia, lagoons more distant from the sea, where, however, the soil is still subject to tidal influence, but is less saline,

FIG. 226. Cocos nucifera, Nipa fruticans, [illegible]
at Singapore

are largely fringed with a short-stemmed palm, Nipa fruticans (Figs. 226 and 227), which occasionally, for instance in Sumatra, alone covers extensive tracts. This variety of mangrove is best distinguished from the true mangrove formation as *Nipa-formation*. Rhizophoraceae hardly ever occur in the Nipa-formation, but a few other mangrove trees, such as Avicennia officinalis, Sonneratia acida, sometimes appear, and very frequently the fern Chrysodium aureum.

Behind the mangrove and Nipa-formation, the land, becoming gradually drier and being free from regular inundation by the tide, shows an increasing number of species belonging to drier saline soil, Hibiscus tiliaceus mixed with Chrysodium aureum being specially abundant (Fig. 228).

Fig. 227. From the Javanese mangrove. In front: Rhizophora mucronata, bearing seedlings. In the background: Nipa fruticans (Nipa-formation). From a photograph by G. Karsten.

The Western Mangrove.

The western mangrove greatly resembles the eastern in its oecological character, but is much poorer in species and much less richly differentiated. It contains four species only:—

Rhizophoraceae: Rhizophora Mangle, Linn. *Combretaceae*: Laguncularia racemosa, Gärtn. *Verbenaceae*: Avicennia tomentosa, Jacq., and A. nitida, Jacq.

The West African mangrove appears to be without Avicennia tomentosa.

Rhizophora Mangle (Figs. 229, 230), like R. mucronata in the eastern mangrove, occupies the outer edge of the formation, whilst Laguncularia racemosa appears particularly at the inner boundary and there frequently forms pure mangrove. The Avicenniae assume an intermediate position. Just as in the eastern mangrove, so in the western, on drier islets a few additional species of plants occur which become dominant in formations transitional to inland formations, and include tropical cosmopolitan species, such as Hibiscus tiliaceus and Chrysodium aureum, but also some purely western species, such as the combretaceous Conocarpus erectus. Epiphytes are scarce in the western as in the eastern mangrove, and are usually confined to a few Bromeliaceae and lichens.

FIG. 228. Mangrove in Samoa. Inner margin on a less saline and less wet soil. On both banks: Chrysodium aureum. To the right: Hibiscus tiliaceus ?. In the background: Cocos nucifera. From a photograph.

v. *DISTRIBUTION OF LITTORAL FORMATIONS IN THE TROPICS.*

Open littoral formations occur throughout the tropics, and in districts with a small rainfall they are almost the only ones. The close woodland above high-tide mark and the mangrove growing within reach of the tide are luxuriantly developed only in districts with abundant rain; and as the atmospheric precipitations decrease they become lower in stature, less close, and poorer in species. Besides this, littoral woodland is exclusively tropical, or is represented in temperate zones only by a few tropical emigrants of stunted form, whereas the open formations agree oecologically with those of higher latitudes.

Up to the present time the *distribution of mangrove* alone has been studied in detail. Within the tropics its distribution nearly agrees with that of rain-forest. The mangrove is absent or poorly developed on coasts the inland vegetation of which possesses a xerophilous character, except where, as at the mouth of the Indus and other large rivers, there is a considerable addition of fresh water to the sea-water. This correlation, in spite of the continuously very wet condition of the substratum, is quite comprehensible when the distinction is recalled between physical and physiological dryness. Sea-water is physiologically dry[1], so that plants that meet their demands for water from it are exposed to the danger of excessive transpiration, and consequently climatic factors counteracting transpiration must necessarily favour the development and spread of mangroves. The air in districts near the sea, even with scanty rainfall, is probably as humid as in those with abundant rain; on the other hand [illegible] which reduces the heating of the foliage due to insola-

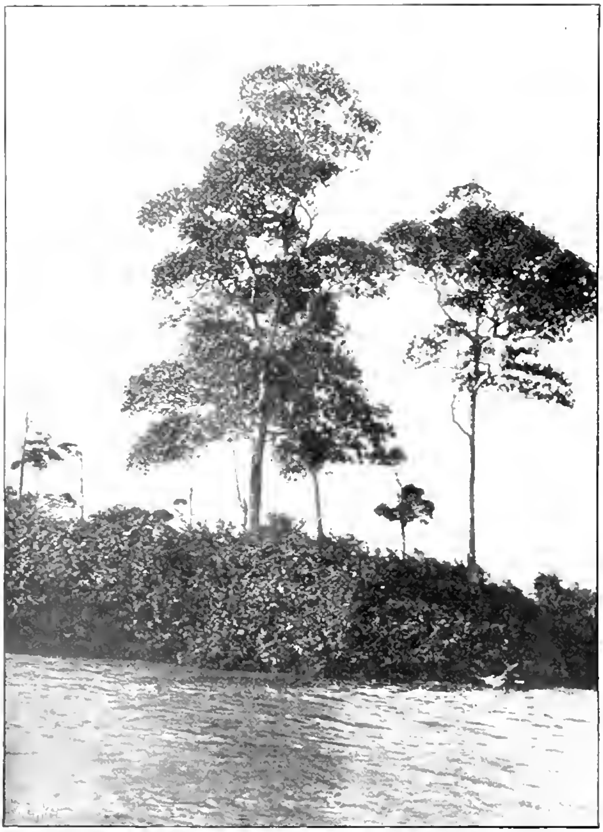

Fig. 229. Mangrove in Florida. View from exterior. Rhizophora Mangle. From 'Garden and Forest.'

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[1] See p. 4.

tion, and consequently the transpiration, is much more considerable and more regular in humid sea-districts than in those with slight rainfall. Dense and frequently repeated *cloudiness apparently represents the most essential climatic condition for the occurrence of mangrove* in the tropics.

Beyond the tropics the limits of the formation as a whole, and those of its individual members, are chiefly determined by temperature:

The North-East limit of the *Eastern Mangrove* as a closed formation, according to Warburg's observations, apparently lies in South Liu-kiu (Iriomotte. 25° N.); Warburg has not seen tall mangrove further North. Even there it is already impoverished and consists of only four species (Bruguiera gymnorrhiza, Rhizophora mucronata, Sonneratia acida, ? Avicennia officinalis); in the form of isolated individuals. Rhizophora mucronata still appears in South Japan (Kagoshima, 32° N.) as the most northerly representative of the Eastern Mangrove flora. In a South-East direction the mangrove continues to the tropic of Capricorn in undiminished luxuriance, but becomes lower in stature and poorer in species on the coast of New South Wales (Avicennia officinalis, Aegiceras). Bushes of Avicennia occur even in New Zealand and as far as Chatham Island (44° S.). The North-West limit of the mixed mangrove lies at the mouth of the Indus; beyond this

FIG. 230. Mangrove in Florida. Interior view. Rhizophora Mangle. From 'Garden and Forest.'

Avicennia officinalis alone reveals itself at a few isolated stations north as far as Sinai. In the South-West direction it continues as a mixed formation to 30° S. in Natal.

The *Western Mangrove* extends in a North-East direction as far as Bermuda (32° N.). but on the American continent only to South Florida (27°–28° N.). I have observed it to the South-East even on the island of Santa Catharina (27° S.), growing as luxuriant mixed bush. The North-West limit, according to Drude's Atlas. occurs in South California. The South-West limit is at 4° S., for the dryness of the climate precludes its further extension southwards.

SELECT LITERATURE.

1. Edaphic Influences in Tropical Inland Country.

Brandis, D. Die Familie der Dipterocarpaceen und ihre geographische Verbreitung. Sitzungsber. d. niederrhein. Gesellsch. für Natur- und Heilkunde zu Bonn. 1896.

Junghuhn, Fr. Java, deszelfs gedaante, bekleeding en invendige structuur. German Edition by Hasskarl. Bd. I. 1852.

Kurz, S. Preliminary Report on the Forest and other Vegetation of Pegu. Calcutta, 1875.

Warming, E. Lagoa Santa. Skrifter a. d. kgl. danske Videnskabernes Selskab. 1892.

Wohltmann, F. Die natürlichen Faktoren der tropischen Agrikultur und die Merkmale ihrer Beurtheilung. Leipzig, 1892.

Zollinger, H. Ueber Pflanzenphysiognomie im Allgemeinen und diejenige der Insel Java insbesondere. Zürich, 1855.

2. The Formations of the Tropical Seashore.

Börgesen, F., og Paulsen, Ove. Om vegetationen paa de dansk-vestindiske oër. Kjobenhavn, 1898.

Cleghorn, H. On the Sand-binding Plants of the Madras Beach. Hooker's Journ. of Botany. Vol. VIII. 1858.

Engler, A. Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete. Theil A. Berlin, 1895.

Goebel, K. I. Die Luftwurzeln von Sonneratia. Berichte der deutschen botanischen Gesellschaft. Bd. IV. 1886.

—— II. Pflanzenbiologische Schilderungen. Theil I. Marburg, 1889.

Haberlandt, G. I. Eine botanische Tropenreise. Leipzig, 1893.

—— II. Ueber die Ernährung der Keimlinge bei viviparen Mangrovenpflanzen. Annales du Jardin Botanique de Buitenzorg. Vol. XII. 1895.

Johow, Fr. Die Mangrovensümpfe. Kosmos. 1884.

Junghuhn, Fr. Java, deszelfs gedaante, bekleeding en invendige structuur. German Edition by Hasskarl. Bd. I. 1852.

Karsten, G. Ueber die Mangrovenvegetation im malayischen Archipel. Bibliotheca botanica. Heft XXII. 1891.

Kurz, S. Preliminary Report on the Forest and other Vegetation of Pegu. Calcutta, 1875.

Pechuel-Lösche, E. Die Loango-Expedition. Abth. III, Hälfte 1. Leipzig, 1882.

Schenck, H. Ueber die Luftwurzeln von Avicennia tomentosa und Laguncularia racemosa. Flora. Jahrg. LXXII. 1889.

Schimper, A. F. W. I. Ueber Schutzmittel des Laubes gegen Transpiration vornehmlich in der Flora Java's. Monatsberichte der Berliner Akademie. Bd. VII. 1890.

—— II. Die indomalayische Strandflora. Botan. Mittheil. aus den Tropen. Heft III. Jena, 1891.

Schweinfurth, G. Pflanzengeographische Skizze des gesammten Nil-Gebietes und der Uferländer des Rothen Meeres. Petermann's Mittheil. 1868.

Warburg, O. Vegetationsschilderungen aus Südost-Asien. Engler's Jahrbücher. Bd. XVII. 1893.

Warming, E. Rhizophora Mangle. Ibid. Bd. IV. 1883.

SECTION II. THE TEMPERATE ZONES

CHAPTER I

GENERAL CHARACTERISTICS OF THE TEMPERATE CLIMATE AND ITS EFFECTS ON VEGETATION AND FLORA

1. General Characteristics of the Temperate Climate. i. *Heat.* Great differences of temperature. Maritime climate and continental climate. Isotherms of January and July. Diurnal oscillations. ii. *Light.* Zone-like differentiation of light. Absorption and diffusion of light in different latitudes. iii. *Atmospheric Precipitations.* Periodicity and amount of precipitation. Significance in relation to the soil. **2. Some General Effects of the Temperate Climate on Plant-life.** i. *Effects of Heat.* Its fundamental significance. Temperatures below freezing-point. Zone with a mild winter and zone with a cold winter. Distribution of species. Mesothermic plants. Lack of uniformity of the oecological optimum temperature. ii. *Effects of Light.* Amount and intensity of light. Fixed lie of leaves in relation to light. Diffuse light in temperate zones. iii. *Effects of Atmospheric Precipitations.* Smaller significance when compared with the tropics. **3. Character of the Flora of Temperate Zones.** General survey of the mesothermic forms.

1. GENERAL CHARACTERISTICS OF THE TEMPERATE CLIMATE.

i. *HEAT.*

THE zones between the tropical and the polar zones deserve the appellation *temperate* solely on account of their mean temperature. From the point of view of the difference between the temperatures of winter and summer they should rather be termed excessive. This is specially true of the north temperate zone. 'Between the tropic of Cancer and the polar circle there is represented almost the entire range of temperature, within which the temperature of the air on the earth's surface ever fluctuates. In Central East Asia the mean temperature in January sinks almost every year to −40° C. and even lower, whilst the temperature in July rises to 35° C. in the Punjab, Mesopotamia, probably also in Arabia, North Africa, and in Arizona and South California. At the same time the absolute extremes of temperature of these countries lie between − 70° and + 50° and even more. As regards oscillations of temperature also, the variability in temperature from one day to another reaches its highest in the north temperate zone; in it, districts with the greatest variability of temperature occur[1].'

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[1] Hann, op. cit., III, p. 3.

Proximity to the sea generally operates as a moderating influence on climate. A mild climate may accordingly be described as a *maritime climate*, an excessive climate as a *continental climate*. Besides the property possessed by masses of water of heating up or cooling down more slowly than solid land, the effects of ocean currents play an important part on the climate of littoral districts and islands. The western parts of the British Isles and the west coast of Norway owe to the Gulf Stream their high winter temperature, that is so remarkable considering their high latitudes; and the east coast of North America is for similar reasons warmer than its west coast. The following table gives the mean temperature for a series of climates:—

MEAN TEMPERATURES (CENTIGRADE) IN DIFFERENT CLIMATES.

Stations 1 to 6 Temperate; 7–8 Semi-temperate; 9–12 Extreme. After O. Peschel.

Station.	Latitude.	Altitude.	Year.	January.	July.	Difference.
1. Hokitika (New Zealand)	42° 42′ S.	3 m.	11·6	15·7	7·2	8·5
2. Falkland Islands . . .	51° 41′ S.		6·1	9·8[1]	2·5	7·3
3. Hobart Town (Tasmania)	42° 52′ S.	10 m.	13·1	17·3	8·8	8·5
4. Dublin	53° 22′ N.	48 m.	9·5	4·7	15·4	10·7
5. Sitka	57° 3′ N.	—	5·7	− 1·0	12·5[2]	13·5
6. Reykjavik	64° 8′ N.	—	3·3	− 2·5[1]	12·1	14·6
7. Dresden	51° 3′ N.	128 m.	9·2	− 0·3	19·2	19·5
8. Buda	47° 30′ N.	153 m.	10·7	− 1·4	22·3	23·7
9. Astrakhan	46° 21′ N.	− 20 m.	9·4	− 7·1	25·5	32·6
10. Irkutsk	52° 17′ N.	460 m.	− 0·1	− 20·5	18·8	39·3
11. Yakutsk	62° 1′ N.	160 m.	− 11·2	− 42·8	18·8	61·6
12. Verkhoyansk	67° 34′ N.	50 m.	− 16·7	− 49·0	15·4	64·4

Annual fluctuations of temperature are much smaller in the south temperate zone than in the north; only the diurnal oscillations in the south temperate zone are as great or greater at certain places, for instance in the interior of South Africa and of Australia.

On the whole, the temperature of the atmosphere diminishes with increasing distance from the tropics, but in a most irregular manner, so that isotherms in the temperate zones exhibit much greater curvatures than within the tropics (see Map IV):—

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[1] February.

[2] August.

For example, the isotherm for January of 0° C. has its most northerly point in America, to the north of Sitka, at about 58°; eastwards it falls rapidly down to St. Louis, its most southerly American point, at 38° 5′, runs with a slight ascent to Washington at 39°, to Philadelphia at 40°, ascends considerably in the Atlantic Ocean, reaches the south coast of Iceland at about 63° 30′, exceeds 70° on the west coast of Norway and there reaches its most northerly point, then runs directly southwards along the west coast of Denmark, across Central Europe (Wilhelmshaven, Bamberg, Munich), then bends towards the east, passes south of Sofia at about 42°, its most southerly point in Europe, then continues, with weaker undulations, in the easterly direction, reaching its most southerly point about 32°, in Central China, where it is 38° south of its most northerly point, then it gradually ascends, traverses South Korea, and reaches its most northerly Asiatic point in the northern part of Nippon at about 38°, which lies therefore only about 6° above its most southerly point and considerably more to the south than on the west coasts of America and Europe.

In the southern hemisphere, north of the Antarctic circle, only a part of Tierra del Fuego and a few insignificant groups of islands, for instance South Georgia, have a July temperature of 0° C. or less.

The July isotherm of 20° C. is the most uneven in the northern hemisphere, though without executing such sharp curvatures as the isotherm of 0° C. It reaches its most southern point on land in California at 31° (descending much more to the south on the ocean), ascends almost due northwards up to about 55° in the north-west, then proceeds westwards with repeated undulations through Canada (Winnipeg 50°, Quebec), through Boston at about 42° 20′, crosses the Atlantic Ocean somewhat north of 40°, aligns the north coast of Spain (about 44°), the west coast of France (Bordeaux), bends eastwards through Paris to Moscow, then straight through Siberia, ascending in East Siberia to Yakutsk (about 62°), its absolutely northernmost point, where it is 31° north of its southernmost point, then falls on the coast of China to south of 40°, its most southerly Asiatic point, and reaches the south point of the island of Jesso.

In the southern hemisphere, the January isotherm of 20° reaches the west coast of America at about 20°, that is to say within the tropics, its northernmost point; it falls along the Andes to South Argentina, runs southwards along the west coast of Africa from the tropic of Capricorn to the Cape of Good Hope, then eastwards, without reaching Natal, to the south coast of Australia, to which it nearly entirely clings, and passes through the north of New Zealand.

