

found recently in a gravel pit in Pony Hollow, twelve miles southwest of Ithaca, N. Y., on the property of Mr. Bert Drake. Unlike most *Mastodon* finds from this region this is not postglacial. It was found in place twenty-four feet below the surface in stratified sand and gravel which was being used in good roads work. The pit is in the base of an extensive terrace whose top follows the valley wall high above the outwash gravel plain which occupies the floor of the valley. The exact origin of this Pleistocene terrace is obscure but it is certainly not later than the end of the ice occupation of the valley and may be earlier.

The tusk was broken in removing the gravel. Two pieces, each about a foot long, from ten to thirteen inches in circumference, were presented to the Paleontological Museum of Cornell by E. A. Dahmen, the road engineer. Three approximate measurements of the curvature of the tusk gave from two feet one inch to two feet eleven inches as the radius of curvature.

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SCIENTIFIC BOOKS

THE TRANSLOCATION OF MATERIAL IN DYING LEAVES¹

THE fact of an autumnal transfer of nutrient matter from leaves was first clearly stated by Sachs, in 1863. Sachs's statement was based on microscopical examinations of the leaves of a series of plants in various stages of their autumnal changes, whereby he determined that starch and chlorophyll disappeared from leaves before their fall. He extended this observation to cover most of the other nutrient materials in the leaf. Swart, however, holds that the solution of this question in its broader sense is to be had only by chemical analyses such as he has made.

According to Swart, the first essential to a correct answer is a correct wording of the problem, as follows:

¹ Swart, Dr. Nicolas, "Die Stoffwanderung in ablebenden Blättern," pp. 1-118, Taf. 5, Jena, Verlag von Gustav Fischer, 1914.

During the autumnal coloring of leaves can there be determined, by chemical analysis, a translocation of nutrient materials during the period extending from shortly before to directly after the close of the yellowing?

It is essential to draw the time limits thus sharply, since this period represents a sharply limited, externally recognizable terminal period in the life of the leaf, which in addition to anatomical variations in the petiole, may be directly recognized by the physiological processes which are indicated to us by the disappearance of the chlorophyll. If we would answer the question as to whether, before the fall of the leaf, there may be demonstrated a transfer of any substances, it is necessary to regard only the period during which the leaf, as indicated by these externally recognizable processes, prepares for its final act. After answering this narrower question, then we should consider the amount of these materials in the leaf at other periods of the year, in order to arrive at a causal explanation of the phenomena.

The necessary chemical analyses fall into two groups: those which extend over the entire vegetative period of the leaves, and those which cover only the period directly before and after yellowing. In most of the former investigations the leaves analyzed began to be removed from the tree at a late period, but quite independent of the exact time when the coloring began and ended. The value of the results of such analyses must, therefore, be estimated with caution since, even in most favorable cases, they can only give us an answer to the question of whether, in general, yellow leaves are poorer in their content of any given substance than green leaves of any earlier period. Thus a maximum or a minimum in the proportion of the given material in the intervening period would give results entirely misleading with reference to the question whose answer is sought.

Another objection to former researches that extend over the entire vegetative period is that very frequently a large number of leaves for study were taken at one time from the same

tree. By this act the metabolism of the remaining leaves is known to be altered. Thus, for example, the rapidity of the translocation of carbohydrates from leaves is increased with the diminution of the number of leaves on the plant; by partial defoliation transpiration from the remaining leaf surfaces is increased, and this is accompanied by a more rapid depletion of starch. The taking in of the nutrient salts is also favored by a diminution in the number of leaves.

If dead leaves are used in the analysis, another source of error is introduced, since substances may be washed out of dead leaves exposed to the weather. In former researches a yellow color has been held to indicate death, and all yellow leaves accordingly designated as dead. Swart discusses these, and other sources of error in all researches on the subject prior to Wehmer's *Kritik* of 1892. He argues with Wehmer that all results published before his paper can be relied upon to only a limited extent, but he disagrees (p. 37) with Wehmer's view that these results argue against the validity of the theory of a depletion before leaf-fall, for he knows of no case where the failure of a translocation has been demonstrated beyond doubt.

