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Foliar Periodicity in Trees

Laubfall und Lauberneuerung in den Tropen. by G. Volken; Ueber die Periodischen
Erscheinungen Tropischer Pflanzen. by G. Klebs

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takes place the tree shows active assimilation; and the maximum absorption of potassium and nitrogen occurs in this period; if "midsummer shoots" are formed, however, this period marks the culmination of potassium and phosphorus increase while that of nitrogen is almost brought to a standstill, that of calcium and of magnesium showing a falling off. Apparently the "midsummer shoots" draw largely upon the reserves stored in the earlier leaves, which contribute to these shoots 24 p.c. potash, 100 p.c. lime, 52 p.c. magnesia, 26 p.c. phosphoric acid, and 62 p.c. nitrogen. In period 4 the absorption of calcium reaches its maximum, and the behaviour of the nitrogen, potassium and magnesia shows that during this period there begins the migration of substances to and from the leaves which has been investigated by Ramann (see below).

(II) Since the mineral substances contained in plants are obtained from the soil and carried largely into the leaves by the transpiration current, it is obvious that actively transpiring leaves will accumulate large quantities of mineral matter. Ramann confirms the conclusion of previous investigators that in autumn there is a migration of mineral substances from the leaves to other parts of the plant. Ash analyses show that in the relatively short interval between the autumn colouring and the death of the leaves there is a rapid transference of nitrogenous compounds, potassium salts, and phosphates from leaf to stem. On the other hand, calcium salts and silica increase in amount in the dying leaf, and the amount of these substances may be twice as great as in normal green leaves. Ramann analysed the leaves of beech, maple, birch, oak, and *Robinia*. His results are of considerable ecological interest; for instance, the well-known fact that beech and oak make rich humus is evidently connected with the fact that their leaves retain more of their nitrogenous and phosphorus-containing compounds than do those of other trees.

(III) In this paper Ramann gives the results of analyses of pear leaves, some of which were killed by frost while others remained uninjured. The former showed diminution in potassium and phosphorus, but an increase in calcium content—exactly as in normal autumn withering, though the migration of substances from the leaves was less marked. The protein content of the frost-killed leaves remained unaltered. The author does not discuss this point, nor does he state whether or not ice was formed in the frozen leaves, but as pointed out by Schaffnit (*Zeitschr. f. Bot.*, 5, 1913, p. 121), with increasing concentration of the cell-sap due to the freezing process there would occur a salting-out or denaturation of the proteins, the latter becoming coagulated and therefore not acted upon readily by proteolytic enzymes even if these survived the cold. Ramann found that the migration of substances into and out of the leaves took place during the short period between the thawing and the perishing of the frozen leaves; but since death of the tissues in non-resistant leaves like those of the pear takes place during the actual freezing and not after thawing, the exit of the potash and phosphoric acid would be simply a postmortem change due to osmotic diffusion and could therefore be effected in a period too short to allow of the conversion and transport of organic nitrogenous substances.

FOLIAR PERIODICITY IN TREES

(I) **Volken, G.** "Laubfall und Lauberneuerung in den Tropen." Berlin (Gebr. Borntraeger), 1912, 142 pp.

(II) **Klebs, G.** "Ueber die periodischen Erscheinungen tropischer Pflanzen." *Biol. Centralblatt*, 32, 1912, pp. 257—285.

Observations by various writers (Treub, Haberlandt, Schimper, Wright, and others) have shown that even in the uniform climate of the tropics many trees show striking periodicity, their growth being interrupted by resting periods instead of proceeding continuously. Schimper (*Pflanzengeographie*, 1898) concluded from his observations that plants in general and of necessity show periodicity, which is independent of climate and is referable to internal causes. Klebs (*Willkürliche Entwicklungsänderungen*, 1903) showed, however, that many plants which under natural conditions have well-marked resting periods may by artificial means be made to grow continuously. It is unnecessary to refer to the well-known work of Johannsen, Molisch,

and others on the methods (etherisation, etc.) for shortening the resting period in various plants; a useful summary of this subject is given by Burgerstein (*Progressus rei botanicae*, 4, 1911, pp. 1—26).

In his work on rhythm in plant development, Klebs (*Sitzungsber. Heidelberger Akad.*, 1911) brought forward additional evidence against Schimper's interpretation, and denied the existence of periodicity independent of external factors. In this paper Klebs deals with his observations on trees in Java, and also on a number of both European and tropical plants, some grown from dry tubers and bulbs and rhizomes, others transported in Wardian cases. From the latter series of observations, little was obtained beyond additions to the growing list of plants whose resting period could be curtailed. In his work in Java, Klebs found that of the various trees introduced from temperate climates into the tropics, some grow without any resting period, in others rest can be annulled by strong stimuli such as defoliation, while in the third group it was found impossible to eliminate the resting period. Though his stay in Java lasted only from November to February, admittedly too short a period for the solution of the problem by means of growth-measurements, his results from defoliation and pot-culture experiments led him to the conclusion that growth, as might be expected, is hampered by low temperature, diminished light intensity, lack of moisture, and inadequate food supply. Of these four factors, Klebs regarded the last (lack of mineral salts) as being the most important; he found, for instance, that trees which normally show continuous growth exhibited a resting period when grown in pots, but could be made to grow on by increasing the supply of salts, and he concluded that the chief effect of the somewhat brutal interference with the plant's life which is involved in removing the leaves was to cause a supply of salts to the growing-points. Cases in which different branches of the same tree behave differently, some being in a state of rest while others are growing, are explained by Klebs in a very simple manner. The plant can obtain only a limited amount of nutritive salts in the soil, but the amount of carbohydrate which it can manufacture is not so limited, hence there is a lack of correlation between inorganic and organic nutrition; the former suffices for certain branches, hence these begin to grow and thus deprive other branches of food so that the latter enter into a resting period.