The diurnal oscillations of atmospheric temperature are usually greater in temperate zones than in the tropics. They attain their maximum in deserts. Thus G. Rohlfs read − 0·5° C. on his thermometer in the morning of the 25th of December, 1878, at Bir Milrha, south of Tripoli, and in the afternoon of the same day + 37·2° C.[1] The diurnal fluctuations mainly depend on the radiation of heat—that of the sun by day, that of the earth by night—and are accordingly much greater with a clear than a cloudy sky. In the former case, particularly in dry districts, they

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[1] Peschel, Physikalische Erdkunde, Leipzig, 1881, II, p. 174.

apparently have a considerable bearing on the processes of vegetation; but observations on this question are not available.

ii. *LIGHT.*

As the non-calorific rays of the sun's energy can act on vegetation exclusively by radiation, the zones denoting the distribution of light—*zones of light-climate*, in contrast to those denoting the distribution of heat, *zones of temperature-climate*—are parallel with the equator: under the heading of light may be included the ultra-violet rays, so far as they act upon the plant. The total intensity of light diminishes uniformly towards the poles, but the length of the day during the greatest part of the vegetative season increases in the same direction—the illumination during the winter sleep is without significance.

DURATION OF DAYLIGHT IN DIFFERENT LATITUDES.

Latitude.	Length of longest day.	Length of shortest day.
30°	13 hrs. 56 min.	10 hrs. 4 min.
40°	14 ,, 51 ,,	9 ,, 9 ,,
50°	16 ,, 9 ,,	7 ,, 51 ,,
60°	18 ,, 30 ,,	5 ,, 30 ,,
66·5	24 ,, — ,,	0 ,, 0 ,,

Owing to the greater length of the day the insolation of a point in the temperate zones during a summer day would be much stronger than that of a point at the equator if absorption by the atmosphere did not likewise increase towards the poles. With the sun in the zenith, the atmosphere allows 81 % of the luminous rays, 75 % of the heat rays, 40 % of the chemical rays to pass; with increasing distance from the zenith, the absorption will naturally become proportionately greater.

Whilst absorption of the sun's rays increases with the distance from the equator, this is compensated to a certain extent by the increase of diffuse light that *pari passu* takes place, so that the sum total of *luminous* energy falling on a point in the temperate zones in summer remains greater than that at the same time at the equator. *Chemical* radiation, on the other hand, in consequence of its stronger absorption becomes considerably weakened. Hence with equal surfaces *a plant of the temperate zone during the vegetative season receives more luminous but less chemical energy than one in the tropics.*

iii. *ATMOSPHERIC PRECIPITATIONS.*

The alternation of dry and wet seasons that is almost general, if not everywhere equally pronounced, within the tropics, is continued beyond them up to nearly 40° N. and S. latitudes. In higher latitudes, districts with precipitation at all seasons of the year predominate, for instance the greater part of Europe, West Siberia, Eastern North America, South Chili, Japan, Kamchatka, New Zealand; yet within the same latitudes there are extensive districts with marked periodicity of atmospheric precipitation, for instance Central and East Asia and Western North America.

The amount of precipitation in the temperate zones attains that in the rainiest tropical points at only a few places. Among districts of any considerable extent which have more than two meters annually there are Assam, a small part of the north-west coast of America, South Chili, a part of Western New Zealand; but besides these there are only a few isolated points, in particular in the Himalayas, also in the Alps, in Norway, and Great Britain. Equal amounts of rainfall, however, in the temperate zones, wet the soil more thoroughly than in the tropics, as they are on the average spread over far longer periods of time and therefore flow off to a smaller extent.

Of great importance in the cold temperate zone is the winter snow, the water melting from which is mostly acquired by the soil.

The formation of dew is generally weaker in the temperate zones than in the tropics; fogs are characteristic of humid and cool districts, near the sea in particular.

2. SOME GENERAL EFFECTS OF THE TEMPERATE CLIMATE ON PLANT-LIFE.

i. *EFFECTS OF HEAT.*

Heat, though it universally determines the very existence of plants, seems to lie concealed in the tropics owing to its uniformity, and, compared with atmospheric precipitations, does not essentially affect the differences in vegetation either in space or time; in the temperate zones, on the other hand, differences in temperature assume both in space and time a considerable importance, that rapidly increases towards the poles, and finally far exceeds that of atmospheric precipitations.

Of special significance in relation to plant-life are temperatures slightly below zero, those in fact that correspond to the freezing-points of the sap, which last, according to its concentration, freezes at temperatures varying from a fraction of a degree to two to three degrees Centigrade below the freezing-point of pure water. In the case of many plants, freezing causes death from cold; others are not indeed killed by the cold, but are injured or killed by the reduced absorption of water owing to the cooling of the soil, even at a temperature only slightly below zero. In Central Europe, for both of the reasons given above, the earliest frosts exert a destructive influence with which we are sufficiently familiar; yet they are less disastrous than exceptional frosts occurring in lower latitudes, where a slight frost at night is more fateful to vegetation than are long and severe periods of winter cold occurring in districts accustomed to annually recurrent low temperatures. Species of plants that are killed or seriously injured by air-temperatures of 0° to 3° C. are far more numerous than are those which withstand − 3° C., but not lower temperatures occurring in nature.

One may reasonably assume that near the tropics it is the winter temperatures which are extremely important in relation to plant-life in the temperate zones, but that at a greater distance from the tropics it is the summer temperatures which are important; so that, for instance, the difference in plant-life between Southern and Central Europe must depend chiefly on the winter temperature, that between Central and Northern Europe on the summer temperature. This consideration leads us to *divide the temperate zones into two belts, one with a mild winter—the warm temperate belt, and the other with a cold winter—the cold temperate belt*: the warm temperate belt is characterized by broad-leaved trees that are evergreen or green during the rainy period, and by only a partial winter-rest of its woody plants; the cold temperate belt is characterized by trees that are bare in winter and green in summer, and by a general winter-rest on the part of its woody plants. The border line between the two belts approximately corresponds to the isotherm of 6° C. for the coldest month.

A more exact coincidence of the border line of the belts of vegetation with the isotherms would possibly be attainable if attention were also paid to the isotherms of the hottest month, as we should exclude from the belts having a mild winter, in the northern hemisphere, districts north of 20° C. isotherm in July, in the southern hemisphere, where heat due to insolation is stronger, districts south of 14° C. isotherm in January, and should incorporate them with the belts having a cold winter. Too much importance, however, should not be attached to such attempts, as an exact coincidence between zones of heat and of vegetation is impossible, at any rate under the present mode of defining climatic factors.

The general effects of temperature on vegetation in the temperate zones are particularly exhibited in the phenomena of periodicity. Indirectly, by its influence on the absorption and emission of water, heat also affects the distribution of woodland and grassland. Special chapters are devoted to both groups of phenomena.

In the distribution of the constituents of the flora, temperature plays a much more important part in the temperate zones than in the tropics, where in this respect it gives way to the action of atmospheric precipitations. The distributional areas of many European, North Asiatic, and North American species of plants have been defined, and correctly, as functions of the temperature.

The flora of the temperate zones as a whole is described as *mesothermic*, although its constituents, as regards their demands on heat, exhibit great differences, which are by no means expressed by the quite temperate mean temperature, nor by the sum total of the degrees of heat. The oecological optimum temperature sometimes exhibits a curve that is nearly as flat as those of tropical plants, but sometimes a steep ascent from low to high degrees of temperature and as steep a descent. Moreover, the absolute minimum of plant-life is proved to be very uneven, whilst data are not yet available regarding the maximum, which is probably just as unequal.

Whilst unequal demands on atmospheric precipitations appear to be limited chiefly to groups of a low rank, from the genera downwards, the relation in regard to temperature is frequently characteristic of groups of a higher rank, so that apart from historical causes the differences in the flora within either of the two temperate zones are greater than within the tropics, where only atmospheric precipitations play an essential part. As regards their floras, in the first place, belts with mild winters are marked off from those with cold winters; in the second place, districts with a maritime climate are distinguished from those with a continental climate.

General considerations on the effects of heat on growth, transpiration, and other functions in the temperate zones must be omitted here, since the great differences in temperature of the temperate zones determine corresponding differences in the vegetative functions.

ii. *EFFECTS OF LIGHT.*

The difference in relation to plant-life between the amount and intensity of light is most strikingly apparent when we compare tropical with temperate zones. Under an equally dense crown of leaves the sum total of luminous energy increases towards the poles, but the ability of plants to live under it diminishes. Shade-vegetation is accordingly much more strongly developed in the tropics than in the temperate zones[1]. The unequal intensity of light in the temperate and tropical zones also induces a different fixed lie of the leaves in relation to the light. In the tropics direct insolation is the controlling factor; leaves arrange themselves obliquely or parallel to the rays, but in the temperate zones they expose their surfaces at right angles to the direction of the brightest diffuse light, regardless of the direct insolation. In spite of the exposed position, the destructive effects of light on chlorophyll are far less in temperate than in tropical zones. The foliage of Scandinavian vegetation is considered to be even of a more intense and pure green than that of Central Europe, although it is almost continuously illuminated during summer.

Many effects of light associated with less high intensities are naturally more strikingly displayed as duration of daylight increases. Thus, the

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[1] See p. 224.

increased production of pigments in flowers and fruits, as well as of ethereal oils, near the north polar circle, is, probably rightly, attributed to the longer duration of light[1].

iii. *EFFECTS OF ATMOSPHERIC PRECIPITATIONS.*

Atmospheric precipitations determine, in the first place, the distribution of woodland, grassland, and desert, also the vegetative character of their individual formations, within the temperate zones; their significance is however somewhat less than in the tropics, for this is evidently dependent on the temperature prevailing at the time of the precipitations, so that, in both temperate zones, districts with summer rain and dry winters contrast most sharply in their vegetation with districts having winter rain and dry summers[2].

An amount of precipitation that in the tropics would occasion a most luxuriant development of vegetation, has no such invigorating effects on plant-life in the temperate zones. This difference depends in particular on the fact that the cold of winter corresponds physiologically to a pronounced dry season, and accordingly sets a decided limit to the surface growth of plant-members.

The periodic phenomena of plant-life, which in the tropics are regulated exclusively by the alternations of moist and dry seasons, are also partially dependent on these in temperate districts with mild winters, although even in such districts change of temperature makes itself felt. Temperature has the greater effect, or is alone effective, in districts with cold winters, according as they possess a dry or a wet summer.

In a similar way, the importance of humidity recedes before that of temperature in the demarcation of the areas of mesothermic species of plants. Only in climates with markedly mild winters are there found groups of plants whose distribution is solely determined by atmospheric precipitations, as is the case in the tropics.

3. CHARACTER OF THE FLORA OF TEMPERATE ZONES.

I will now give a condensed summary of the mesothermic groups of forms, which are treated in a manner like that adopted when dealing with the tropical zones, and from the standpoints already given on p. 226.

Thallophyta.

Algae are even less developed in temperate than in tropical terrestrial floras, except when they combine with fungi to form *Lichenes*, which rapidly increase in the number of their species and individuals, as the climate

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[1] Schuebeler, op. cit., p. 83.

[2] See Part III, Sect. II, Chaps. III–V.

becomes cooler, and together with mosses play the chief part as epiphytes and lithophytes in forests, particularly of the cold temperate belt, as well as on rocks and stones. It has been already stated[1] that, in the temperate zones, *Fungi* exhibit many more large forms belonging to the Ascomycetes and Basidiomycetes than in the tropics, and they are therefore more conspicuous, in spite of apparently weaker development.

Bryophyta.

Bryophyta, in particular *Musci*, constitute in the temperate zones much more essential constituents of the vegetation than in tropical lowlands. In particular, moist cool districts with a maritime climate, for instance Western New Zealand, the Atlantic coasts of Europe, the North Pacific coasts of America, Tierra del Fuego, are very rich in mosses.

Pteridophyta.

Filicineae are dependent on conditions of existence similar to those of mosses, but require more heat and are therefore chiefly developed in humid warm temperate districts. New Zealand is distinguished above all other countries of the earth for the abundance of its ferns. Systematically the temperate fern-flora is less rich than that of the tropics, as it is nearly or entirely devoid of several orders that occur in the tropics and possesses no order peculiar to itself. The *Cyatheaceae* exhibit only a few temperate species, which chiefly inhabit the southern warm temperate belt; their arborescent forms, although represented by a few species only, are a principal constituent of the flora of Tasmania (Fig. 231) and of New Zealand, less of that of South Africa. The *Hymenophyllaceae* exhibit a similar reduction and similar distribution. The *Polypodiaceae* are much more dominant in temperate zones than in the tropics.

The *Lycopodiaceae* and *Equisetaceae* play only a subordinate part in the temperate zones.

Gymnospermae.

Abundance of gymnosperms and their wide distribution as socially growing forest-trees distinguishes at the first glance the temperate from the tropical flora. This important part is played only by *Coniferae*[2]. *Cycadaceae* (Fig. 232) are far poorer in species and are rarer than in the tropics, and the small family of *Gnetaceae* is represented by a few species of Ephedra alone. The most extensive coniferous forests are those of the cold belt of the north temperate zone; they consist almost exclusively of Pinaceae (Pinus, Abies, Picea, Larix; in North America also Taxodium, Sequoia; in Japan also Cryptomeria); the Taxaceae (Taxus, Ginkgo) are

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[1] See p. 226.

[2] See the distribution of Coniferae in Drude's Atlas, No. II.

FIG. 231. Dicksonia antarctica in the temperate rain-forest in Tasmania. From a photograph.

To face p. 4[illegible]]

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quite subordinate. The conifers of the south temperate zone are also chiefly Pinaceae, yet not of the sub-families Abietoideae and Taxodioideae, as in the north, but chiefly Araucarioideae (Araucaria, Agathis). The Taxaceae (Podocarpus, Dacrydium), particularly in the eastern hemisphere, are more important constituents of the forest in the south than in the north.

FIG. 232. Zamia integrifolia in Florida. From a photograph by H. G. Webber.

Monocotyledones.

In the warm temperate belts, as in the tropics, Monocotyledones are represented not only by grasses and other herbs, but also by tall and striking forms, which belong chiefly to Liliaceae and Amaryllidaceae, and only to a very slight extent to the Palmae and Bambuseae so prominent in the tropics owing to their size, and do not belong at all to the Pandanaceae and Scitamineae. Thus species of Aloe are in particular characteristic of South Africa (Fig. 233), species of Yucca (Fig. 234), Dasylirion and Agave of warm North America, species of Xanthorrhoea of Australia (Fig. 235), Cordyline australis, attaining 10 meters in height, of New Zealand (Fig. 236), and the gigantic dragon-tree, Dracaena Draco, of the Canary Islands.

Mesothermic *Palmae* are not numerous, and are confined to a few warm tracts, where they are rarely prominent, at least in the wild state. Their most familiar and most widely spread representative, Phoenix dactylifera, is not known wild; Pritchardia filifera, which is often planted as an ornamental tree, is confined to a few valleys in South California. Of tall-stemmed palms Sabal Palmetto (Fig. 242) (Florida to North Carolina) is probably the single one that is common within its distributional area. In company with it two or three dwarf palms (Sabal serrulata, S. Adansonii appear, and often form a dense thicket, as does Chamaerops humilis on the Mediterranean coast.

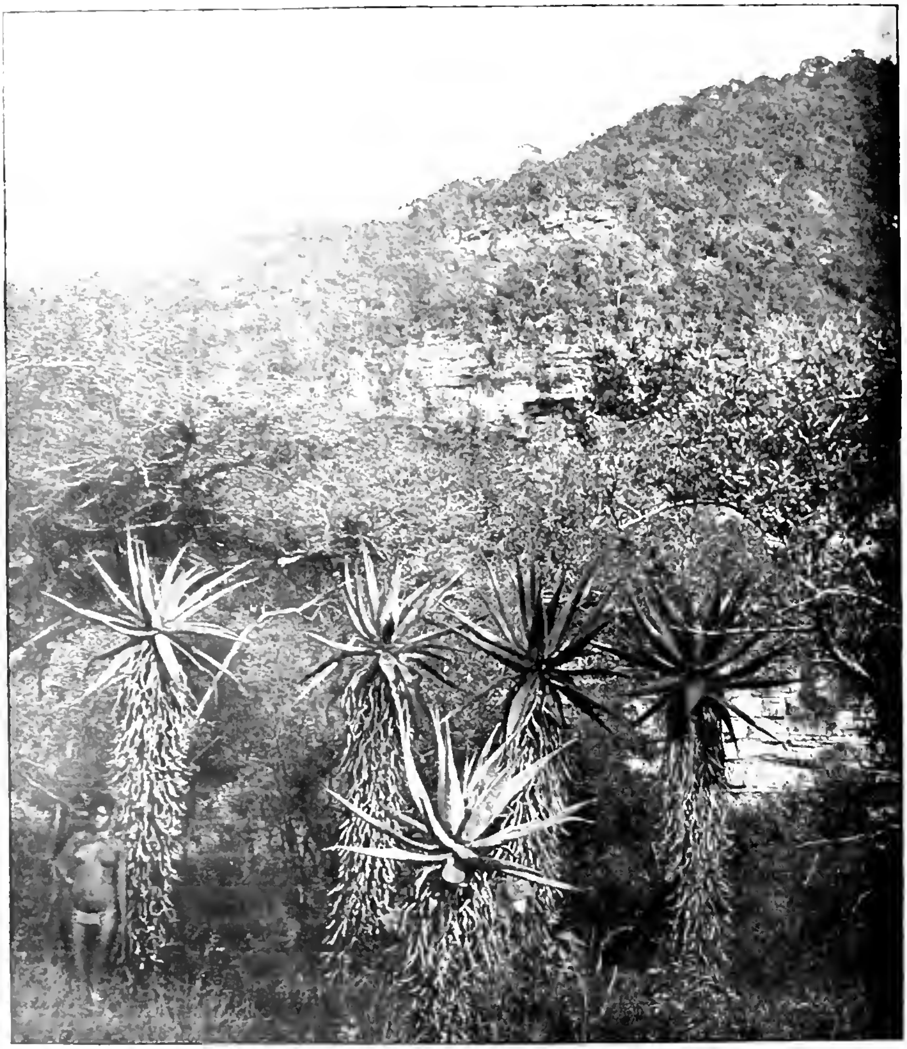


FIG. 253. Aloe in a forest-landscape in Natal. From a photograph.