In his own researches Swart employed the method devised by Stahl, of cutting out, with a die (or a cork-borer), portions of the leaves for analysis, thus avoiding the troublesome and inaccurate measuring of the area of an entire leaf. Tabular statements of the results of several analyses are given on pages 59 to 67, the material including leaves of *Anthurium*, sp., *Liriodendron Tulipifera*, *Ginkgo biloba*, *Laserpitium latifolium*, *Paroithia persica*, *Æschylus Hippocastanum*, *Salix capræa*, *Sorbus intermedia*, *Quercus* sp., and others. These analyses show that the leaves in the brief period preceding their fall and during their coloring, had suffered a loss of nitrogen, phosphoric acid and potassium, and these losses, especially in the case of nitrogen and phosphoric acid, were quite considerable. These results confirm *in toto* those of former investigators. The slight loss of magnesia in individual cases may, in the opinion of the author,

be attributed to variations in the analyses, in consequence of the inequality of the research material. Iron remains rather constant.

It is worthy of note that calcium, silica, phosphoric acid and chlorine, materials which at other times become richer in leaves, increase only a little, or not at all. From this it may be inferred that, in general, in the last vital period of leaves, only slight additional quantities of nutrient salts are taken in from the soil. On the other hand, the two analyses of *Laserpitium* (as shown in the table, page 67), in so far as they are comparable, indicate that the composition of leaves may vary considerably in different years.

No general law or principle can be formulated from the known behavior of nitrogen, phosphoric acid and calcium. Such an inference must be based on a study of all the investigations bearing on the subject. The fact that the literature contains certain contradictions as to the behavior of calcium, serves only to indicate (in so far as the researches have been carried out with sufficient care) that the behavior of any given substance is not uniform, but varies, within wide limits, according to the plant and the external conditions.

In consideration of the rather considerable losses, especially of nitrogen and phosphoric acid, suffered by the leaves studied by Swart, he finds himself in entire agreement with the view for which Ramann and Stahl contend, namely, that the loss of substances suffered by leaves before their fall is wholly restricted to their period of yellowing. Microscopic investigations of yellowed leaves (pages 70-96) also substantiate this conclusion.

The second chapter is devoted to The Coloring of Leaves. Having demonstrated that the translocation of nutrient materials, resulting in a permanent loss of these substances from the leaves, takes place in the relatively short period of a few weeks' duration, marked externally by the loss of chlorophyll, the author now turns his attention to this period, in order to ascertain how far a study of the yellowing of leaves would lead to the same conclusions as did the chemical analyses.

The period of yellowing or of coloring in

general, in which are completed those processes which are associated with the degeneration of the leaves, varies in length (according to the species of plant) from a few days to several months. In unusually dry, or in wet cold years (*e. g.*, 1911 and 1912 in Germany), this period began several weeks earlier than normally, and was of briefer duration. Under these conditions the loss of substance which leaves suffer through autumnal translocation is notably less than under normal conditions, especially when an early night frost brings the life of the leaf to an abrupt end.

That the vascular bundles exert an influence upon the process of change of color is evidenced by the fact that the change always begins in those parts of the parenchyma that are farthest from the veins, and spreads thence by degrees, first to the smaller veins, then to the main veins, reaching the petiole last of all. As the yellow color spreads the stomata (as Stahl has shown) quite generally become closed.

Swart then asks what has become of the chlorophyll, where the yellow color has appeared, and notes that this question can not be considered to advantage, except in the light of the newer conceptions concerning the nature of chlorophyll. Then follows a review of the chlorophyll studies of Sorby, Tswett, Willstätter, Kohl, Czapek and others. According to Kohl (1902), there belong to the yellow pigments of chlorophyll, carotin and two xanthophylls, α and β . Tswett (1903) distinguished in addition to carotin, three xanthophylls, α , α_1 , β . From subsequent researches of Willstätter we have become better acquainted with two of these yellow accompaniments of chlorophyll. One is an unsatisfied carbohydrate, of the composition $C_{40}H_{56}$, identical with the carotin of carrots. The second, the xanthophyll of older authors, is an oxide of carotin, with the formula $C_{40}H_{56}O_2$. Both pigments are crystallizable. According to Willstätter, both these yellow pigments play no rôle in photosynthesis, but are concerned in respiration, and with this view Swart agrees.

