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CONTENTS:

Abscission. By Francis E. Lloyd - - - - - - - - 61
Gall Midges as Forest Insects. By E. P. Felt - - - - - 76
Excursions - - - - - - - - - - - - - - 79

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THE OTTAWA NATURALIST

VOL. XXVIII. AUGUST-SEPTEMPER, 1914 Nos. 5 and 6.

ABSCISSION.

By Francis E. Lloyd.

(Continued from page 52)

This dependence upon external conditions is frequently illustrated by the behaviour of plants in temperate and boreal regions. The weather conditions about Montreal during October and November of the year just past (1913) were peculiar, and they were reflected in the behaviour of shrubs and trees. Many of them began to push out their spring flower buds, and in some instances (*Hydrangea*) partially opened their flowers, while the usually prompt disappearance of foliage in many trees and shrubs was much delayed. The poplars were especially noticeable, retaining their leaves even in exposed situations so that many were retained far into November, while a few still remain at the present writing. *Ampelopsis Veitchii* was also noteworthy in this respect, the conditions having been such that, in some cases, a full half or more of the leaf complement still remains adherent, though dry and dead (February, 1914). I examined these plants and found that the process of abscission had been started, but had been prevented from completion.[9] Perhaps, having been delayed by the unusual prolongation of warm weather, the abscission was overtaken by a sudden change and stopped by killing the leaves, whereas, normally, the abscission would have been completed before such intervention. It is possible that an examination of such trees as the black-jack oak, which often fails to shed its leaves, would throw light on this habit. A red beech, planted on the campus of McGill University, constantly retains its leaves, but those especially on the shorter lateral shoots. According to my late colleague, Professor Alcock, this tree shows each year an increasing

[9] Tison found that the marcescent leaves of Hamamelis differed from the normally caducous in having an incomplete abscission mechanism or it is not even initiated.

tendency in this direction. I am able to confirm this observation as regards 1912 and 1913. This last year, the plant has retained practically all its leaves except those on the outermost new shoots. It would have occasioned less surprise if the change in tendency of leaf shedding has moved in the opposite direction. I find in this plant also, that a partial abscission layer was formed.

The indefinite prolongation of green foliage in plants which show definite periodicity in temperate regions is not difficult to attain under experimental conditions. Flammarion (26) caused seedlings of *Quercus robur* to retain their leaves by transfer to a greenhouse. By removing the lower leaves from a shoot, Dingler (27) was able to postpone abscission of its upper leaves The age of the organ thus enters in as a factor. The cotton plant in the open field begins to show a decreasing activity in mid-summer, even in mid-Alabama. The exact date in 1911 at Auburn was August 14th. When kept under constantly favourable conditions, as in a greenhouse, its period may be prolonged very greatly. I have grown it for over a year, without any evidence that it could not have been kept in activity for a still longer period. The guayule, *Parthenium argentatum*, and its congeners, *P. hysterophorus*, *P. lyratum* and *P. incanum*, may be similarly controlled. The shrubby species show a periodicity related to rainfall in their natural habitat (the Chihuahuan Desert), but it was found possible in the driest part of a very dry year to stimulate the plant to renewed growth by cutting back the branches, thus showing that the moisture supply alone was the limiting factor, and when the balance between outgo and income was disturbed in favour of the latter, growth became possible. *Ampelopsis Veitchii* normally sheds tendrils only at the close of the season, but I found them being shed during dry weather from plants which spread over boulders (New York Botanical Garden, July, 1913) and were so exposed to high temperature and isolation. Such examples very much strengthen the view that the periodic phenomena of growth and leaf-fall stand in a delicate relation to the environmental factors, a disturbance in any one of which is sufficient to induce a change in behaviour. The analysis of this relation is possible only, as Klebs has said, by experimental means. We may, therefore, profitably examine this aspect of our problem, in order to see what results are at present available.

THE RELATION OF ABSCISSION TO EXTERNAL FACTORS.

The intricacy and much detail of the work which has been done, far too little as it, at present, may be, will prevent more than a rather curtailed summary, but sufficient, it is hoped, to direct attention to the chief results.

Transpiration. It has been a readily attained and rather generally accepted view that the abscission of leaves may be induced by disturbances in the water relations. The promptness with which many desert plants lose their foliage with approaching drought and their readiness to refoliation, even though stimulated thereto by such moisture as might be absorbed by their branches from rain (Lloyd, 28), as I have shown experimentally to be the case in *Fouquieria*; the dropping of leaves by houseplants on too meagre or too generous watering, both go to show that, directly or indirectly, such conditions may induce abscission. The early shedding of tendrils in *Ampelopsis*, above cited, may have been due to excessive transpiration. That merely reduction of water content of the leaf is, however, inadequate, in itself, to produce the result is shown by the fact that daily "incipient drying" and actual wilting, which we know from observation (Lloyd, 29), (Livingston and Brown, 30) to occur, is not followed by any such result. Desiring to produce abscission by reducting the water supply to organs known to be able readily to be caused to shed, I did the following experiments: A large sector (90°) of tissue was removed in a dozen cases from the stem below the insertion of the tendril in *Ampelopsis Virginiana*, and it was found impossible to induce abscission, although it will occur in cut branches in 36 or 48 hours in a moist chamber, without measureable loss of turgor, though doubtless there was some. The wounds healed, and they were later examined microscopically, and all the vascular supply to the tendrils was found to be extirpated for a distance of 5 to 10 mm. The water supply must then have passed around the wound, travelling laterally below and above it, yet either without the least prejudice to its movement or quantity, which is difficult to believe, or, if such prejudice obtained, without inducing abscission.