Tree-forms of *Bambuseae* appear in the temperate zones chiefly in Japan. The other mesothermic Monocotyledones are almost without exception herbaceous, and to a certain extent quite essential constituents of grassland, of desert, and of the herbaceous flora clothing the soil of woodland. The importance of *Gramineae* is everywhere recognized; *Cyperaceae* and *Juncaceae* are widespread; *Liliaceae*, *Amaryllidaceae*, *Iridaceae*, and to a less extent *Orchidaceae*, are important constituents of the dry districts in the warm temperate belts; in the hotter parts of extra-tropical America *Bromeliaceae* possess a few very common species, for instance Tillandsia usneoides, and in Chili species of Puya.

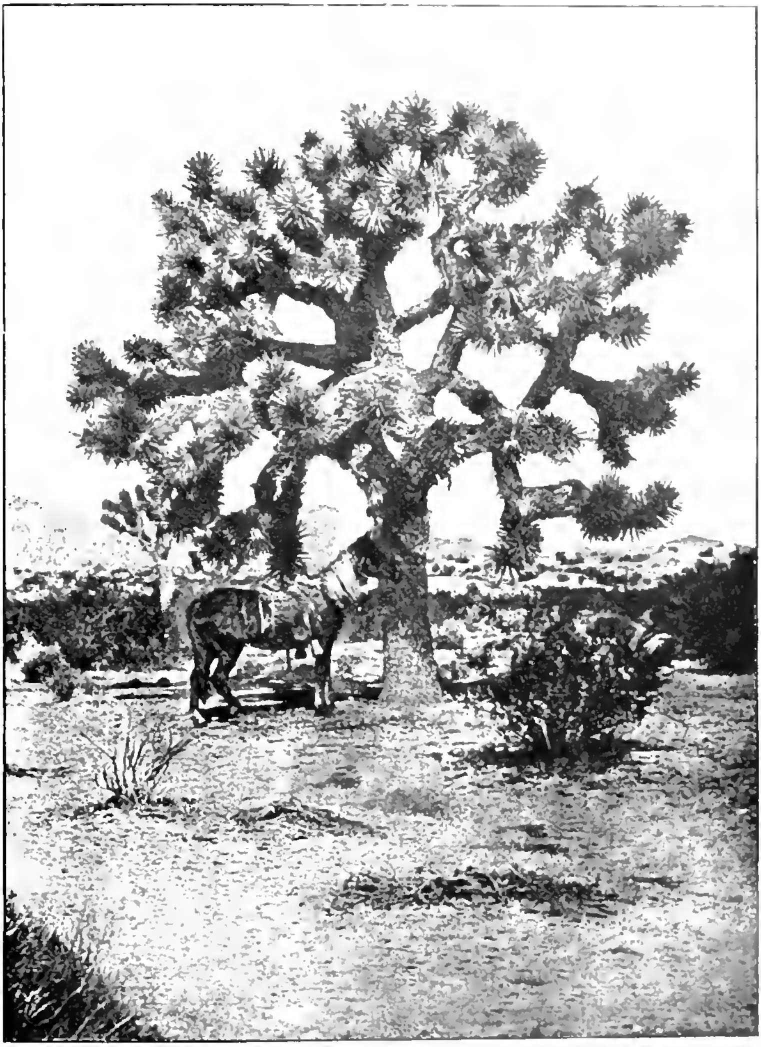
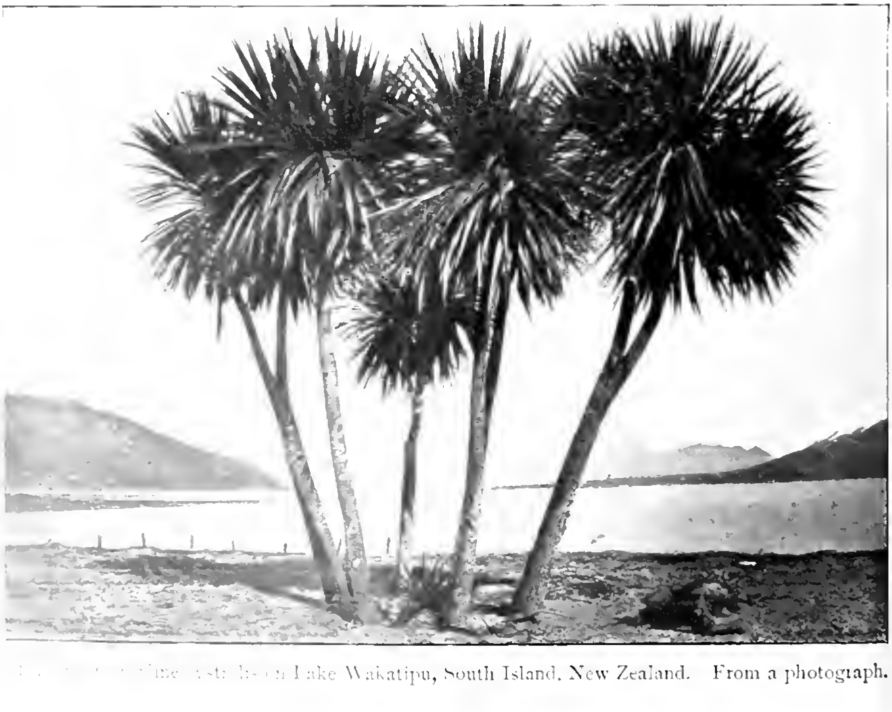


FIG. 234. Yucca arborescens in the Mohave Desert, California. After Coville.

FIG. 235. Xanthorrhoea sp. on the river banks near Sydney. From a photograph.



[illegible] line australis on Lake Wakatipu, South Island, New Zealand. From a photograph.

Dicotyledones.

The group of Dicotyledones includes a much smaller number of tree-species in the temperate zones than it does in the tropics, and the forests composed of Dicotyledones are much less mixed. This is especially the case in the cold temperate belts, where broad-leaved forests usually present almost pure woods of certain Amentaceae, whilst in approaching the tropics the number of tree-species becomes greater and their admixture more uniform. Dicotyledonous shrubs are very rich in forms in the warm temperate belts; on the contrary, woody lianes are very feebly represented. The distribution of herbaceous Dicotyledones on grassland and in the shade-flora of woodland is about the same as in the tropics.

Next to the Coniferae, *Amentaceae*, in particular species of Fagus and Quercus, in the southern zone species of Nothofagus, to a less extent a few other species (Castanea, Carpinus, Betula, Juglans), are the most important constituents of the forests in temperate zones. In stations where edaphic conditions are the controlling factors, woods of other Amentaceae appear, especially species of Salix and Alnus on wet soil, species of Betula on sandy soil and on sphagnum-moor.

In the temperate zones as compared with the tropics, the *Urticineae* are of subordinate importance as trees (Ulmus, Celtis, Morus); herbaceous forms are commoner (Urtica, Parietaria, Humulus).

Of the two families of the *Polygoninae*, the Piperaceae are almost completely absent, whilst the Polygonaceae are much more numerous than in the tropics, and appear particularly in grassland and open situations.

Centrospermae: the Chenopodiaceae, as inconspicuous shrubs and herbs, rarely as small trees, are very common and rich in forms on saline soil, particularly on steppe and desert, but also on manured land. The Caryophyllaceae occur in both zones, in the southern only as Alsinoideae: they form important constituents of grassy tracts and of the herbaceous ground-flora of woodland. The Nyctaginaceae occur in the warm temperate belts of America, and the Aizoaceae are in particular important constituents of the South African flora.

Among the *Polycarpicae*, the purely mesothermic Ranunculaceae take the foremost place in temperate zones, chiefly in the northern zone. The Magnoliaceae are represented by a few forest trees in Japan, Himalaya, and North America; only the widely distributed Drimys Winteri reaches South America. The Lauraceae overstep both the tropical limits and form important constituents of warm temperate woodland, but in the cold temperate zones they are represented by only a few species (Laurus Sassafras in North America).

The *Rhoeadinae*, with the exception of the Capparidaceae, are mostly mesothermic, and are in particular richly represented by Cruciferae in both temperate zones. The Papaveraceae and Fumariaceae are almost exclusively north temperate; the Capparidaceae are confined to the dry districts of the warm belts; and the few Resedaceae are mainly Mediterranean.

Of the family *Cistiflorae*, the Cistaceae are mesothermic and chiefly inhabit Mediterranean countries, the Violaceae occur in both temperate zones, the mainly tropical Ternstroemiaceae reach their northern limit in China and Japan (Camellia), the Tamaricaceae chiefly inhabit Mediterranean countries and Central Asiatic deserts.

The almost wholly American Cactaceae, which alone compose the *Opuntinae*, are abundantly represented not only within the tropics, but also in the warm temperate belts, and are of extreme physiognomic importance in the desert flora, particularly of North America.

The temperate *Columniferae* belong chiefly to the Malvaceae, which occur in the form of shrubs and herbs both in the north and in the south. The chief large extra-tropical genus of Tiliaceae is Tilia; its species are forest trees of the north temperate zone. The pre-eminently tropical Sterculiaceae are represented in temperate Australia by the Lasiopetaleae.

The *Gruinales*, although the majority of them are mesothermic, are only of subordinate importance in the composition of the vegetation of the globe, if we except the Geraniaceae, which possess numerous species in both hemispheres, but especially in South Africa (Pelargonium). The other temperate Gruinales belong to Linaceae, Oxalidaceae, Balsaminaceae, and Tremandraceae, which last are confined to Australia.

The *Terebinthinae*, with few exceptions, require heat, and in their mesothermic forms therefore are confined to the belts with mild winters, where most of them in large numbers inhabit dry districts. The Zygophyllaceae are mainly halophytes of desert districts in both hemispheres; the Rutaceae, particularly as shrubs, form the principal constituents of xerophilous woodlands, specially in South Africa and Australia. The mainly tropical Anacardiaceae play a part similar to that of the Rutaceae, but they are specially important in the Mediterranean flora (Pistacia, Rhus—the latter genus is also North American and East Asiatic).

The *Aesculinae* are represented by tree-species of Acer in the north temperate forests, specially those of North America, China, and Japan. The Hippocastanaceae are likewise mainly North American; Aesculus Hippocastanum is, however, distributed from Greece to North India. Only a few Sapindaceae occur.

The *Frangulinae* contribute numerous species, particularly to the shrubby vegetation of both temperate zones, for instance chiefly in America species of Ilex (Aquifoliaceae), also several Celastraceae such as species of Euonymus in the northern zone, species of Gymnosporia in South

Africa; finally, numerous Rhamnaceae, particularly belonging to the genera Rhamnus (Europe, North Asia, North America), Phylica (South Africa), Ceanothus (California). The mainly tropical Vitaceae are mostly represented as lianes, but also by aberrant forms in the warm temperate belts. Vitis vinifera is indigenous in Mediterranean countries, most other species of Vitis in North America.

Tricoccae: the Euphorbiaceae are not so important in temperate as in tropical floras; yet some of their species, specially those of the genus Euphorbia, are very widespread in the most diverse formations. Buxus sempervirens (Mediterranean countries, Atlantic Europe, temperate Asia) and Empetrum nigrum (north temperate and polar zones) are the commonest representatives of the Buxaceae and Empetraceae.

The *Thymelacinae* (Thymelaeaceae, Penaeaceae, Proteaceae) are by a vast majority mesothermic, but the most of them are confined to the warmer belts. Their chief centre is in the dry districts of South Africa and Australia.

Umbelliflorae: the Umbelliferae are almost exclusively mesothermic and form a chief constituent of the flora of the north and south temperate zones, specially in grassland formations (Fig. 237). Drude shows that of the three sub-families into which he has divided the Umbelliferae, the Hydrocotyloideae are austral, the Saniculoideae both austral and boreal, the Apioideae boreal as regards most genera. The Araliaceae are for the most part megathermic, but yet are richly represented in the warmer districts outside the tropics. Europe possesses only one species, Hedera Helix. The small family Cornaceae is almost exclusively north temperate.

Of the *Saxifraginae* the Crassulaceae are chiefly inhabitants of dry hot districts and are strongly developed in South Africa. The but slightly homogeneous Saxifragaceae are represented in both temperate zones by dissimilar groups of forms, as are also the Hamamelidaceae. A few allied families (Cunoniaceae, Bruniaceae, Pittosporaceae) are indigenous chiefly in the southern zone.

Rosiflorae: the Rosaceae are almost exclusively mesothermic and form an important component of the north temperate flora; the south temperate zone possesses only a few genera, which are however in some instances rich in species (Acaena in South America, Cliffortia in South Africa). Roseae, Prunoideae, and Pomoideae are boreal.

Of the three families of *Leguminosae*, the Papilionaceae are by far the most important in the temperate zones; within which they are richly represented in the most widely different formations. The Mimosaceae are limited to the warm temperate belts and are extremely important in xerophilous woodland, specially in South Africa, Australia (Acacia), and Argentina (Mimosa). Only a few Caesalpiniaceae overstep the tropics (Cercis, Ceratonia Siliqua, Gleditschia).

Among the *Myrtiflorae* the Myrtaceae assume the first rank in the temperate as in the tropical zone; they are confined to the mild-winter belt, and only in Australia (for instance Eucalyptus) do they play a prominent part. The Onagraceae are specially West American (for instance Fuchsia), and the Lythraceae, although represented everywhere, are never dominant. Punica inhabits warm temperate Western Asia.

The *Hysterophyta* are still less important in the temperate than they are in the tropical floras. They are limited to a few Aristolochiaceae, Santalaceae and Loranthaceae, and to one or two Rafflesiaceae and Balanophoraceae.

The *Ericaceae* possess social species in Calluna vulgaris and different species of Erica, which compose extensive shrub-formations, termed heaths, specially in the north cold temperate belts. Most of the species of Erica are however indigenous in South Africa. North America also is very rich in Ericaceae. The Epacridaceae are characteristic constituents of the south temperate zone, specially in Australia, and never occur in the north temperate zone.

Of the three families of *Primulinae*, the Myrsinaceae are almost absent from the temperate zones; the purely mesothermic family of Primulaceae exhibits numerous species, chiefly boreal; and that of Plumbaginaceae plays an important part in steppes and deserts with saline soil and on the sea-shore, and it also is chiefly boreal.

The *Contortae* possess an almost purely mesothermic group of forms in the Gentianaceae, which, represented by species of Gentiana, inhabit both the temperate zones: also a mainly mesothermic family in the Oleaceae, whose home is chiefly in East Asiatic and North American forest districts. The families of Asclepiadaceae and Apocynaceae, which are rich in forms in the tropics, become very subordinate in the temperate zones; the Loganiaceae are almost entirely absent.

The *Tubiflorae* are, in their families Boraginaceae (with the exception of the Cordiaceae), Polemoniaceae, and Hydrophyllaceae, mostly inhabitants of the temperate zones, the Polemoniaceae and Hydrophyllaceae being chiefly in America. The Convolvulaceae are less numerous than in the tropics.

The Scrophulariaceae include the mainly mesothermic forms of the *Personatae*, and are richly represented in both temperate zones: while the Solanaceae are much less numerous than in the tropics. The smaller families of Orobanchaceae, Utriculariaceae, and Plantaginaceae are of slight significance, and the almost purely megathermic large families of Bignoniaceae, Gesneraceae, and Acanthaceae have even slighter importance.

Of the two families of the *Labiatiflorae*, that of the Verbenaceae is mainly megathermic and of slight importance in the warm temperate belts only: whilst the Labiatae are chiefly mesothermic, and are represented by numerous and sometimes very common species. They are richly developed, especially in Mediterranean countries.

Rubiinae: the family of Rubiaceae, which is strongly developed in the tropics, becomes quite subordinate in the temperate zones and by far the majority of its forms are herbaceous. The much smaller families of Caprifoliaceae and Valerianaceae are almost entirely mesothermic and boreal, but never form important constituents of the vegetation.

The Compositae play at least as important a part in temperate floras, as in the tropics; here also they prefer grassland districts. Their sub-families to some extent inhabit both zones, but are in part exclusively or chiefly attached to one of them. Thus the Liguliflorae and the Cynareae are mainly boreal, the Labiatiflorae are austral and almost exclusively American. The two other families of the *Aggregatae* are mesothermic, the Dipsaceae being mainly north temperate, the Calyceraceae South American.

LITERATURE.

The climatic data are chiefly taken from **Hann's** Handbuch der Klimatologie, 2nd ed., 1897, and his Atlas der Meteorologie, 1887; also from **Woeikof**, Die Klimate der Erde, Jena, 1887.

The data regarding geographical distribution of mesothermic groups of forms are taken from the Natürliche Pflanzenfamilien of **Engler** and **Prantl**.

CHAPTER II

PERIODIC PHENOMENA OF VEGETATION WITHIN THE TEMPERATE ZONES

Introduction. 1. Metabolism and Interchange of Energy in Mesothermic Plants at Different Seasons. i. *Periodicity in the gean-tree.* Processes that are visible externally. Development of the flower-buds in the gean-tree. Grand periods and temperature. Season of rest and temperature. Carbohydrates in the periods of activity and repose. Effects of temperature on the solution and re-formation of starch. ii. *Starch-trees and Fat-trees.* Causes of the formation and disappearance of fat. iii. *Theory of Forcing.* The two conditions of protoplasm. The resting condition prolonged by low temperatures. Suppression of growth in length. Oecological optimum temperature in the active period coinciding with the natural temperature. iv. *Periodicity of Herbaceous Plants.* The sweetening of potatoes. v. *Cold and Drought.* Similar effects of winter period and dry period. **2. Periodic Aspects of Vegetation.** i. *General Considerations.* Winter phenomena. Plants flowering in winter in Japan. Cold and the development of flowers. ii. *Periodic Phenomena in the South Temperate Zone.* Chili. South Africa. South Australia.

INTRODUCTION.