Returning now to the question as to the behavior of these green and yellow pigments,

during the yellowing of the leaves, Swart rejects the hypothesis that the green ones disappear from the leaves, while the yellow ones, as such, remain behind. As to whether the chlorophyll is merely translocated as such, or whether it first undergoes a decomposition, there is no *a priori* reason for considering the first alternative as correct, while at the same time no instance is known where the colorless rhizomes of our perennial plants become green in winter. Observations of the bark of girdled branches above the girdling, as compared with the bark below the girdling, also give negative results, and so on this ground also, we may reject the hypothesis of a translocation of chlorophyll as such.

If, however, the chlorophyll suffers a disintegration, then either the disintegration products are removed from the leaf, or else they remain where formed. Stahl (1909) showed that the former is the case, and demonstrated that the separation of a leaf from the stem, or portion out of the leaf blade, caused a marked retardation of the yellowing in the leaf or isolated portion. The same result was obtained on trees in the open, in the case of leaves at the commencement of color change, by separating a part of the blade from direct connection with the vascular bundles, by a cut or simply by pinching. Swart has repeated these experiments with the same results as those obtained by Stahl. For their firmer establishment, there is needed only the application of the law of mass action. Swart, therefore, concludes, with Stahl, that the chlorophyll passes from the leaves into the stem in the form of its disintegration products.

The question of the fate of the yellow coloring matters is next considered. Kohl held that the yellow pigment that remains behind in yellowed leaves consists of carotin and also of the xanthophylls, α and β , found by him in green leaves, but that the yellow pigment of the normal green chloroplasts remains unaltered during the autumnal color changes. In direct opposition to this Tswett, by means of his adsorption method, found that, in most cases, the larger part of the yellow pigments in yellowed leaves represents a new formation,

which he provisionally designated as autumn-xanthophyll. The question as to whether it is simple or complex, Tswett did not solve. If Tswett's idea is correct, then it is highly probable that we have to do here with a derivative of the normal yellow pigment of the leaf—possibly with a further oxidation product of carotin. Swart refers to the contrast (first noted by Stahl) in the behavior of the yellow and green pigments, and the biological significance of yellowing and etiolation, showing how the yellow pigments containing the elements C, H, and O, remain in the leaf, while the green pigments, which contain also N and Mg (two elements whose retention by the plant is more important than that of the other three), are transplanted back into the plant before the death of the leaves.

Here is a lack of agreement with the results of the chemical analyses, which show that the magnesium is not removed from yellowing leaves, and a satisfactory explanation of this contradiction in favor of the results above recorded is not at hand. One may consider that the magnesium contained in chlorophyll represents only a very small part of the entire amount of that element which is present in leaves, so that, considering the variations which the results of the analyses always show, the translocation of this small part may be often not noticeable in the end result. Unless we abandon the idea of a translocation of the chlorophyll in the form of its disintegration products, we must establish the fact that the magnesium very probably takes no part in this movement.

Swart then gives attention to the changes in the cell contents of the yellowing leaves disclosed by a microscopical examination. Four different processes (to which Sachs first called attention) are studied: (1) The destruction of the outer form of the chlorophyll grains, (2) the disintegration of the green pigment, (3) the translocation of the chlorophyll substance, (4) the translocation of the starch. These processes, which may occur in any order or simultaneously, are studied and described. Contrary to Mer, Swart believes that the oil, formed by the disintegration of the chloro-

phyll, remains in the leaf at the time of leaf fall. Wide variations are noted in the behavior of the starch. In some leaves which have just begun to turn yellow, very little starch was found, while in others, quite yellow, the yellow portions were found to be full of starch. Swart confirms the observations of Mer as to the sequence of steps in the disappearance of the starch, namely, first from the parenchyma cells of the leaf blade, then from the veins of the blade, and finally from the vascular bundles of the petiole. Small traces of starch remain with the intact chloroplasts in the guard cells of the stomata. It is not strange that traces of starch remain in completely yellowed leaves, when we recall that the solution of starch is greatly inhibited by the very low temperatures which often occur suddenly in autumn, and that there is also a high content of insoluble carbohydrate, as shown by chemical analysis.