(I) Volkens continued his observations at Buitenzorg for eight months (December to July) and brought together a large amount of interesting material; his daily records were carried on after his departure by de Moehy, so as to complete a full year. The data thus collected refer mainly to leaf-production, leaf-fall, and the intervening resting period; no observations were made as to the soil factors (mineral content, etc.), but records were kept of temperature, rainfall, atmospheric humidity, and insolation. He found that in tropical trees, as in those of temperate climates, leaf-fall is effected by means of an absciss-layer and is preceded by colour change—Schimper had described the leaves of *Ficus glabella* as falling while still quite green, but Volkens states that this never occurs, either in the species mentioned or in any other case. In many cases exfoliation is complete and may take place in a remarkably short time—in four to eighteen days in *Ficus variegata*; or it may take from three to nine months—in such cases there are often great differences between the different branches, the leaves either falling singly or in periodic batches and their fall being accompanied by production of new leaves so that two, three, or more generations of leaves may be present at a time. When leaf-fall proceeds branch by branch, it usually begins at the apex of the crown and progresses downwards, but apparently without definite relation to the light-conditions affecting the different branches.

The author distinguishes from the true evergreens the various transitional cases in which there is a distinct resting period, involving arrest of assimilation and transpiration, though the leafless condition usually lasts only for a few days (very rarely for two months or more). In the evergreens two main classes are recognised—(1) those showing marked periodicity, all the buds opening simultaneously, and (2) those in which the opening of buds proceeds throughout the year.

From his observations, Volkens concludes that it is impossible to correlate the periodicity of trees in Java, and the tropics generally, with climatic changes; the temperature factor is excluded owing to its remarkable uniformity throughout the year, and though many of the trees become leafless during the period of maximum rainfall, others show regular half-yearly periods or irregular periodicity quite independent of rainfall—in short, neither in the case of indigenous nor in that of introduced trees could Volkens find a definite relation between dry

period and leaf-fall, and he confirms Schimper's conclusion that periodicity in tropical trees depends not upon external but upon internal factors, concerning which it is impossible at present to say anything definite.

(II) In his recent work, Klebs describes his new observations on plants brought from Java and cultivated at Heidelberg. Some of these showed continuous growth, even during winter when it was impossible to give them optimum conditions for growth; young plants of species which in Java show definite periodicity also showed continuous growth at Heidelberg, while in a third group the leaves were produced in crops interrupted by resting periods, though all were grown under uniform conditions. He reiterates his view that in the majority of cases, if not in all, the resting period of tropical trees must, since the meteorological conditions show such remarkable uniformity, be referable to variations in the absorption and distribution of mineral salts. He cites observations by Volkens and other writers as supporting this view; for instance Volkens found that shoots arising from the base of the stem or from the thicker branches remain covered with leaves when the rest of the tree is leafless; Los showed that the stool shoots of old *Tectona* trees, as well as young trees of the same species, remain leafy during the dry season; Wright found that in a number of species periodic leaf-fall begins when the tree has reached a certain age and becomes more pronounced as the trees become older. On Klebs' view, such cases are readily explained—the young trees or young shoots are able by their more vigorous absorption and transport of water to obtain a better supply of salts. Moreover, his experiments show that in most cases the resting period can be eliminated by manuring as well as by defoliation, which on his view act by influencing the food supply.

In reviewing the two papers by Volkens and Klebs cited above, Jost (*Zeitschr. f. Bot.*, **4**, 1912, pp. 643—650) expresses the view that while Volkens has laid too much stress upon the temperature and water factors and has not taken the mineral supply into consideration, too little is known regarding the distribution of salts in the soil and in the plant at different periods to justify the acceptance of Klebs' view that, granting uniform climatic conditions, the incidence of a resting period is determined by discrepancy between organic and inorganic food supply. Jost further argues that we have no proof that such discrepancy, or deficit of mineral salts, is actually conditioned by external factors, and that the various kinds of foliar periodicity may be simply an outcome of the "specific structure" of the plants; granted that the resting period can be curtailed or even annulled by the supply of mineral salts, it does not follow that lack of mineral salts is the cause of the resting period—one might as well conclude from etherisation experiments that the resting period is due to lack of chloroform!

Without going farther into this controversy, it may be said that much of the more recent work in this branch of physiology goes to support the view put forward by Klebs. Lakon (*Zeitschr. f. Bot.*, **4**, 1912, pp. 561—582) has shown that the buds of various European trees can be made to burst into premature growth by supplying the cut twigs with Knop's culture solution. Like Klebs, this writer sees in the culture solution a stimulus which activates enzymes rendered inactive by the accumulation of reserve food substances. Whether all the other methods of forcing the growth of perennating plants by shortening the resting period are to be explained on this theory of the activation of enzymes by various stimuli (narcosis, mechanical injury, injection of water and other liquids, etc.) remains to be proved by critical experiments.

COLD AIR DRAINAGE AND PLANT DISTRIBUTION

Shreve, F. "Cold air drainage." *Plant World*, **15**, 1912, pp. 110—115.

The author has been engaged in studying the physical factors which influence the distribution of vegetation in the Santa Catalina Mountains, in south-western Arizona, and has found that important differences occur in the temperature limits of stations at similar altitudes but differing in their relations to the ridges and valleys of the mountain slopes. These differences he attributes to the fact that valleys and cañons are frequently occupied by a stream of cooled air, and he discusses the influence of the "cold air drainage" thus set up upon the distribution of the vegetation.