EVEN at a short distance outside the tropics, indeed occasionally within them, for instance in South China, the periodic change of temperature makes its influence felt on vegetation. With otherwise equally favourable conditions as regards moisture a retardation in the phenomena of plant-life is unmistakable, and the times of flowering are rigidly associated with the alternation of cold and hot seasons. Such dependence is specially evident in plants when they are transplanted from higher into lower latitudes. Thus the periodic phenomena of introduced Central European broad-leaved trees in Madeira, where the mean temperature of the coldest month (January) is 15° C. and that of the hottest (August) 22·2° C., resemble those in their native country; and Viola odorata in Santa Catharina (South Brazil) produces its entomophilous flowers, according to F. Müller, from March until December, but at the height of summer usually bears cleistogamous flowers only.

The lower the winter temperatures, the greater of course becomes the difference in the vegetation in the cold and hot seasons respectively, in particular where there is a moist summer-climate. In districts with a dry summer, for instance the steppes, and to a still greater degree in deserts, not only the difference in the temperature but also that in the moisture comes into play.

The following considerations relate chiefly to the cold belt of the north temperate zone, as at present precise physiological observations on the warm or sub-tropical belts are lacking; at the same time, in the sub-tropical belts we have to deal with the same phenomena as occur further north, though in a less pronounced form.

1. METABOLISM AND INTERCHANGE OF ENERGY IN MESOTHERMIC PLANTS AT DIFFERENT SEASONS.

i. *PERIODICITY IN THE GEAN-TREE.*

A description will not be given here of periodic phenomena easily visible without detailed investigation, such as foliation and defoliation, the development of the flowers and the maturing of the fruit, as these are generally known. But quite recently we have begun to gain a better insight into these processes, by means of physiological experiments and of the microscope, and thus to prepare the way for their explanation. It is to be hoped that a careful consideration here of these investigations may stimulate similar observations and experiments in other climates.

The periodic phenomena in a cold temperate climate appear on the whole to run the same course throughout the entire vegetable kingdom, except in annuals and a few plants that are constantly in blossom. Yet in details manifold differences reveal themselves, so that it seems advisable to direct our attention first of all to a definite example. The gean-tree, Prunus avium, appears to be eminently suitable, as it has been thoroughly investigated by several authors, specially by Askenasy and A. Fischer, and at any rate noticed by others; it can moreover serve as a type of the majority of our broad-leaved trees.

Roughly considered, the *season of activity* and the *season of rest* of the gean-tree in South and Central Germany *include each about six months*—the active period from about the middle of April to the middle of October, the resting period during the remainder of the year.

During the period of rest, the branches are leafless and bear only scaly buds, which, as will be shown hereafter, are nearly always actually growing. This growth is however usually extremely slow, and in default of exact measurements is first noticeable towards the end of the period of rest as swelling.

The most significant moments *during the active period* are, as regards the reproductive functions, the flowering time in April or May, and the ripening of the fruit in June or July. The vegetative phenomena[1] that

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[1] Askenasy, op. cit.

are externally visible fall into three periods: (*a*) a period of growth of the foliage-buds (April–May), (*b*) a period of assimilation during which axes and roots grow in thickness[1] and the winter buds are formed (May–September), and (*c*) a period of retardation and decline terminating in the autumnal leaf-fall. Amongst all these phenomena, that of the development of buds, especially of the flower-buds, has proved best adapted for the study of the periodic phenomena in their separate details.

According to Askenasy, who was the first to conduct a thorough investigation into these matters, the development of the flower-buds of the gean-tree is distributed over two periods, which are separated by a period of rest, or rather of extremely slow growth. The period of rest, at Heidelberg, lasts from about the end of October to the beginning of February, that is to say about three and a half months; it is therefore considerably shorter than the period included between the more striking features of defoliation and sprouting of the buds that is usually described as the period of rest. Next year's foliage-buds are already laid down at the flowering time; those of the flowers in the course of July.

The growth of the buds during the first growing period, i. e. during the summer and early autumn, is very slow and uniform up to the commencement of the period of rest, when it becomes almost nil.

At the beginning of the second or spring period of growth progress is at first still slow, but becomes gradually more rapid, and finally so rapid that, towards the end of their development, the flower-buds in 6–10 days increase to double and treble their fresh weight. Growth is constantly accelerated till shortly before maturity, but is retarded immediately before its close. The whole development therefore affords a splendid example of Sachs' grand period of growth.

In the increase in size of the buds water naturally takes a greater share than does dry material. Of the total weight of freshly blown buds $\frac{7}{8}$ may be placed to the credit of spring growth. $\frac{1}{8}$ to that of summer growth. The dry weights however are in the ratio of $\frac{3}{4} : \frac{1}{4}$. A hundred buds during the spring period increase in dry weight by 6 grammes. If the tree possesses 200,000 flower-buds—mostly too low an estimate—for their formation 12 kilos. of dry material are necessary.

The curve of growth of the gean-flower, characterized as it is by a sudden sharp ascent, is only occasionally, and then merely to a certain extent, dependent on temperature. Any influence of temperature is not discernible during the summer period, and even during the spring period *variations of temperature cannot alter the course of the curve of growth.* In other words, if the temperature in February be higher than in March,

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[1] According to von Mohl, roots continue their circumferential growth, however slowly, during winter.

the growth in March will still be more energetic than that in February and proceed with increasing rapidity. If however we compare several years with one another, the influence of temperature appears very plainly, as the curve in a warm spring is steeper and leads to an earlier flowering than in a cold spring. At the same time Askenasy has not taken into account very low temperatures, which are not uncommon in March; it remains for botanists to investigate the course of the grand period, in the case of slight frosts in spring—severe frost is known to kill the growing buds.

The dominating influence of inherent characters over the effects of temperature is still more remarkable than the features exhibited by the grand period; this is revealed in the fact that a rise of temperature in October does not awaken the resting buds into activity, whereas it does so from the end of November onwards, and is the more effective the nearer the commencement of the rise is to the end of the normal resting period. The phenomenon cannot be due to growth having taken place in the interval, for the increased weight of the buds from the beginning of October to the end of November is hardly appreciable, and the stalks of the buds apparently remain at the same stage of development.

In illustration of the above we may give the following short tabular statement regarding the sprouting of branches of the gean-tree; there are no early dates in the table, as the experiment was first begun in December.

SPROUTING OF BRANCHES OF THE GEAN-TREE UNDER A RISE OF TEMPERATURE. (After Askenasy.)

Date of placing in the hot-house.	First flower opened.	Number of days elapsed.
14 December	10 January	27
10 January	28 January	18
2 February	19 February	17
2 March	14 March	12
11 March	21–22 March	10½
23 March	31 March	8
3 April	8 April	5

To the external periodicity revealed in the phenomena of growth there is a corresponding internal periodicity in the processes of metabolism[1]. From the moment when the leaves are fully grown until their fall, a continual stream of assimilated matter flows from the green cells into the branches and stem. Products of assimilation free from nitrogen, which we alone consider, because those containing nitrogen are too little known, travel in the form of easily diffusible glucose; on the way, this

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[1] Alf. Fischer, op. cit.

is however occasionally converted into starch (transitory starch). The path of this stream of glucose is always the same. It is determined in the leaves by the elongated parenchyma-cells of the nerves and petiole, and in the axes is confined to the cortical parenchyma. From the cortex the stream flows horizontally into the wood, where the parenchyma-cells gradually fill with starch, whilst the vessels retain as such the glucose they have received from the parenchyma. There is no descending current of assimilated matter in the wood.

The commencement of leaf-fall indicates in the tree the moment at which the tree contains the greatest amount of assimilated matter (*autumnal maximum*). From now onwards up to the beginning of the next vegetative season a continual diminution in that amount takes place, at first slowly, but finally very rapidly.

Immediately after reaching its autumnal maximum, which is also specially that of starch (autumnal starch-maximum), the assimilated matter within the axes is distributed in the following manner:—The parenchyma of the cortex and of the medullary rays is rich in starch and glucose; the cambium contains neither. The wood contains much starch but no glucose in its living cells, much glucose but no starch in the vessels. The medullary sheath is rich in both substances; on the other hand they occur in the pith here and there only.

Shortly after leaf-fall the starch completely disappears from the cortex, as it is converted partly into glucose and some fat, partly into some still unknown bodies (species of sugar). The wood is somewhat poorer in glucose than during summer, but shows no perceptible diminution in the quantity of starch it contains.

The buds at the time of the starch-maximum contain no glucose, but the scales are rich in starch, and the pith still more so. The embryonic organs are devoid of starch and glucose.

Towards the end of winter, even before any externally visible changes indicate the commencement of the vegetative season, activity commences in the interior of the tree. The cortex free from starch becomes again filled with this substance, clearly at the cost of the glucose and of the unknown bodies formed during autumn (spring starch-maximum). This condition is only of short duration. The starch is again partly converted into glucose and this flows into the vessels. In the vessels the current of sap sets itself in motion and provides the buds—hitherto poorly supplied with water and nutriment—with water and glucose.

Even in the buds, movements in the reserve-material have taken place during the winter-sleep. The starch has left the pith, where it was at first so abundant, and has now accumulated in the embryonic leaves and flowers, from which hitherto it had been absent. It is reserve-material, and just suffices for the first stages in the flushing of the buds, that is, up to the conclusion of the swelling period. The later rapid and vigorous growth up to the completion of maturity takes place at the expense of the glucose carried thither by the vessels from the branches and stem.

The opening of the buds consumes a considerable part of the carbohydrates that are stored in the axes. The starch, which just before was so abundant, undergoes an extensive diminution, which however is in part accounted for by conversion of starch into glucose that is not used. This spring-minimum of the carbohydrates, especially of starch, is of short duration, as very soon fresh quantities of assimilated material are produced by the young leaves and conducted to the food-reservoirs. Thus commences the accumulation that culminates in the autumnal maximum.

In the above paragraphs, processes of metabolism have been described that come into play partly in the period of rest, during the cool and cold seasons. The question arises how far they are directly dependent on the temperature[1] or how far determined by inherent hereditary characters. Experiments show that *both temperature and inheritance co-operate.*

The disappearance of starch from the cortex at the commencement of winter is a direct effect of low temperatures, for it does not occur in the twigs of trees that are exposed during the period in question to higher temperatures, in rooms or in plant-houses. The reformation of the starch is likewise a function of the temperature, for when the temperature is sufficiently high (minimum 5° C., optimum 25°–30°), it commences in a few hours, and even in the smallest pieces of cortex, so long as they possess uninjured cells. The cooling down to 2° C. of such branches in which reformation of starch has taken place causes the starch to disappear again.

The connexion between the phenomena just described and the temperature is evident, but the temperature is not the sole controlling factor, for if it were so the starch would disappear, even in summer, after an artificial reduction of temperature. This however is not the case.

ii. *STARCH-TREES AND FAT-TREES.*

The woody plants of the cold temperate zones, so far as is known, all behave in the main like the gean-tree. In details however they exhibit many differences. Independent of the generally known external differences in periodicity, a group of *starch-trees* and another of *fat-trees* have been established on the basis of their respective conditions in winter, as revealed in Russow's investigations. In the starch-trees, to which chiefly hardwoods—among others the gean-tree—belong, at the commencement of winter only very little fat is produced at the expense of the starch, which in the cortex is converted into glucose and unknown bodies, but

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[1] See p. 48.

in the wood remains unaltered. In the group of fat-trees, which are chiefly soft-wooded species, such as conifers, birches, and lime-trees, *all the starch in the cortex and wood is converted into fat*, and this condition lasts until spring, when the fat is reconverted into starch.

The formation of fat from starch, and of starch from fat, like the changes mentioned above in the cortex of the gean-tree, are dependent, on the one hand, on inherent characters possessed only during the season of rest, and, on the other hand, on the temperature. The production of fat does not take place while the atmosphere is warm, and any fat that may be present is then converted into starch.

iii. *THEORY OF FORCING.*

The protoplasm of the plants of temperate zones exists in two conditions, one active and one quiescent. The regular periodic alternation of these conditions, as in the tropics, is occasioned by inherent hereditary characters, and they are distinguished by the difference in their behaviour in relation to temperature, as well as by other features.

In active protoplasm, by means of higher temperatures stimuli are set up that induce the processes of growth, whereas lower degrees of heat result in a general cessation of growth.

In quiescent protoplasm even optimum temperatures do not call forth phenomena of growth; on the other hand, changes of temperature produce a reaction in the form of metabolic changes, and these are induced in part by lower and in part by higher temperatures.

The quiescent condition of the protoplasm is of much shorter duration than its active condition, and by no means persists through the whole normal period of rest. This period of rest is in its second and greater part a direct result of low temperature, and it may accordingly be shortened in this part by a rise in temperature. The *forcing of plants* depends on this circumstance. On the contrary, the first part of the period of rest, which in the gean-tree lasts from the middle of October to the end of November, but in other woody plants is often shorter (for instance Forsythia viridissima) or longer (Fagus sylvatica), depends exclusively on inherent characters and is not influenced by a rise of temperature. It is quite useless, and even harmful, to try to begin forcing before the end of this necessary period of rest, as buds even under the most favourable temperature remain in their winter condition. Transition from the one condition to the other is slow, and forcing will be in any one case more rapid the more imminent was the completion of the change of the quiescent protoplasm into active protoplasm. Low temperatures accelerate the transition.

Horticultural experiments, purely practical in nature but none the less valuable on that account, made particularly on fruit-trees with the object of accelerating development (forcing), most clearly demonstrate the existence of a period of rest that is independent of external influences. These experiments have also determined the optimum temperatures for the development of the flowers and fruits of temperate trees, and though not adequately appreciated they have put an end to a chaos of false statements regarding the connexion between temperature and periodicity.

Most fruit-trees are suitable for forcing only after a few frosts, which accelerate the transition to the active condition, so that, for instance, the forcing of the peach-tree cannot be commenced before January; in Belgium, however, it succeeds from November onwards. The vine, on the other hand, comes into a condition in which it can be forced at temperatures somewhat above zero.

When forcing is commenced the temperature need by no means be high, and, at most, should not exceed 6° to 8° C. It is gradually raised, but never actually above the temperatures prevailing in nature during the corresponding stages of development. Higher temperatures cause abnormal features, such as excessively long shoots, defective formation of wood, atrophy of flowers, and so forth. It is especially necessary that the temperature be kept low during the flowering time, and, in the case of stone-fruits, during the stoning, otherwise the flowers or young fruits drop off. The growth of the fruit, however, demands higher temperatures than does the development of the flower-buds, but for late autumnal fruits (grapes) moderate final temperatures are again necessary.

Night-temperatures must be kept from 2 to 4 centigrade degrees lower than day-temperatures; otherwise hypertrophic phenomena set in.

It follows from the above-mentioned and other phenomena that the optimum temperatures for the processes of growth in length are higher than those for other processes—such as the formation of flower, the development of wood—so that higher temperatures favour the former at the expense of the latter. Experience in the cultivation of temperate woody plants in warmer zones completely confirms this; as there also growth is greatly accelerated[1]. Light retards growth, and it is possibly owing to this fact that forced plants withstand higher temperatures by day and in the sun than by night or on a cloudy day.

The general results of the experience of practical men amount to this, that in the case of our fruit-trees the degrees of temperature naturally prevailing during the vegetative season approximately correspond to the optimum for the formation of flower and fruit, as well as for the formation of wood, but are below the optimum for the processes of growth of foliage-shoots. Hence the forcing of fruit-trees is generally confined, in the first place, to the abolition of that portion of the period of rest that is due to low temperatures, and, in the second place, to imitating as closely as possible the temperatures prevailing during the different stages of

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[1] See p. 48 ff.

the normal period of growth. For the plum alone temperatures somewhat higher than those prevailing in spring and summer in Central Europe are favourable for the development of flower and fruit, so that, in contrast to other fruit-trees, the period from the opening of the buds to the ripening of the fruit can be considerably shortened. Pynaert's table of temperatures suitable for forcing the peach-tree has already been given[1], and is worthy of study on account of its importance and comprehensiveness.

What is true of the fruit-trees in Central Europe is also certainly true of the great majority of the woody plants, as of the whole indigenous flora. In other words, *the flora of the temperate zones during the vegetative season enjoys an oecological optimum temperature, so that all the functions work harmoniously side by side.* It accordingly follows, as has been already explained, that a transference to a climate with a higher or lower temperature causes discordant changes, at any rate to begin with. Subsequently, in certain species, *acclimatization* is secured by adaptation to the new conditions of temperature[2], provided these conditions do not differ too greatly from those of the native home.

iv. *PERIODICITY OF HERBACEOUS PLANTS.*

That the facts already established in reference to woody plants are also true of perennial herbs is proved by all our experience, which has taught us in particular that in perennial herbs, as in woody plants, there is a resting period due to inherent causes, and that a series of metabolic changes also take place in them, like those which proceed in woody plants.

Müller-Thurgau has thrown much light on the periodicity of the potato. The well-known sweet taste of frozen potatoes is not, as is generally supposed, a consequence of the frost, but sets in at temperatures between 0 and +6 C. as a consequence of the conversion of part of the starch into sugar (glucose, invertose). Müller-Thurgau is of opinion that we may possibly infer from this phenomenon that in the potato there is a continual process of solution and of formation of starch, and that the formation demands higher temperatures than the solution, so that when near freezing-point there is an accumulation of sugar which at a higher temperature would be converted into starch. Against this view the fact may be urged that the production of sugar is essentially associated with the winter; in September and October there is no production of sugar, or the production is carried on to a much less extent than it is later in the year.

We have evidently to deal with phenomena quite similar to those in woody plants. In this case too, as a consequence of inherent causes, the winter and the summer conditions periodically alternate with each other in the protoplasm. During the winter condition low temperatures between 0 and +6 C. cause a considerable transformation of starch into sugar, whereas during the summer condition they only exert a weak and inhibitory action. Just as in the case of

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[1] See p. 45.