As to the behavior of the plasma itself, Swart failed to confirm the observation of Kienitz-Gerloff that only disorganized remnants of plasma are to be found in yellowed leaves. The mesophyll cells give the impression of being very poor in plasma, in comparison to the parenchyma of the vascular bundles, but the plasma utricle and the nucleus remain intact. The cells of the leaf, even after leaf-fall, are by no means dead. That a translocation of nitrogenous substance occurs (as the chemical analyses conclusively demonstrated), was also determined by the microscopical study. This may be associated with a destruction of the plasma and a transfer of the disintegration products, but Swart could find no evidence of a translocation of the plasma itself, as held by Kienitz-Gerloff.

In 1860, von Mohl showed the untenableness of Schacht's view that the death and fall of the leaf was caused by the formation of the abscission layer of periderm at the leaf-base, for in many plants this layer does not form, and in the cases where it is present the vascular bundles are not interfered with by its formation. Observations to the same effect by Tison were confirmed by Swart, who considers that there is no longer any doubt that the forma-

tion of the abscission layer does not interfere with the translocation of materials between stem and leaf, although, as Tison demonstrated, thyloses may form in the vessels, and callus in the sieve tubes, but other observed changes (lignification, cork formation and stoppage by wound-gum) take place only after the leaf has fallen.

To test Tison's statements as to the formation of thyloses and callus, Swart employed indigo-carmin, a stain that does not penetrate the protoplast, and is not poisonous (like eosin) in concentrated solution. Branches containing leaves that had begun to turn yellow, as well as green leaves, were placed in deep blue solutions in light, and the penetration of the stain followed by observing cross sections. In all cases, within a few hours or longer (varying according to the species or the length of the branch), the stain had advanced into the vascular bundles of the petiole, and even into the veins of the blades of the yellowed leaves. The stain appeared earlier in the green than in the yellow ones, although the green ones were farther away, and this may be explained by the stoppage of the stomata above described. In how far the closing of the stomata or the changes in the leaf base are to be considered as the primary cause of the diminished suction in the yellow leaves was not determined. The fact remains that any considerable stoppage of the path of liquids is not the rule. The observation that completely yellowed leaves often remain for many days in their exposed places on the tree without becoming dry, leads us to the same conclusion. The author also finds that the leptome elements of the vascular bundles are not cut off by the abscission layer, so that the transportation of substances from the leaf is not hindered in that manner. These facts meet all objections to the transportation theory based on the argument that the abscission layer, being formed before yellowing begins, prevents the passage of materials to and from the leaf.

We are accustomed in our thoughts always to associate leaf fall with a degenerative

change of color; but that leaves out of account the periodic or the continual leaf-fall outside of temperate regions, and even often in autumnal leaf-fall, where we observe, especially on certain trees, that many leaves fall when still green, or only half colored. On more careful investigation, however, these latter cases are found to be due to some unfavorable external conditions, such, for example, as frost, which may cause a rupture of the leaf by the formation, at night, in the abscission layer, of ice crystals which thaw on the following day. Other causes mentioned are storms, sudden increase of turgor in the active zone, disease of the roots or of the leaves themselves, and the leaving of collected plants for too long a time in the collecting case. Thus it is seen that plants shed their leaves, not alone when they have ceased their function as organs of nutrition, but also when the life of the plant is threatened, especially as a result of too great transpirational activity.

Mention is made of such trees as the beech, hornbeam and oak, many or most of whose leaves remain on during the winter, on account of their failure to form the abscission layer until the following spring.