[2] On acclimatization, see p. 49.

woody plants, at a high temperature starch is regenerated at the expense of products, sugar in this instance, into which it was at an earlier stage converted. The production of sugar during winter is not necessary for the further development of the potato, but has an accelerating effect on it. It must be due to other causes that potato-buds do not develop further in autumn. Sachs has put forward the attractive hypothesis, that in this and other similar cases it may be a question of the gradual formation of ferments; an experimental proof of this suggestion has not yet been attempted[1].

v. *COLD AND DROUGHT.*

In their action on vegetation cold periods display an unmistakable likeness to dry periods. That this likeness is not specious, but is founded on the organization of the plant, appears from the circumstance that both factors frequently influence periodicity in a quite similar manner and can replace one another. Thus forcing is accelerated if water is withheld for some time before the commencement of winter cold: the winter period of rest then commences and terminates sooner[2]. Persistent drought hastens the defoliation of our deciduous trees. The buds of woody plants and herbaceous perennials are no more induced to open by moisture during the dry season than are winter buds by higher temperatures, so long as a certain time determined by inherent causes has not been reached. Plants richly provided with reserve-material blossom in the tropics chiefly during the dry season and immediately after it, but in temperate zones chiefly in the spring. Many trees that blossom normally in the cold season have after a dry summer a second weaker flowering. Closer investigation regarding metabolism during the period of vegetative rest that is due to drought will show how far analogies between metabolic changes and movements of reserve-material correspond to these external analogies.

2. PERIODIC ASPECTS OF VEGETATION.

i. *GENERAL CONSIDERATIONS.*

The variety in the aspect of vegetation that changes with each season is mainly due to periodic phenomena. The most conspicuous changes in the vegetative organs are exhibited by woody plants at the autumnal leaf-fall. But among evergreen plants also there is in many cases a not unessential difference between the appearance in winter and in summer, as many Coniferae assume a brownish-yellow colour, others, as well as some broad-leaved species, a brownish-red one. Such a change of colour

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[1] See also Lidforss, op. cit.

[2] Müller-Thurgau, II, p. 901; Pynaert, op. cit., p. 263. According to Pynaert, the result is not quite certain.

follows only after frost, and is confined to leaves exposed to the direct rays of the sun. The yellow colour is due to a partial decomposition of the chlorophyll, the red colour is caused either by a red pigment in the chlorophyll-corpuscles (Thuya, Buxus), or by anthocyan in the cell-sap (Ilex, Hedera, Mahonia)[1]. Many species of Pinus assume a characteristic appearance in winter because their fascicled needles become adpressed to the twigs, owing to certain hitherto unexplained physiological causes.

In contrast with woody vegetation, evergreen species predominate in the herbaceous vegetation, so that meadows retain their fresh green appearance in mild winters and present yellow tints only during persistently hard frost. Many herbs however develop anthocyan during the winter, but as this discoloration is usually absent from grasses, it is far less apparent than among woody plants. Many herbaceous perennials are only transitorily green; the death of the subaërial shoots frequently happens even during summer, and is therefore probably due to inherent causes.

It is well known that flowers are never entirely lacking at any season, as during mild weather many species, like Bellis perennis, Senecio vulgaris, Veronica hederaefolia, blossom even in winter. True winter-flowering plants, however, do not occur in the markedly cold belts of the temperate zones; the species just mentioned flower really throughout the year and still more freely in the warmer seasons. On the other hand, the warmer belts produce a number of plants whose flowering season falls in the months from November to February. Rein[2] makes the following remarks regarding the winter-flora of Japan:—

'Towards the end of October the woodland that is green in summer is leafless, as with us [i. e. in Central Europe], and there are only a few plants that have not entered upon their winter rest. These are chiefly shrubs and trees that are green in winter . . . the flowering of which occurs during the earliest winter months. Among them are Olea Aquifolium, Sieb. et Zucc., Aralia japonica, Thunbg., and some other Araliaceae, which blossom in November; Thea chinensis, Sims, and Camellia Sasanqua, Thunbg., whose flowering time is in November and December, and whose last buds are killed by night-frosts; a few species of Daphne, which blossom in January and February; and above all Camellia japonica, which in this season sometimes affords the surprising spectacle of bearing simultaneously flowers and snow, but whose flowering time is prolonged until April.

'Among herbs we find still fewer species whose flowering time falls in late autumn or actually extends into winter proper; among such are a few Compositae, especially Pyrethrum and Aster.'

Even in the warmer belts winter-flowering plants are scanty. The

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[1] Schimper, op. cit., p. 166.

[2] Rein, op. cit., p. 155.

commencement of the true flowering season usually coincides with that of the vegetative season in spring and ends with the cessation of this season in autumn. The beginning and end of the flowering season are dependent to a great extent on the temperature, and therefore not only fail to coincide at different places, but also in different years at the same place. But the action of the inherent rhythm always proves stronger than that of temperature. so that the awakening of vegetation very often occurs at a lower temperature than does its falling asleep.

It has been already shown[1], that in the temperate zones low temperatures usually favour the inception of reproductive organs, and that the growth of these organs is completed in very many instances within lower limits of temperature, or at any rate possesses a lower optimum than is the case with foliage-shoots. The dissimilar action of temperature on the reproductive and vegetative organs respectively has not only been proved experimentally, but is also apparent in nature, especially in lower cryptogams and mosses, the sexual activity of which very often coincides with winter, whilst their vegetative activity occurs during the warm months. In phanerogams this connexion is less clear, owing to a number of opposing circumstances. Thus, many herbaceous plants can commence forming flowers only after they have assimilated the needful material; the formation of assimilating organs however, like assimilation itself, demands higher temperatures. Other plants again are adapted to certain pollinators and flower at a time when these are active. In spite of such limitations, the favourable influence of low temperatures on the reproductive organs in relation to the periodicity of phanerogams is unmistakable when we consider those plants alone that produce the plastic materials for the manufacture of flowers in the preceding vegetative season.

It is well known that, in the temperate zones, most herbaceous perennials belonging to the Liliaceae, Amaryllidaceae, Iridaceae are early-flowering; in Mediterranean countries Orchidaceae and Araceae also are among the earliest spring-flowering plants. Many Dicotyledones with rhizomes or roots rich in nutriment, such as Anemone, Helleborus, Eranthis, Corydalis, Ficaria, behave similarly. A few bulbous plants flower in autumn, such as Colchicum autumnale, Spiranthes autumnalis, Crocus sativus, Cyclamen europaeum. The majority of trees are also early-flowering and frequently open their flowers earlier, and therefore at lower temperatures, than their leaves. The indigenous examples, with which the ivy as a late-flowering plant is included, are sufficiently well known. I had noticed the same feature in the much richer tree-flora of North America, and an analysis of the flowering times of the trees in Asa Gray's Manual of the Botany of the Northern United States has confirmed my observations. Of 141 species referred to in the above work as being trees or arborescent shrubs—

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[1] See p. 48.

I have not considered true shrubs—110 commenced flowering from March until May, 25 in June, 6 in July; in August merely the close of the flowering time of a few July-flowering trees occurred. The connexion between the opening of the flowers and the cooler temperatures appears specially striking, if we consider that spring is colder in the Northern States of America than in South and Central Germany, so that May in Boston is scarcely comparable with April in the Central Rhenish districts.

ii. *PERIODIC PHENOMENA IN THE SOUTH TEMPERATE ZONE.*

The literature to which I have access contains but few data regarding the periodic phenomena of the south temperate zone.

A pamphlet of Hann's on the climate of Central Chili gives the following information. In June (corresponding to our December) the almond-trees flower, also wild violets, hyacinths, Ranunculi, Acacia cavenia. In July and August, Datura arborea, Richardia aethiopica, Heliotropium (peruvianum?). In August there blossom cherries, peaches, plums, Acacia lophanta, a species of Fumaria, and a number of indigenous Amaryllidaceae and anemones. Pear-trees and apple-trees blossom in the first half of September; fig-trees and Lombardy poplar are fully in foliage by the end of this month. Lilac, Gladiolus byzantinus, carnations, and a number of other garden-plants develop their flowers in October. By the middle of November the first strawberries are ripe: olive-trees flower in this month. Wheat and barley are harvested in December: strawberries, figs, cherries, melons, apricots ripen. In March and April beans, capsicums, and potatoes are collected: grapes are ripe enough to be picked between the 20th and 30th April.

TEMPERATURE AND RAINFALL IN SANTIAGO.

	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.
Temp. Cent. .	18·2	18·9	18·4	16·4	13·1	9·6	7·8	7·3	8·3	10·7	13·0	15·8
Rainfall in mm.	6·4	0·0	1·3	2·5	13·7	51·6	100·2	105·8	70·4	41·8	17·9	14·9

Reiche[1] makes the following remarks about the vegetation of Rio Maule (about 35° S.): 'The commencement of the cycle of vegetation may conveniently be reckoned from the flowering of Oxalis lobata; this happens in April, after the termination of the summer drought, and reaches its climax in May. During this period, under the influence of the first rains, the hitherto yellowish or reddish brown steppe, which was either bare or covered with the parched remains of vegetation, becomes clad with green verdure. The latter consists of seedlings of Erodium cicutarium, Lupinus microcarpus, Medicago denticulata, as well as the leaves of Scilla, Achyrophorus, Soliva, Briza and other grasses. During the actual rainy season the campo retains its green tint, slightly interrupted by flowers; here and there appear Stenandrium dulce (rose coloured), or from August onwards, Anemone decapetala (white or blue). From September onwards the picture becomes more embellished every day: at first the numerous fiery red corollas

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[1] Reiche, op. cit., II. p. 26.

of Habranthus phycelloides attract attention principally on the mountain sides; then Triteleia porrifolia dominates, and in October and the beginning of November, the chief flowering season of the year, it becomes impossible to name any plants that are specially prominent. But even then the first signs of the desiccation and death of the vegetation appear on specially exposed points, particularly in the disappearance of the species of Tillaea and of Poa annua. At the same time, from the end of September or the beginning of October the deciduous trees (Fagus obliqua, poplars, fruit-trees) become adorned with new leaves and eventually with flowers. From the end of October onwards, the abundance of flowers steadily decreases; Alstroemeria Ligtu and Habranthus chilensis, locally with the Compositae Triptilion spinosum and Cephalophora plantaginea, again impart a floral beauty that lasts till December. Finally, Noticastrum Haplopappus, Madia sativa, Wahlenbergia linarioides, Cephalophora aromatica, Boisduvalia concinna, with occasional stragglers of other species, remain as the last flowering herbs in the otherwise brownish-yellow tract. The reappearance of Oxalis lobata finally heralds the appearance of a new vegetative period. In the ravines occupied by numerous shrubs, and in the forests, this cycle of change is less marked; but it is quite apparent both in the vegetation of herbaceous perennials and in the vital activity of woody plants (sprouting, flowering, fruiting).'

Just as in Central Chili, so also near Cape Town, there are flowers at every season, but chiefly in spring; September is the month that is richest in flowers; autumn is poor in blossom. According to Thode[1], winter (May–July) is characterized by the flowering of Oxalidaceae; spring (August–October) particularly by that of Compositae, Iridaceae, Ficoideae, Proteaceae; summer (November–January) by that of Geraniaceae and Crassulaceae; and autumn (February–April) by that of Amaryllidaceae. East Cape Colony also has chiefly spring flowers.

According to Behr[2], herbaceous plants in South Australia flower shortly after the end of the rainy season; the Eucalypti and Acacia retinodes in spring; the Loranthi in the midst of the dry season. The scrub blossoms chiefly at the beginning of the dry season, in September, October, and November, but also throughout its whole duration; on the other hand, the rainy season is very poor in flowers (Astroloma and others). The grassland puts on the whole of its floral beauty all at once, at the beginning of summer.

In the districts enumerated above, which in some cases possess summer rain, and in others winter rain, the beneficial influence of the cool temperature on the development of flowers is universally revealed in the form of an after-effect. In other respects conclusions regarding the effective factors cannot be drawn from such scanty data.

SELECT LITERATURE.

Askenasy, E. Ueber die jährliche Periode der Knospen. Botanische Zeitung. Bd. XXXVII. 1877.

Behr, H. Über die Verhältnisse der südaustralischen Flora im Allgemeinen. Linnaea. Bd. XXII. 1847.

Brandis, D. Effect of Seasons upon the Flowering of Plants. Indian Forester, 1882. Also Nature, 1882.

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[1] Thode, op. cit.

[2] Behr, op. cit., p. 552.

Candolle, A. de. Les effets d'une même température sur une même espèce au nord et au midi. Comptes rendus de l'Acad. des sciences de Paris. Tome LXXXII. 1875. p. 1369.

Drude, O. Deutschlands Pflanzengeographie. Bd. I. S. 425. The literature of phaenology of Central Europe is cited.

Fischer, Alf. Beiträge zur Physiologie der Holzgewächse. Pringsheim's Jahrbücher. Bd. XXII. 1890.

Gray, Asa. Manual of the Botany of the Northern United States. 5th edition. New York, 1868.

Hann, J. Beiträge zur Klimatologie von Südamerika. Zeitschrift der österr. Gesellschaft für Meteorologie. Bd. V. 1870.

Heer, O. Ueber die periodischen Erscheinungen der Pflanzenwelt in Madeira. Verhandl. der Schweizerischen naturforsch. Gesellsch. in Glarus, 1851. Also Annals and Magazine of Natural History. Vol. X. 1852.

Hoffmann, H. I. Phänologische Untersuchungen. Giessener Universitätsprogramm. 1887.

—— II. Witterung und Wachsthum, oder Grundzüge der Pflanzenklimatologie. Giessen, 1857.

Jacob, G. Untersuchungen über zweites oder wiederholtes Blühen. Inaug. Diss. Giessen, 1889.

Kienitz, M. Vergleichende Keimversuche mit Waldbaum-Samen aus klimatisch verschieden gelegenen Orten Mitteleuropas. Müller's Botanische Untersuchungen. Bd. II. 1879.

Lidforss, Bengt. Zur Physiologie und Biologie der wintergrünen Flora. Botanisches Centralblatt. Bd. LXVIII. 1896.

Linsser, C. Die periodischen Erscheinungen des Pflanzenlebens. Mémoires de l'Académie de Saint-Pétersbourg. 7e série. Vol. XI, 1868; XIII, 1869.

Ludwig, Fr. Lehrbuch der Biologie der Pflanzen. Stuttgart, 1895.

Mangin, L. Observations sur le développement des fleurs dans les bourgeons. Journal de botanique. Tome II. 1888.

Molisch, H. Untersuchungen über Laubfall. Sitzungsberichte der Wiener Akademie. Bd. XCIII. 1886.

Müller-Thurgau, Herm. I. Ueber Zuckeranhäufung in Pflanzentheilen in Folge niederer Temperatur. Landwirthschaftliche Jahrbücher. Bd. XI. 1882.

—— II. Beitrag zur Erklärung der Ruheperioden der Pflanzen. Ibid. Bd. XIV. 1883.

Pynaert, Ed. Les serres-vergers. Traité complet de la culture forcée et artificielle des arbres fruitiers. 4e édition. Gand, 1888.

Reiche, K. I. Zur Kenntniss der Lebensthätigkeit einiger chilenischen Holzgewächse. Pringsheim's Jahrbücher. Bd. XXX. 1896.

—— II. Die Vegetationsverhältnisse am Unterlaufe des Rio Maule (Chile). Engler's Jahrbücher. Bd. XXI. 1896.

Rein, J. J. Japan: Travels and Researches. 2nd English edition. London, 1889.

Schimper, A. F. W. Untersuchungen über die Chlorophyllkörner und die ihnen homologen Gebilde. Pringsheim's Jahrbücher. 1885.

Schuebeler, F. C. Die Pflanzenwelt Norwegens. Christiania. 1873–1875.

Thode, J. Die vier Jahreszeiten am Cap. Naturwiss. Wochenschrift. 1892.

Warming, E. Beobachtungen über Pflanzen mit überwinternden Laubblättern. Vorl. Mittheil. Botanisches Centralblatt. Bd. XVI. 1883. p. 350.

Wiesner, J. Untersuchungen über die herbstliche Entlaubung der Holzgewächse. Sitzungsberichte der Wiener Akademie. Bd. LXIV. 1871.

CHAPTER III

WOODLAND CLIMATE AND GRASSLAND CLIMATE IN THE WARM TEMPERATE BELTS

1. General. 2. Subtropical Districts. Florida. South Brazil. Paraguay. **3. Warm Temperate Districts without a Dry Season.** Climate of the temperate rain-forest. South Japan. West Chili. New Zealand. Grassland climate of the Falkland Islands. **4. Temperate South Africa.** Rain-provinces and vegetation-provinces. The south-west coast with winter rains. Climate of the evergreen sclerophyllous woodland. The south and east coast with spring and summer rains. Climate of savannahs. Interior of Eastern South Africa (Transvaal and Orange River Colony) with summer rain. Climate of the steppes. **5. Warm Temperate Districts with a Moist Summer.** Intermediate climate in North Argentina. Park landscapes. Climate of the pampas. Climate of the thorn-woodlands (espinal) of West Argentina. Climate of grassland in South-East and East Australia. **6. Warm Temperate Districts with a Moist Winter.** Climate of evergreen sclerophyllous woodland. South-West and South Australia. Central Chili. Mediterranean countries. California. **7. Conclusion.**

1. GENERAL.

THOSE parts of the temperate zones bordering on the tropics and alone meriting the appellation *subtropical* exhibit scarcely marked characteristics, and ally themselves with tropical districts when the climate is very humid, and with the true temperate districts when it is dry. With increasing distance from the tropics a new factor intervenes, the cold of winter, which, though acting more indirectly than atmospheric precipitations and subordinate to them, assists in determining the differentiation of the vegetation in oecological districts. It is no longer, as in the tropics, a matter of indifference whether the rainy season occurs in summer or in winter, but the rainy season is responsible for an essential distinction in the oecological conditions of the vegetation.

Excluding the less characteristic subtropical districts, the warm temperate districts may be subdivided into three groups, namely, those without any dry season, those with a moist summer, and those with a moist winter. Intermediate districts, usually of slight extent, with spring or autumnal rains, sometimes ally themselves more to districts with a moist winter and at other times to those with a moist summer.

2. SUBTROPICAL DISTRICTS.

Temperate districts bordering on the tropics, up to about 30° latitude, are chiefly occupied by desert. In them high-forest districts prevail over only a limited area. Concerning the climatic condition of these high-forest districts I cannot give a satisfactory account from the literature before me; a rainfall of 130–150 cm., with the corresponding atmospheric humidity, appears sufficient for fairly rich forest growth. Nevertheless, countries with true high-forest—of course omitting fringing-forest—are not inferior to the tropics in their rainfall.

Florida, clad with extensive forests, which are however not very lofty or luxuriant, appears to have a rainfall of 130–140 cm. (Fort Brook 136 cm.); the coast of the Gulf of Mexico to the east of the Mississippi has 147 cm.; whilst the Bahamas, with merely bushy and shrubby woodland, have 120 cm. only (Nassau 118 cm.). All these countries have chiefly summer rain; the winter however is also very humid.

Tropical rainfall and tropical forest growth appear to the south of the tropics, in South America for instance on the Brazilian coast (Joinville, Blumenau) up to about 30°, and in the interior, in Paraguay (Asuncion) and along the Andes, up to about 25° S.

Subtropical High-forest Climate.

SOUTH AMERICA.

(From Meteorol. Zeitschr., 1891, p. 272; and Zeitschr. d. österr. Gesellsch. f. Meteorol., 1877, p. 333.)

	JOINVILLE. 26° 19′ S., 49° 43′ W.			BLUMENAU (1889). 26° 55′ S., 49° 9′ W.				ASUNCION (PARAGUAY). 25° 16′ S., 57° 40′ W. 98 meters above sea-level.			
	Temperature. (1877–83).		Rainfall (1890).	Temperature.		Rainfall.		Temperature.			Rain-fall.
	6 a.m.	2 p.m.	Amount in mm.	Mean.	Daily Range.	Amount in mm.	Days (7 yrs.	Mean.	Max.	Min.	Amount in mm.
Jan. .	22·1	27·3	362	27·6	4·5	195	10·3	26·7	38·3	19·4	68
Feb. .	22·1	27·4	227	26·1	4·5	154	12·3	28·3	38·9	16·7	99
March	21·4	26·5	224	25·0	3·7	189	12·7	27·5	35·6	18·6	91
April .	18·7	23·8	217	22·1	5·3	235	10·4	23·1	33·8	14·2	175
May .	15·5	20·7	142	18·6	6·4	191	8·3	20·0	28·9	9·7	168
June .	14·8	19·5	156	15·2	8·0	15	6·7	15·6	26·1	6·9	201
July .	14·5	19·3	90	17·6	5·9	57	6·7	21·1	30·0	10·6	98
Aug. .	14·4	19·8	121	16·2	7·7	118	7·1	23·3	33·3	13·3	27
Sept. .	16·1	20·5	189	17·8	7·7	161	9·4	25·6	36·7	15·0	132
Oct. .	17·4	22·6	184	20·7	8·4	137	7·2	28·1	38·8	16·1	307
Nov. .	19·6	24·3	147	22·7	9·8	127	10·0	27·8	39·0	20·0	250
Dec. .	20·6	26·0	186	26·4	7·9	247	8·2	27·2	37·8	17·8	467
Year.	18·1	23·1	2245	21·3	6·6	1826	109·3				2083

The rainfall in Blumenau is very variable. It consisted, on the average of 1868–74, of 1,406 mm.; 1875–80, of 1,676 mm.; in the year 1888, of 2,149 mm.; in 1890 of 1,333 mm.

In North Argentina, as will hereafter be shown, less rainfall than 120 cm. with great frequency of precipitation causes grassland (savannah) to predominate, and, wherever the soil is somewhat moister, scattered tracts of savannah-forest.

3. WARM TEMPERATE DISTRICTS WITHOUT A DRY SEASON.

Of warm temperate rainy districts those with rain throughout the year—even if this is for the most part unequally distributed—show the greatest agreement with tropical districts. Provided the rainfall is sufficient, they are clad with forest that resembles tropical rain-forest, but is less rich in forms, and is also less luxuriant, and will be styled *Temperate Rain-forest*. It occupies merely small tracts, in contrast with the tropical rain-forest. In the lowlands it is confined to South Japan, Tasmania, West New Zealand, and South Chili. Its occurrence in highlands is described in detail in Section IV.

The southernmost island of Japan, as well as the south-eastern part of Nippon, as far north as Tokyo, have very mild winter temperatures and abundant rain at all seasons of the year, with a maximum in the hot months. The atmospheric humidity is always very considerable.

Temperate Rain-forest Climate.

SOUTH JAPAN—TOKYO.

35° 40′ N., 139° 44′ E. 24 meters above sea level. 1 (1876) to 4 years (1873–6).

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1878, p. 26.)

	Temperature.			Rel. Humidity.	Cloudiness.	Rainfall. Amount in mm.	
		Mean Max.	Mean Min.				
	1876	1873–6	1873–6	1873–6	1876	1876	1873
January . .	4·0	16·9	– 3·8	70	3·5	68	93
February . .	1·6	12·2	– 6·9	68	5·5	115	65
March . . .	3·3	13·2	– 5·3	63	5·7	116	50
April . . .	8·1	20·2	– 3·7	70	5·8	141	80
May . . .	12·2	22·4	0·6	71	6·0	122	63
June . . .	17·0	27·0	5·4	75	6·5	152	46
July	18·5	28·8	12·0	82	7·5	276	256
August . . .	24·3	32·0	16·5	83	5·4	150	71
September .	26·7	33·3	18·3	80	5·3	65	210
October . .	22·6	29·9	13·8	84	7·7	359	486
November .	14·7	24·1	4·3	78	5·2	158	202
December .	9·1	20·0	– 1·5	72	3·2	38	67
Year . . .	13·6	33·9	– 7·2	74·7	5·6	1760	1690

Rainfall in 1874, 1,697 ; in 1875, 1,742 mm.

JAPAN—NIIGATA.

37° 55′ N., 139° 10′ E., 6·5 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1883, p. 71.)

	Temperature (10 years).			Rainfall (7 years).	
	Mean of the Terms.	Mean Max.	Mean Min.	Amount in mm.	Days.
December . . .	5·2	12·9	− 0·6	178	10·9
January . . .	2·2	9·0	− 2·6	110	11·4
February . . .	2·9	10·2	− 3·2	77	8·6
March	5·8	16·4	− 1·1	105	8·9
April	10·7	22·9	3·1	99	6·8
May	16·1	27·4	8·0	106	5·7
June	21·0	29·4	12·5	126	5·8
July	26·0	34·0	19·0	204	7·1
August	27·2	34·8	21·0	103	6·2
September . .	22·9	31·4	14·6	167	8·2
October . . .	15·5	24·6	7·4	197	8·9
November . .	9·8	19·3	2·9	216	10·3
Year	13·8	35·0	− 4·3	1688	98·8

WEST CHILI—ANCUD.

41° 51′ S., 74° W., 15 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1872, p. 11.)

	Temperature (1 year).	Rainfall (3 years).		Bright Days (3 years).
		Amount in mm.	Days.	
December . . .	12·8	149·7	12·3	12·3
January . . .	13·4	155·0	11·7	14·0
February . . .	13·9	147·3	7·3	14·0
March	9·9	216·0	18·0	8·0
April	10·2	303·5	20·0	3·5
May	9·7	466·5	22·0	2·0
June	7·0	619·5	24·0	2·5
July	8·1	366·0	19·0	4·5
August	7·9	474·0	21·0	3·7
September . .	8·0	196·7	11·7	12·0
October . . .	10·4	107·3	9·0	9·7
November . .	12·6	196·9	17·7	7·7
Year	10·3	3397·5	193·7	93·9

WESTERN NEW ZEALAND.

(After Hann in Zeitschr. d. österr. Gesellsch. f. Meteorol., 1871, pp. 281, 345.)

	TARANAKI (North Island). 39° 4′ S., about 23 meters above sea-level.		HOKITIKA (South Island). 42° 42′ S., about 25 meters above sea-level.	
	Temperature. Mean.	Rainfall. Amount in mm.	Temperature. Mean.	Rainfall. Amount in mm.
December . . .	17·1	125·0	14·8	309·1
January . . .	18·7	81·8	15·0	226·1
February . . .	18·6	101·8	15·5	250·7
March	16·9	65·5	13·6	171·5
April	15·2	89·4	12·0	218·7
May	12·6	196·1	9·6	161·8
June	11·0	150·2	7·8	209·3
July	10·4	160·0	7·3	244·8
August	10·0	131·5	7·5	231·9
September . .	11·8	133·4	9·6	149·3
October . . .	13·2	151·6	10·8	340·4
November . .	15·0	123·4	12·3	322·3
Year	14·2	1509·7	11·3	2835·9

A constantly humid, warm temperate district, with rain insufficient for forest growth, occurs only in the Falkland Islands. As the rain is extraordinarily frequent, the islands possess a splendid climate for grassland, and are actually for the most part covered with grass.

Warm Temperate Grassland Climate.

EASTERN NEW ZEALAND—CHRISTCHURCH (SOUTH ISLAND).

42° 33′ S., 6½ meters above sea-level.

(After Hann in Zeitschr. d. österr. Gesellsch. f. Meteorol., 1871, pp. 281, 345.)

	Rainfall. Amount in mm.	Temperature. Mean.		Rainfall. Amount in mm.	Temperature. Mean.
December .	41·2	15·9	July . . .	62·2	6·2
January . .	58·7	16·6	August . .	58·9	6·6
February .	60·2	16·6	September .	29·5	9·8
March . .	44·5	14·4	October . .	54·4	11·7
April . . .	46·0	12·6	November .	54·1	14·0
May . . .	57·9	8·9	Year . .	648·6	11·6
June . . .	81·0	6·3			

Mean annual maximum temp. 31·2. Mean annual minimum temp. −3·8.

FALKLAND ISLANDS—STANLEY HARBOUR.

51° 41′ S., 57° 51′ W.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1881, p. 299.)

1875–1877.	Temperature.			Relative Humidity. 9 a.m.	Cloudiness. 9 a.m.	Rainfall.	
	Mean Max.	Mean Min.	Mean.			Amount in mm.	Days.
January . .	11·7	4·7	8·2	76	7·4	50	21·0
February .	13·4	6·2	9·8	72	7·2	69	21·3
March . .	12·8	5·6	9·2	76	7·2	55	19·3
April . . .	12·4	6·0	9·2	81	6·6	43	18·3
May . . .	9·5	3·6	6·6	84	6·4	51	22·3
June . . .	7·0	2·2	4·6	90	6·9	43	19·3
July . . .	5·3	1·2	3·3	91	7·6	37	20·0
August . .	4·8	0·2	2·5	91	7·2	47	20·3
September .	5·6	0·6	3·1	88	6·7	30	22·0
October . .	7·3	1·5	4·4	81	6·2	29	15·7
November .	8·0	2·0	5·0	82	7·7	34	21·3
December .	10·3	3·9	7·1	76	7·9	29	15·3
Year . .	9·0	3·1	6·1	82	7·1	517	236·1

4. TEMPERATE SOUTH AFRICA.

Countries in which the climate as regards rain varies at short distances are naturally more instructive for the study of the connexion between the rain-climate and the character of the vegetation, than are others of greater extent and where other climatic conditions vary as well. Extra-tropical South Africa is in this respect extremely important; data regarding its rainfall are very accurately known, thanks to Dove's observations, and its flora has in essentials retained its original character. It appears that the provinces as planned by Dove according to rainfall are at the same time oecological vegetation-provinces.

To the south of the littoral strips of the Karroo desert, from about 30° S., the precipitation, which is scanty north of this latitude[1], rapidly increases. The south-west coasts of Cape Colony have 60–75 cm. of rainfall, chiefly as winter rain; the summer is dry. The relative humidity of the air is high. The vegetation consists of low xerophilous evergreen woody plants with small leathery leaves. Although also occurring elsewhere as scattered constituents of the vegetation, *such sclerophyllous plants*[2] *are characteristic of*

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[1] See Chap. IX, Deserts.

[2] See p. 9.

warm temperate districts with wet winters and dry summers, where alone they form the chief mass of the vegetation.

Warm Temperate Sclerophyllous Woodland Climate.

SOUTH-WEST AFRICA—WELLINGTON.

33° 38′ S., 19° 0′ E., 120 meters above sea-level.
(After Dove, op. cit., p. 33 ff.)

	Temperature (4½ years).		Relative Humidity (6⅓ years).	Rainfall in mm. (8 years).	Cloudiness (3 years).
	Mean.	Range.			
January .	22·9	12·1	61	11·9	2·6
February .	22·7	11·4	65	19·3	2·7
March . .	21·3	12·4	67	24·4	3·0
April . .	18·1	11·9	75	46·0	3·7
May . . .	13·9	9·2	81	105·7	5·3
June . . .	11·9	9·4	82	88·1	4·9
July . . .	11·5	9·2	84	93·0	4·6
August . .	11·8	9·8	83	76·5	4·4
September .	14·1	10·7	77	77·2	4·2
October .	16·8	11·4	72	59·4	4·0
November .	19·4	11·8	66	21·3	3·1
December .	20·9	12·4	63	30·7	2·9
Year . .	17·1	10·9	73	653·5	3·8

	CAPE TOWN. 33° 56′ S., 18° 29′ E., 11 meters above sea-level. (After Dove, op. cit., p. 33 ff.)			CLANWILLIAM. 32° 10′ S., 18° 53′ E., 100 meters above sea-level. (After Dove, op. cit., p. 36 ff.)			WORCESTER. 32° 40′ S., 19° 27′ E., 240 meters above sea-level. (After Dove, op. cit., p. 37 ff.)		
	Temperature (30 years).		Rainfall in mm. (43 yrs.).	Temperature (9 years).		Rainfall in mm. (13 yrs.).	Temperature (3½ years).		Rainfall in mm. (18 yrs.).
	Mean.	Range.		Mean.	Range.		Mean.	Range.	
January . .	20·8	13·1	16·8	23·6	19·8	8·9	22·2	16·3	5·1
February .	20·8	12·8	15·7	23·1	20·1	5·6	21·9	15·1	19·8
March . .	19·3	13·0	24·1	21·6	19·6	7·9	20·8	14·7	10·7
April . .	17·3	9·7	46·7	17·9	18·2	12·7	17·7	14·9	23·4
May . . .	14·6	7·8	98·8	14·5	13·7	42·2	13·4	13·1	48·0
June . . .	13·1	8·3	112·5	11·4	15·2	36·1	11·8	12·2	53·3

	CAPE TOWN.			CLANWILLIAM.			WORCESTER.		
	Temperature (30 years).		Rainfall in mm. (43 yrs.)	Temperature (9 years).		Rainfall in mm. (13 yrs.)	Temperature ($3\frac{1}{2}$ years).		Rainfall in mm. (18 yrs.)
	Mean.	Range.		Mean.	Range.		Mean.	Range.	
July . . .	12·6	9·8	88·6	10·8	15·4	41·9	10·8	11·9	54·4
August . .	13·2	9·5	83·6	11·9	15·5	23·9	12·8	11·8	32·0
September .	14·2	10·1	55·1	15·1	18·8	16·5	14·3	12·7	30·7
October .	16·1	11·7	41·1	18·4	19·1	19·3	16·7	13·2	38·4
November .	18·0	11·9	28·5	20·4	18·7	10·2	18·7	14·4	14·7
December .	19·8	12·3	20·0	22·3	19·1	6·4	20·4	15·4	7·1
Year . .	16·6	10·9	631·5	17·6	17·8	231·6	16·8	13·8	337·6
	Relative humidity (30 years), Jan. 67, June 81, year 74.						Relative humidity ($3\frac{3}{4}$ years), Jan. 59, July 78, year 68.		

SOUTH COAST—MOSSEL BAY.

34° 11′ S., 22 9′ E., 32 meters above sea-level.
(After Dove, op. cit., p. 55.)

	Temperature ($9\frac{1}{2}$ years).		Relative Humidity ($5\frac{3}{4}$ years).	Rainfall in mm. (9 years).	Cloudiness (5 years).
	Mean.	Range.			
January .	21·2	7·8	76	16·5	4·2
February .	20·9	6·9	78	52·8	4·9
March . .	19·3	6·9	83	48·5	5·6
April . .	17·5	7·0	83	27·2	4·1
May . . .	15·8	7·5	82	38·1	4·6
June . . .	14·4	8·3	79	22·9	3·4
July . . .	13·3	7·7	82	42·4	3·6
August . .	13·7	7·8	82	40·4	3·7
September .	14·9	7·8	80	40·1	4·8
October .	16·5	7·4	78	38·9	4·3
November .	17·7	7·5	78	20·8	4·6
December .	20·1	7·5	73	18·5	4·1
Year . .	17·1	7·6	79	407·1	4·2

Eastward of the dry western district the mountains are so near the coast, that only a narrow flat strip separates them from the sea. *On short strips, in the Knysna district, the annual rainfall attains* 100–110 *cm. Here the coast is covered by evergreen high-forest.* This is, however, confined to the humid valleys, whilst the drier hill-spurs are covered with shrubs. In this case, therefore, the inferior limit of rainfall sufficient for high-forest apparently is hardly reached, and the existence of the high-forest is associated with water in the soil.

To the east of the Knysna forest, the annual rainfall again falls to the amount it shows on the west coast, that is to say, 50–70 cm. *The rain, however, is no longer winter rain, but chiefly falls in spring and autumn, and does not fail at any season. There is also a complete change in the vegetation. The sclerophyllous woods disappear and are replaced by grass savannahs with small acacias.* Forest is confined to the river banks.

Warm Temperate Grassland Climate.

EAST CAPE COLONY LITTORAL SAVANNAH.

(After Dove, op. cit., p. 55 ff.)