The red pigment of the anthocyan group, occurring in solution in the cell-sap, and to which the autumn landscape owes its special charm, is also formed at other seasons. Its appearance before the death of the leaf is restricted to a relatively small number of species, and then it does not replace the yellow pigment, but only masks the latter. It often occurs in mature leaves when there is no outward indication of initial degeneration, such, *e. g.*, as the disintegration of chlorophyll. An active assimilation, combined with a migration of carbohydrates induced by nocturnal cold, is a *conditio sine qua non* for the accumulation of sugar in the cell-sap, which, in turn, is the antecedent condition for the formation of the red pigment. Thus it is that we have the most beautiful red colors in autumn when cold nights alternate with warm days.

There follows a brief discussion of Pick's theory that the presence of anthocyan in leaves

favors the digestion of starch and the translocation of carbohydrates, and especially that it increases the activity of the starch-digesting enzyme. Wortmann disagreed with this, but Stahl, in his researches with variegated leaves, found a satisfactory explanation of the favorable influence of the red pigment on the process of the translocation of materials. The formation of red pigment in leaves in spring and fall, and in high mountains, in summer, is associated with low temperatures which retard the translocation of the photosynthate, and thus decrease the activity of photosynthesis. Stahl's thermoelectric investigations with red-spotted leaves demonstrated an increased absorption of heat in those parts of the leaves containing anthocyan. On the basis of these results, Stahl modified Pick's thesis as follows:

In the heat-absorbing red coloring matter of leaves the plant possesses a medium for accelerating the transformation of matter and energy.

Contrary to the light-shield theory, which holds that the anthocyan is a protection against the destructive effect of a too intensive light on the chlorophyll, Stahl's theory, especially in view of the favoring of the process of translocation, has the advantage of either giving biological significance to the red pigment in autumn leaves, or of pointing the way to investigations of the metabolism in autumn-red leaves.

It remains to be proved whether the favoring influence of the red pigment on the translocation of material may actually be demonstrated by comparative chemical analyses, or, in other words, whether and in how far red leaves, under the same conditions, suffer a more thorough emptying out than do other leaves on the same plant which have not formed the red pigment. Swartz's analyses of green, yellow and red leaves of *Parottia persica*, with reference to nitrogenous contents showed that, before leaf-fall, the red leaves are more thoroughly emptied than the yellow ones.

If a leaf is dropped from the branch shortly after its color has turned (be the color either yellow, red or white) the cells still remain alive, except in a few cases where *pari passu*

with the loss of chlorophyll a brown pigment spreads over the leaf-surface. The outer appearance and also the microscopical characters indicate that the cells by no means contain merely disorganized matter, but maintain their complete vital functions until the appearance of the brown and black color, which indicates the death of the leaf. Thus, with Tswett, Swart concludes that the color change of leaves is not a postmortem decomposition, but a physiological process, and that we have to distinguish two phases in the change of color, viz., the *necrobiotic*, with its yellow, red and white tints, and the postmortem, characterized by the appearance of brown and black color.

But Swart holds that the theory of translocation does not stand and fall with the question as to whether the leaf during yellowing becomes dead or not, for, as he has shown in the investigations here recorded, the translocation of material still takes place from the portions of leaves that have already entered upon change in color. Nevertheless, Swart adds, the theory, in consideration of certain cases, must suffer a certain limitation.

A chapter on final considerations (pp. 97-117) concludes the book.

C. STUART GAGER

SPECIAL ARTICLES

ON THE ORIGIN OF THE LOESS OF SOUTHWESTERN INDIANA¹

THE gallant defenders of the grand old aqueous theory of loess deposition seem to be retreating southward, though their rear-guard vigorously contests every district yielded. Just now they seem to be crossing the Ohio River. Rumor has it that a strip on the north side of the river in southwestern Ohio is still being claimed; southwestern Indiana² has been in their undisputed possession for 10 years; and the latest publications on the geology of western Kentucky and southeastern Missouri contain such words as "the writer may state his

¹ Published by permission of the Director of the United States Geological Survey.

² *Bull. Geol. Soc. Am.*, Vol. 14, pp. 153-176 and the Patoka folio U. S. Geol. Survey.