	PORT ELIZABETH. 33° 57′ S., 25° 37′ E., 55 meters above sea-level.				EAST LONDON. 33° 20′ S., 27° 55′ E., 10 meters above sea-level.			
	Temperature (11 years).		Rainfall in mm. 18 yrs.	Relative Humidity (6½ years).	Temperature 6⅓ years).		Rainfall in mm. (6 years).	Relative Humidity 3⅓ years).
	Mean.	Range.			Mean.	Range.		
January . .	21·1	7·8	20·8	74	21·4	7·1	66·5	79
February . .	20·9	7·6	35·8	77	21·3	6·7	45·5	84
March . . .	19·7	7·3	54·6	81	20·4	7·1	92·5	82
April . . .	17·7	7·7	47·2	78	19·0	8·8	64·8	80
May . . .	16·2	8·0	60·5	77	17·6	9·3	66·8	79
June . . .	14·7	9·1	47·5	72	15·6	10·3	37·1	74
July	13·6	8·8	53·3	74	14·8	11·4	36·8	72
August . .	14·3	8·3	52·3	77	15·6	10·1	54·4	74
September .	15·2	6·7	53·8	78	17·2	8·0	53·3	79
October . .	16·5	7·8	59·2	76	18·0	7·4	69·1	81
November .	18·4	8·1	52·3	74	19·4	7·6	81·0	83
December .	20·1	8·2	38·9	74	20·9	8·1	23·9	78
Year . . .	17·4	7·9	576·2	76	18·4	8·4	691·7	79

East London belongs to the east coast of Cape Colony. As we proceed in a north-easterly direction, we enter Natal, and, with it, *a district with summer rain*, but rain is also abundant in the spring. There is very little rain in winter.

The rainfall increases along the coast of Natal up to over 100 cm. (Durban, 1,036 mm.); inland however, even at a slight distance from the sea, it only amounts to about 60–75 cm., just as on the south coast of Cape Colony.

KING WILLIAM'S TOWN.
32° 51′ S., 27° 22′ E., 400 meters above sea-level.
(After Dove, op. cit., p. 84 ff.)

	Temperature.		Relative Humidity (6½ years).	Rainfall in mm. (16 years).	Cloudiness (5 years).
	Mean (7 years).	Range (9 years).			
January .	21·2	13·7	75	58·8	4·9
February .	21·2	13·2	75	90·2	4·9
March . .	19·1	12·4	83	86·1	6·2
April . .	16·6	13·9	79	49·8	3·6
May . . .	14·0	14·6	76	43·2	3·0
June . . .	11·6	15·6	73	13·7	2·1
July . . .	11·3	16·4	73	37·3	2·2
August . .	12·4	15·3	74	28·7	2·7
September .	14·7	14·9	75	34·0	4·6
October .	16·6	13·9	75	63·0	4·9
November .	18·1	13·2	72	62·7	5·0
December .	20·3	14·7	70	69·3	4·8
Year . . .	16·4	14·3	75	638·8	4·1

Possibly at an earlier period, as Thode suggests, the more rainy littoral tract was covered with forest. The latter may then have borne the character of an inconsiderably luxuriant rain-forest. The less rainy interior, on the other hand, is true savannah with acacias and some other trees, except on the mountains (which will not be discussed here), where richer precipitations here and there produce forest growth.

Warm Temperate Grassland Climate.

NATAL—PIETERMARITZBURG.
29° 35′ S., 30° 20′ E., 640 meters above sea-level.
(After Dove, op. cit., p. 84 ff.)

	Temperature (10 years).		Relative Humidity (8 years).	Rainfall in mm. (9 years).
	Mean.	Range.		
January .	22·0	7·8	74	106·7
February .	22·1	7·5	76	113·5
March . .	20·9	8·8	75	87·1
April . .	18·3	8·9	73	37·3
May . . .	14·9	11·7	69	22·6
June . . .	12·8	13·2	66	6·6

	Temperature (10 years).		Relative Humidity (8 years).	Rainfall in mm. (9 years).
	Mean.	Range.		
July . . .	13·2	13·5	63	5·3
August . .	15·7	12·3	63	6·6
September	18·2	10·4	67	36·6
October .	18·9	8·7	74	83·8
November .	20·8	8·3	75	112·3
December .	21·3	7·8	76	124·7
Year . .	18·3	9·8	71	743·1

Whilst the western half of the interior of South Africa exhibits the character of a desert, the eastern half (Orange River Colony and the Transvaal) is covered with grassland, which, in correspondence with the dry cold of winter that is hostile to trees, is not savannah but steppe[1]. Here the winter is very poor in rain, and most precipitation occurs from November to March, as the following percentages show.

DISTRIBUTION OF RAINFALL THROUGHOUT THE MONTHS OF THE YEAR IN PERCENTAGES IN ORANGE RIVER COLONY AND TRANSVAAL.

(After Hann, Handbuch, III, p. 365.)

	Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Upper Orange River Colony, 1,350 meters above sea-level. Annual rainfall, 53 cm.	16·7	18·1	16·9	6·3	4·8	2·7	2·5	2·1	4·2	5·5	10·1	10·1
Transvaal, 850 meters above sea-level. Annual rainfall, 64 cm.	26·3	17·3	12·6	4·4	3·0	2·0	0·8	1·5	1·4	4·9	12·1	13·7

If we neglect the deserts, which will be described further on, and the rain-forests, which in South Africa are insufficiently known and unimportant, we obtain the following general propositions that hold good generally for the warm temperate belts:—

1. *The western coast of temperate South Africa has a wet winter and a dry summer; the vegetation consists of xerophilous evergreen sclerophyllous woodland.*

2. *The southern and eastern coasts and the eastern interior have a*

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[1] Cf. pp. 171, 173.

relatively dry winter season and a moist warm season (spring to autumn); the vegetation consists of grassland (savannah or steppe).

5. WARM TEMPERATE DISTRICTS WITH A MOIST SUMMER.

Eastern South America south of 30°, hence in particular Rio Grande do Sul, Uruguay, and Argentina, may be climatically distinguished from most of the warm temperate districts already referred to, by the prevalence of summer rain; in this it is comparable with Natal. In the littoral district and in the lower parts of the La Plata basin a marked dry season does not occur. but a dry season appears during winter in the greater part of the interior.

In North Argentina, as well as along the base of the Andes, as also in the more easterly provinces of Entre Rios and Corrientes, wide tracts of country have a rainfall ranging from 100 to 120 cm. There, high-forest, savannah-forest, savannah, and steppe contend for the mastery; local influences determine the victory and lead to richly varied tracts of park-like country.

Climate of the East Argentine Park-like Country.

CORRIENTES.

About 27° 30′ S.

(From Meteorol. Zeitschr., 1894, p. 356.)

1880–1889.	Temperature.		Rel. Humidity.		Cloudiness.		Rainfall.		Calm.
	7 a.m.	2 p.m.	7 a.m.	2 p.m.	7 a.m.	2 p.m.	Amount in mm.	Days.	
January .	24·8	28·9	78	61	3·6	6·0	183	5·8	0
February .	24·1	28·6	76	60	3·7	5·5	110	3·5	0
March . .	23·4	27·9	80	65	3·8	5·6	108	4·9	1
April . .	19·5	23·4	80	68	4·4	5·0	118	4·7	1
May . .	16·2	19·9	81	72	4·3	4·8	95	3·0	1
June . .	13·8	17·5	82	74	4·8	5·0	48	2·4	1
July . .	13·8	18·2	83	73	5·0	4·9	43	1·9	1
August .	15·5	20·2	79	65	3·5	4·0	20	1·0	0
September	17·0	21·7	78	64	4·4	4·7	73	4·6	0
October .	19·5	24·1	77	63	4·1	4·9	111	4·2	0
November	22·3	26·2	76	63	4·1	4·8	113	5·6	1
December	24·3	28·4	76	63	3·6	5·1	151	5·0	1
Year . .	19·5	23·8	79	66	4·1	5·0	1173	47·5	1

TUCUMAN. 26° 50′ S., 430 meters above sea-level.	Rainfall in mm.	SALTA. 24° 46′ S., 65° 24′ W., 1,200 meters above sea-level.	Rainfall in mm.
January	267·0	Winter	0·0
February	217·0	Spring	199·3
March	209·0	Summer	763·4
April	39·0	Autumn	179·6
May	27·0		
June	0·0		
July	9·0		
August	0·0		
September	0·0		
October	37·0		
November	56·0		
December	197·0		
Year	1060·0	Year	1142·3

Further south the annual rainfall, except at isolated spots, sinks below 100 cm. The eastern half of Argentina has at most 70–100 cm. of rainfall; in the west the precipitations are less, they sink to 20 cm. and even fewer, and the country assumes a desert character (the *western monte* of Lorentz).

The eastern parts of Uruguay and Argentina, that lie nearer to the Atlantic, have an annual rainfall mostly as high as 70–100 cm., and are clad with pure steppe (pampa). West of the pampas there stretches as far as the Cordilleras, an extensive district of thorn-woodland with a rainfall decreasing to the west: this is the *monte-formation* of Lorentz, *espinal-formation* of Hieronymus. This woodland district is subdivided into a subdistrict relatively rich in precipitations, the *eastern monte* of Lorentz, with about 40–70 cm. rainfall, and another, poor in precipitations, that to a great extent may be described as desert. The rainfall ranges from less than 20 cm. at the base of the Andes (Pilciao 13 cm., San Juan 7 cm.) to about 40 cm. on the borders of the eastern monte.

Many explorers have been surprised that the eastern humid district should produce only grass, but the drier western one woods. They did not know the difference between a grassland- and a woodland-climate, nor how grass can hold its own against wood, in a climate that suits it. In the pampas district grass is driven out only where water is very abundant in the soil, as for instance along the banks of rivers. In fact, as the tables show, *the pampas climate is a perfect grassland-climate*, with its rainfall not more than moderate but well distributed, and its humid moderately warm vegetative season. In addition, the strong winds of the pampas, with moderate atmospheric humidity, represent a factor hostile indeed to woodland but innocuous to grassland.

The spread of the grass towards the east is opposed by the reduced rainfall, and, as may be inferred from the considerable number of hours of sunshine, by its less equable distribution in time : this latter is revealed by statements of travellers, who describe the climate as dry compared with that of the pampas. That the climate in the espinal-formation is directly unfavourable to grass appears from the observation of Lorentz that grasses rarely reoccupy clearings to any large extent ; indeed they frequently spring up only under the shelter of trees from a soil resembling a threshing-floor in its bareness.

That woods thrive under such circumstances is a consequence of the accommodating power of xerophilous thorn-bush. There is also in their favour that, in opposition to the pampas, calms predominate over windy weather.

North Patagonia climatically resembles West Argentina, and possesses a similar vegetation, chiefly formed of shrubs, which are very scanty in the desert-like interior.

Warm Temperate Grassland Climate.

PAMPAS.

SAN JORGÉ (CENTRAL URUGUAY).

32° 43′ S., 56° 8′ W., 122 meters above sea-level.

(From Meteorol. Zeitschr., 1886, p. 324.)

1881–1884.	Temperature.			Rel. Humidity.		Strength of Wind.	Sunshine Hours.	Rainfall.	
	Mean Max.	Mean Min.	Daily Range.	9½ a.m.	3½ p.m.			Amount in mm.	Days.
December	34·2	5·6	15·5	60	46	2·2	308	88	8·2
January .	37·3	7·8	15·8	64	50	1·5	336	91	7·2
February .	35·6	8·2	16·2	63	45	1·5	319	26	3·0
March . .	35·3	6·1	14·3	74	57	1·7	267	96	7·5
April . .	29·4	2·1	12·6	78	68	1·6	224	131	8·2
May . .	23·8	− 1·3	11·1	82	70	1·2	188	83	7·0
June . .	21·8	− 2·8	10·2	90	77	1·7	142	125	11·0

1881–1884.	Temperature.			Rel. Humidity.		Strength of Wind.	Sunshine Hours.	Rainfall.	
	Mean Max.	Mean Min.	Daily Range.	9½ a.m.	3½ p.m.			Amount in mm.	Days.
July . . .	23·4	– 3·1	10·2	88	73	2·1	171	82	9·7
August . .	26·9	0·3	10·8	83	73	2·1	200	87	8·8
September	29·2	0·7	11·2	79	66	2·5	204	126	9·2
October .	29·3	2·3	12·6	76	67	2·1	252	71	9·0
November	31·9	4·7	13·4	69	57	1·9	294	101	6·8
Year . .	37·3	– 3·3	12·8	75	62	1·85	2905	1107	95·6

February, 1884, had a mean daily range of temperature of 17·8 degrees, but was also very dry (mean humidity only 33 %), with 1·3 mean cloudiness and 338 hours of sunshine. A frequent change between extreme degrees of humidity is characteristic of San Jorgé. The rain falls usually in a few heavy showers. The number of rainy hours in Central Uruguay is very small.

MATANZAS.

34° 49′ S., 58° 37′ W.

(From Meteorol. Zeitschr., 1894, p. 356.)

1877–1889.	Temperature.				Rel. Humidity.		Rainfall. Amount in mm.	Calms in %.
	7 a.m.	2 p.m.	Mean Max.	Mean Min.	7 a.m.	2 p.m.		
January .	23·4	30·9	38·4	16·1	68	60	92	5
February .	21·3	30·0	36·5	14·1	69	60	58	7
March . .	19·6	27·5	34·0	12·3	70	60	97	9
April . .	13·6	21·4	27·4	5·7	67	59	83	2
May . .	10·1	18·0	23·4	3·1	64	61	73	0
June . .	8·5	15·1	20·6	1·6	62	61	73	0
July . . .	8·3	15·0	21·2	1·7	61	64	55	0
August . .	9·8	17·3	25·1	2·8	66	66	64	0
September	11·3	18·6	26·9	4·5	67	67	83	0
October .	15·4	22·2	28·9	8·3	70	68	71	0
November	19·6	26·4	33·5	11·7	69	65	69	0
December	22·1	29·3	36·6	13·8	70	65	110	0
Year . .	15·2	22·6	39·1	0·5	67	63	928	2

SAN ANTONIO DE ARECA.
34° 12′ S., 59 30′ W.,
43 meters above
sea-level, 1879–1881.

SALADO.
35 44′ S., 59 5′ W.,
15 meters above
sea-level, 1878–1882.

DOLORES.
36 19′ S., 58 20′ W.,
10 meters above
sea-level, 1878–1882.

Other
Pampas
localities.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1884, p. 530, also p. 382; 1895, p. 105.)

	Tempera-ture.	Rainfall. Amount in mm.	Tempera-ture.	Rainfall. Amount in mm.	Tempera-ture.	Rainfall. Amount in mm.	Annual Rainfall. Amount in mm.
January .	22·6	114	21·7	110	21·2	121	
February .	23·8	32	22·0	39	21·6	122	
March . .	21·5	91	19·3	40	19·1	45	AYACUCHO, 37 7′ S., 59 30′ W., 635·6
April . .	16·0	31	14·2	41	15·2	37	
May . . .	12·4	58	11·1	60	12·2	36	
June . . .	10·0	72	8·8	76	7·5	73	
July . . .	9·5	36	8·3	47	8·9	41	BAHIA BLANCA, 38° 45′ S., 62 11′ W., 15 meters above sea-level, mean of 1860 1879, 488
August . .	11·5	26	10·6	47	10·6	60	
September	12·7	58	12·2	56	12·1	45	
October .	16·1	81	15·7	58	15·2	88	
November	20·4	58	19·2	105	18·9	73	
December .	23·8	139	22·3	94	21·4	64	
Year . .	16·3	796	15·5	773	15·3	805	

Warm Temperate Climate for Thorn-Woodlands.

WEST ARGENTINE ESPINAL-WOODLAND.

CORDOBA.
31° 25′ S., 64° 12′ W., 437 meters
above sea-level.
(From Meteorol. Zeitschr., 1891, p. 386.)

LA RIOJA.
29 20′ S., 67 15′ W., 540
meters above sea-level.
1878–1881.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1884, p. 530.)

	Mean Temperature, 1873–87.	Rel. Humidity, 1881–7.	Mean Rainfall. Amount in mm., 1873–88.	Sunshine Hours, 1886 8.	Mean Temperature.	Rainfall. Amount in mm.
January .	23·0	65	115	306	24·9	41
February .	22·4	63	89	244	24·9	57
March . .	20·3	72	96	227	20·9	144
April . .	15·9	69	33	190	17·1	24
May . . .	12·9	67	16	229	13·1	15
June . . .	9·9	67	5	153	9·8	2
July . . .	10·0	60	2	191	9·7	7
August . .	12·7	55	9	229	12·8	17
September	15·0	55	25	187	15·3	24
October .	17·6	61	56	252	19·0	49
November	20·2	64	113	300	23·5	44
December .	22·3	63	107	277	25·7	33
Year . .	16·9	63	666	2785	18·3	457

CATAMARCA.

28° 28′ S., 65° 56′ W., 545 meters above sea-level.

(From Meteorol. Zeitschr., 1894, p. 357.)

1881–1888.	Temperature.		Rel. Humidity.		Cloudiness.	Rainfall. Amount in mm.	Bright Days.	Cloudy Days.	Wind Velocity.	Calms.
	7 a.m.	2 p.m.	7 a.m.	2 p.m.						
January .	25·4	32·5	57	38	4·0	67	4	2	2·0	14
February .	23·3	30·7	61	39	3·7	27	4	2	1·9	16
March . .	21·7	29·5	66	44	3·4	29	8	3	1·9	20
April . .	15·1	23·4	71	51	2·8	21	10	7	1·5	9
May . .	10·9	21·2	74	46	3·1	11	20	1	1·2	37
June . .	6·7	14·1	81	59	5·0	6	14	15	1·0	35
July . .	7·5	17·4	68	38	3·1	0	18	2	1·5	33
August .	10·9	21·8	62	39	2·7	4	27	1	1·6	35
September	15·6	24·9	55	32	3·3	2	23	4	1·8	20
October .	18·6	27·6	56	35	3·5	24	14	4	2·3	8
November	21·8	30·2	55	34	3·8	47	19	1	2·8	14
December	24·9	31·1	54	37	3·9	32	8	1	2·8	18
Year . .	16·9	25·4	63	41	3·5	270	14	4	1·9	23

Extra-tropical East and South-East Australia have rain at all seasons of the year, but with a relatively dry winter (in particular August); the maxima are during late summer on the coast, during spring and autumn in the interior. The rainfall, except on mountain-slopes, is too small for rain-forest. The absence of dry periods during the spring months whose favourable conditions of temperature give the climate the impress of a good grassland-climate, and the mildness of winter, in spite of its relative dryness, renders growth of trees possible. Consequently *the type of vegetation is that of savannah*, and along the coast, in accordance with the increased precipitation, it passes into savannah-forest; in the interior, however, with a decrease in precipitation, it passes into steppe, which in its turn, as the drought increases, is replaced by desert.

Warm Temperate Grassland Climate.

EXTRA-TROPICAL EAST AND SOUTH-EAST AUSTRALIA.
(After Hann, Handbuch, III. p. 382.)

	Meters above Sea-level.	Mean Temperature. Jan.	April.	July.	October.	Year.	Annual Rainfall. Amount in cm.
N. S. WALES, COAST:							
Lismore, 28° 50′ S., 153° 21′ E. .	15	25·4	20·9	14·1	21·9	20·4	157
Sydney, 33° 51′ S., 151° 11′ E. .	45	21·4	17·6	10·9	16·9	16·6	128
N. S. WALES, INTERIOR:							
Narrabri, 30° 20′ S., 149° 46′ E. .	230	28·6	19·8	9·8	20·8	19·8	70
Dubbo, 32° 18′ S., 148° 35′ E. .	260	25·0	17·2	8·2	16·8	16·8	59
Deniliquin, 35° 32′ S., 145° 2′ E.	95	24·0	16·3	7·8	15·7	15·9	44
VICTORIA, COAST:							
Gabo Island, 37° 35′ S., 149° 30′ E.	15	18·1	16·0	10·4	13·4	14·4	96
Portland[1], 38° 21′ S., 141° 32′ E.	10	17·2	14·6	10·0	14·3	14·1	82
VICTORIA, INTERIOR:							
Sandhurst, 36° 47′ S., 144° 17′ E.	230	22·3	15·2	7·7	14·2	14·9	57
Echuca, 36° 5′ S., 144° 50′ E. .	100	23·8	15·7	8·7	15·0	15·8	47

[1] Uncertain.

RAINFALL IN PERCENTAGES.
N. S. WALES. VICTORIA.
(After Hann, Handbuch, III, p. 389.)

Station.	Coast.		Mountains.	Inland.			Inland.	Coast.
South Lat.	30·3	35·1	34·5	31·3	31·6	34·4	36·9	38·5
East Long.	152·5	150·6	149·5	148·3	144·2	144·6	145·1	145·0
January .	10·3	7·9	8·4	9·4	9·9	7·3	5·9	5·6
February .	12·8	10·6	9·5	11·3	10·0	6·3	6·4	5·4
March . .	12·4	10·2	8·1	10·5	12·7	9·0	7·3	6·1
April . .	9·6	11·7	7·2	8·2	10·3	9·1	8·7	8·1
May . . .	7·8	9·9	8·1	9·0	9·2	10·4	9·3	10·7
June . . .	7·5	10·2	9·6	8·1	8·5	10·5	9·6	10·9
July . . .	6·9	7·7	7·4	5·9	5·6	7·2	7·9	9·9
August . .	5·4	5·1	7·0	6·0	5·6	8·5	8·6	9·8
September	5·8	6·7	8·8	7·6	7·8	8·9	9·5	9·9
October .	6·0	7·2	9·0	7·5	8·9	9·3	10·9	9·3
November	6·8	7·0	9·1	7·9	7·4	8·0	8·5	7·8
December	8·7	5·8	7·8	8·0	5·1	5·5	7·4	6·5
Year. cm.	127	111	90	61	35	42	58	85

6. WARM TEMPERATE DISTRICTS WITH A MOIST WINTER.

Several climatic districts of the north and south warm temperate belts possess a climate similar to that of South-West Africa ; an absolutely similar oecological type of vegetation corresponds to this climate. Woodland is characteristic of it.

South-West and South Australia are included in these districts.

Warm Temperate Sclerophyllous Woodland Climate.

SOUTH-WEST AUSTRALIA—PERTH.

31° 57·4′ S., 115 52° E., 14·3 meters above sea-level.

(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1882, p. 285.)

1880.	Temperature.		Relative Humidity.	Rainfall.		Mean Cloudiness.
	Mean Max.	Mean Min.		Amount in mm.	Days.	
January .	36·1	18·9	64	7	5	3·9
February .	32·8	17·2	67	18	4	6·3
March . .	26·7	15·0	73	29	6	4·7
April . .	25·0	12·2	68	84	12	5·5
May . . .	21·1	9·4	82	85	13	4·2
June . . .	18·3	6·7	80	182	16	3·4
July . . .	18·3	6·7	74	95	10	3·2
August . .	18·9	8·3	75	159	17	6·1
September	22·2	9·4	66	65	14	4·2
October .	22·2	8·9	71	26	9	4·0
November	26·7	12·8	64	54	7	3·4
December	30·0	13·9	69	2	3	2·3
Year . .	24·8	11·6	71	806	116	4·3

According to five years' (1876–1880) observations at Perth the mean annual rainfall is 822 mm.

At ten stations in 1879: Fremantle 655, Albany 770, Vasse 604, Bunbury 785, Geraldton 472, Guilford 891, Newcastle 312, Northam 211, York 317, Sinjarrah 754 mm.

There is considerable climatic and phyto-oecological analogy between the South-West African districts described above and Central Chili. The Karroo desert corresponds to the desert of Atacama. South of the latter, precipitations become heavier and continue to increase steadily with the distance from the tropic of Capricorn. Santiago has 33 cm., Talca, somewhat further south, 53 cm. The rain falls chiefly in winter, summer is rainless.

Warm Temperate Sclerophyllous Woodland Climate.

CENTRAL CHILI SANTIAGO.
33° 27′ S., 70° 41′ W., 519 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1885, p. 367.)

1873-1881.	Temperature.		Rel. Humidity.		Rainfall.		Bright Days.
	Mean Max.	Mean Min.	Mean.	Mean Min.	Amount in mm.	Days.	
December	29·7	8·8	67	34	5	0·9	21·2
January .	30·4	10·4	69	39	1	1·0	23·3
February .	29·4	9·1	72	41	3	0·9	21·0
March . .	28·0	6·8	75	38	5	1·1	20·4
April . .	25·3	3·3	80	42	24	3·2	15·1
May . . .	21·8	1·1	83	41	47	5·7	11·3
June . .	18·3	− 0·6	87	45	77	6·1	8·5
July . . .	18·4	− 0·8	87	49	81	8·6	9·3
August . .	20·3	− 0·7	85	50	37	6·1	10·6
September	22·5	2·0	84	40	38	6·3	11·6
October .	24·8	4·2	79	42	14	3·7	12·2
November	28·3	6·7	73	38	6	1·3	17·7
Year . .	30·8	− 1·7	78	28	327	44·9	182·2

and besides 73·1 half-bright days.

The most extensive district with winter rain, that of the *Mediterranean countries*, occurs in the northern hemisphere. It is true that in its northern parts late autumn and early spring are for the most part humid, but this is devoid of oecological significance on account of the low temperature at the time.

The rainfall is very unequal. It lies mostly between 60 and 90 cm., but still, here and there, it rises above 100 cm., whilst in the eastern part of the African littoral district it sinks so low that deserts extend down to the seashore.

The vegetation again consists of sclerophyllous woodland.

Warm Temperate Sclerophyllous Woodland Climate.

MEDITERRANEAN DISTRICT.
NIKOSIA, IN THE INTERIOR OF CYPRUS.
35° 11′ N., 33° 22′ E., 150 meters above sea-level.
(From Meteorol. Zeitschr., 1880, p. 431.)

	Temperature.			Relative Humidity.	Cloudiness.	Rainfall.	
	Mean.	Mean Max.	Mean Min.			Amount in mm.	Days.
January .	10·0	23·0	0·2	84	4·6	101	11·8
February .	9·8	21·5	− 0·1	84	5·1	94	11·8
March . .	12·8	4·7	2·4	81	4·0	31	7·4

	Temperature.			Relative Humidity.	Cloudiness.	Rainfall.	
	Mean.	Mean Max.	Mean Min.			Amount in mm.	Days.
April . .	16·7	29·2	3·8	78	3·7	29	4·5
May . . .	20·9	32·4	7·9	74	2·5	16	4·3
June . . .	25·0	37·8	11·3	67	1·1	10	1·4
July . . .	26·8	38·3	13·1	68	0·8	3	0·3
August . .	27·8	39·4	14·0	66	0·7	2	0·5
September	26·0	38·1	12·3	73	1·0	1	0·6
October .	22·0	34·2	8·7	76	1·9	9	2·3
November	16·2	29·0	4·1	82	3·4	50	6·5
December.	12·3	25·3	1·1	85	3·7	59	7·8
Year . .	18·9	40·6	– 0·4	76	2·7	405	59·2

ATHENS.

37° 58′ N., 23° 44′ E., 102·7 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1884, p. 481.)

1859–1882.	Temperature.			Mean Rainfall in mm.	Rainy Days[1].	Cloudy Days.
	Mean.	Mean Max.	Mean Min.			
December.	9·87	12·81	7·66	69·4	10·9	5·3
January .	8·20	10·87	3·97	52·6	9·8	5·0
February .	8·89	12·63	5·09	37·9	8·0	4·0
March . .	11·33	14·19	6·64	36·7	8·2	4·3
April . .	15·04	17·80	10·69	19·1	6·3	1·9
May . . .	19·95	22·24	17·53	24·5	5·1	1·0
June . . .	24·45	26·65	22·75	10·8	2·3	0·5
July . . .	27·00	28·19	25·36	7·4	1·6	0·1
August . .	26·75	28·91	25·68	10·7	1·9	0·1
September	23·42	25·67	20·49	15·4	2·6	0·4
October .	18·75	20·74	16·63	53·1	7·1	2·1
November.	14·02	12·67	8·74	70·4	8·9	3·8
Year . .	17·30	18·16	16·41	408·0	72·8	28·5

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[1] With measurable precipitation.

ROME.

41° 54′ N., 12° 28′ E., 31 meters above sea-level.
(From Meteorol. Zeitschr., 1886, p. 409.)

	Temperature.			Rainfall.		Cloudiness.	Relative Humidity.	Wind Velocity.
	Mean.	Mean Min.	Mean Max.	Amount in mm.	Days.			
December .	7·4	− 1·3	16·0	82	11·5	5·2	75	204
January .	6·7	− 1·8	15·3	74	11·8	5·0	74	200
February .	8·1	− 0·5	16·7	60	10·5	4·9	73	180
March . .	10·3	1·3	19·0	64	11·5	5·5	68	226
April . .	13·9	4·7	23·1	60	10·6	4·6	65	189
May . . .	17·9	8·5	28·5	55	9·7	4·3	61	195
June . . .	21·9	12·8	31·3	38	7·5	3·5	61	197
July . . .	24·6	15·2	34·0	17	3·6	1·8	56	210
August . .	24·3	14·9	34·2	29	5·0	2·1	58	199
September	21·3	11·8	30·6	70	8·6	3·4	64	177
October .	16·6	6·6	26·0	106	11·1	4·6	71	181
November	10·9	1·2	20·0	114	12·8	5·4	74	201
Year . .	15·3	− 3·2	35·0	769	114·2	4·2	67	197

MALAGA.

36° 43′ N., 4° 27′ W., 23 meters above sea-level.
(From Meteorol. Zeitschr., 1890, p. 198.)

1878–1885.	Temperature.		Relative Humidity.	Rainfall.		Windy Days.	Bright Days.
	Mean Max.	Mean Min.		Amount in mm.	Days.		
January .	21·2	3·5	70	70	4·9	1·7	12·8
February .	23·2	5·7	69	50	4·5	2·2	11·0
March . .	24·6	6·4	68	84	7·1	2·2	10·9
April . .	27·8	8·6	61	68	7·1	2·3	6·6
May . . .	31·1	11·0	61	28	4·3	1·2	16·3
June . . .	35·2	15·3	60	13	1·9	0·6	22·2
July . . .	38·0	18·3	62	3	0·8	0·3	20·5
August . .	38·7	18·1	62	5	0·8	0·0	23·8
September	34·8	15·0	62	27	1·8	1·8	20·0
October .	29·0	10·2	65	64	4·6	3·8	13·8
November	25·5	6·6	68	87	4·6	2·2	14·0
December .	21·6	4·0	70	102	5·8	2·3	14·0
Year . .	40·0	2·2	65	607	48·2	20·8	193·9

LISBON.

38° 43·2′ N., 9° 8·3′ W., 102·3 meters above sea-level.
(From Zeitschr. d. österr. Gesellsch. f. Meteorol., 1878, p. 127.)

1856–1875.	Mean Temperature.	Relative Humidity	Cloudiness (0—10).	Evaporation in mm.	Rainfall.	
					Amount in mm.	Days.
December .	10·2	79	5·0	57	91	12·6
January .	10·3	81	5·7	55	98	15·4
February .	10·9	76	5·0	69	94	12·5
March . .	12·4	70	4·7	118	88	12·0
April . .	14·6	70	5·0	141	48	9·7
May . . .	16·6	69	4·6	172	56	10·0
June . . .	19·5	64	3·3	244	14	4·7
July . . .	21·2	62	2·0	263	3	1·8
August . .	21·7	61	1·9	270	9	2·0
September	19·9	67	3·6	189	34	7·2
October .	16·9	73	4·8	121	87	11·0
November	13·5	78	5·4	74	109	13·0
Year . .	15·6	70·9	4·2	1774	731	112·0

TANGIER.

35° 42′ N., 5° 55′ W.
(From Meteorol. Zeitschr., 1887, p. 27.)

1880 1885.	Temperature.			Days.		Rainfall.		Storms. Mean.
	7 a.m.	12 noon.	9 p.m.	Bright.	Dull.	Amount in mm.	Days.	
December .	11·2	14·5	12·3	11	11	110	10·0	3
January .	11·6	15·2	12·6	9	13	118	11·7	6
February .	12·5	16·1	13·2	9	10	90	12·0	4
March . .	13·5	17·0	13·9	10	11	128	15·2	6
April . .	15·0	18·1	15·1	9	9	119	13·2	4
May . . .	17·9	21·1	17·6	14	7	63	8·2	5
June . .	21·0	24·0	20·2	17	3	7	2·5	3
July . . .	23·0	26·3	22·7	21	4	3	1·7	4
August . .	23·1	27·2	23·4	21	4	9	0·8	4
September	20·4	24·4	21·0	18	3	10	2·2	3
October .	17·3	21·0	18·1	12	9	85	9·3	3
November	14·3	18·2	15·4	11	9	73	7·5	2
Year .	16·7	20·2	17·1	162	93	815	24·3	47

The north temperate zone possesses, along the coast of *California*, another *district with winter rain and a dry summer*, to which also *corresponds a xerophilous vegetation of sclerophyllous woods.*

The annual rainfall at San Francisco is 55 cm., at Monterey 40 cm.; the percentage distribution over the months, according to Woeikoff, for the whole of California is:

DISTRIBUTION OF RAINFALL THROUGHOUT THE MONTHS OF THE YEAR IN PERCENTAGE IN CALIFORNIA.

(After Woeikoff, Die Klimate der Erde, I, p. 389.)

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
20	14	16	8	4	0·3	0·1	0·1	0·5	2	11	24

Full meteorological tables such as those given above do not appear to exist for California. The mean winter temperature at San Francisco is 10·5° C., that of the summer 14·8° C.

7. CONCLUSION.

The three forms of rain-climate of the warm temperate belts distinguished in this chapter can be reduced to two types as regards the conditions of existence of the vegetation.

The *first type* meteorologically considered is indeed composed of very heterogeneous elements, as it includes districts with nearly uniform humidity, together with others possessing rain chiefly in winter and early summer, but with dry late summers, and others again with dry winters and wet summers. The character common to all these is that high temperatures favourable to vegetation coincide with abundant precipitations even if only during the early summer. *The climate during the hot months therefore resembles a tropical climate and impresses a quasi-tropical character upon the vegetation.* Here we find types of vegetation quite similar to those of the tropics and associated with similar conditions as regards atmospheric precipitations. Very abundant precipitations cause the production of *temperate rain-forest*; rainfall less considerable but occurring during the vegetative season, particularly in the form of frequent rain in early summer, brings forth *grassland*, and, owing to the mild winter temperature, makes it assume the tropical form of *savannah*, which with increasing rainfall then passes over into *savannah-forest*. Irregular precipitations during the period of vegetation interrupted by dry seasons, exclude grassland and cause the occurrence of the most accommodating of all woodland types, *thorn-woodland*, as forest, bush, or scrub. Still greater drought brings forth *desert.*

In districts belonging to the *second type*, the rainy season coincides with cool winter temperatures. The latter are below the optimum for a number of vegetative processes, including growth, and in some of the districts concerned occasionally below the minimum. The summer is very dry.

Such climatic conditions are confined to these climatic districts belonging to the warm temperate belts, and accordingly the oecological character of their vegetation, particularly the prevalence of evergreen xerophilous woodland, is without analogy in the tropical zones, or in the belts with a cold winter in the temperate zones.

SELECT LITERATURE.

The meteorological tables are from—

Zeitschrift der österreichischen Gesellschaft für Meteorologie. I–XX. 1866–1885.

Meteorologische Zeitschrift der deutschen und österreichischen meteorologischen Gesellschaft. 1882–1896.

The general descriptions are chiefly based on—

Hann, Handbuch der Klimatologie, second edition, 1897; and Atlas der Meteorologie, Gotha, 1887.

In reference to South Africa—

K. Dove, Das Klima des aussertropischen Südafrika. Göttingen, 1888.

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