For some time I held the view that the peculiar anatomical relation in the flowering branch of the cotton was responsible for much of the boll-shedding. The view had been expressed that the shedding of fruit by orchard trees, said more often to occur near the ends of the branches, is due to the more favourable position of the proximal, since these are nearer the source of supplies.[10] The occurrence of the vascular tissue in an organ of limited secondary thickening (the flower-stalk) alongside that in one of unlimited secondary thickening, namely, the functionally chief axis, seemed to supply a possibility for an increasing prejudice to the water supply of the boll as growth of the whole

[10] Sorauer, P. Abwerfen der Früchte. Handbuch der Pflanzenkrankheiten.

shoot proceeds. Indeed, the much more restricted secondary thickening of the vascular tissues to the boll strengthened my belief. But experimental evidence is all against it. I removed large sectors of tissue from the axis below leaves and below bolls, in twenty cases[11] on August 19th. On the 21st one boll was shed, but the injury had been made beneath the corresponding leaf. On the 22nd one, and on the 23rd two bolls were shed, the injury having been made beneath them. After this there was no shedding till the 28th, when two more bolls fell, beneath which the operation had been done. In no case was the leaf affected, and the shedding of bolls later than August 23rd must in any event be excluded. The bolls were all small when shed, as the operations were done when the flowers were open. It can be shown that the number of losses is accountable for in other ways, and we must conclude that disturbance due to wounding is absent.

On the other hand, Balls (33), working in Egypt, was able to cause practically complete shedding of leaves, flower-buds and bolls within four days by pruning the roots, and so limiting the ability of the plant to take up water. I have repeated the experiment with positive, but less striking and perhaps not unequivocal results, in North Carolina. Cultivation, which unavoidably causes some damage to the shallower lateral roots, is believed by planters to be responsible in part for shedding. Such treatment as root-pruning is certain, if at all extensive, to cause visible wilting in an unusual amount, and too great a loss in this manner may interfere with the mechanism of abscission. It would seem that, if a reduction of water activates the process it must be when only in a small measure, such as we may suppose happens in cut branches when kept in a moist chamber, a method which was used even by von Mohl (34) in his studies. The relation is, at the present moment, a puzzling one. In the case of flowers, Hannig was unable to find any effect on the rate of abscission beyond that of ordinary laboratory air, buds, open flowers and young fruits falling away equally rapidly in both. Fitting arrived at the same conclusion, from which we may argue that the greater loss of water by evaporation, supposedly attributable to drier air, has no effect on the abscission of the corolla. This organ is, however, especially resistant, as is shown by the fact that a cotton flower-bud, removed on the evening before opening, will open and remain turgid on a laboratory table for an entire day, even though the bracts and calyx wilt and even wither. And I have observed that the petals of desert plants (*e.g.*, *Sidalcea*) remain turgid while the whole plant shows marked wilting during the hottest period of the day. The fact

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[11]Exp. 11, West Raleigh, N.C., Aug. 19th, 1913.

that abscission may occur under water (poplar, maple, horse chestnut, etc.) is, of course, to be accounted for in some other way than reduction of water.

In general, therefore, we must conclude, in view of the effects of drought upon trees and shrubs, that there is a relation between lack of water and defoliation, but it is not possible to attribute abscission directly to a reduction of water content, such as may be measured. It may, however, result indirectly by the disturbance of some other relation. As we shall see, very slight departures from the normal condition of the environment in other regards are sufficient to cause or to hasten abscission.

MECHANICAL CAUSES OF ABSCISSION.

This apparently indirect effect is further exemplified in the abscission response to mechanical stimuli. For convenience we regard as mechanical, stimuli such as shaking and wounding, though we cannot consider these as working directly.

Shaking. It is to Darwin (35) that we owe the observation that, if the flower stalk of the mullein (*Verbascum*) is sharply jarred the corollas will presently fall off. Fitting, having satisfied himself that the falling of the corolla was not due to accident or to the movement of the calyx, as held by Devaux, found by repeating Darwin's experiment, that separation was consummated in from 45 seconds to 5 minutes, but for the most part in from 1 to 3 minutes. This is equally true of young and older flowers, so that it is not due to their age. He found a similar behaviour in *Geranium pyrenaicum*, with a reaction time of from 30 seconds to 6 minutes. This phenomenon has been little studied, and only few plants are known to show it.

Wounding. The importance of the effect of wounding on abscission will at once be realized in view of the great economic losses occurring each year from the dropping of buds, flowers and fruits from the plants of our orchards and gardens, as a result of insect and other injury in the form of wounds. Young peaches, when wounded by curculio, drop. The great loss to cotton growers in Alabama, Louisiana and Texas, and the great financial disturbances accompanying it, caused by the boll-weevil, to which must be added the immense expenditures involved in scientific research in finding a way out of the difficulty, have caused a highly dramatic interest to attach to the problem. This case will serve, therefore, as a good example for the present discussion.

The boll-weevil lays its egg in a young "square" or flower bud. In from 1 to 22 days[12] the square falls to the ground, the

[12] I am indebted to the United States Bureau of Entomology, through the courtesy of Dr. L. O. Howard and Dr. W. D. Hunter, for the use of valuable data on the shedding of bolls after weevil injury.

average time being from 8 to 10 days. A very peculiar feature, but following also on other causes, occurs in squares just previous to falling, namely, an outward movement of the bracts (flaring). Sometimes, if abscission does not intervene, the bracts will move inwardly again. This movement is of very great theoretical interest, since it indicates that there is no lack of turgor (though it does not prove it), and, if this be true, an undue loss of water, it is probable, is not a factor. It is evident, from the data which are at hand, that there is some relation between the amount of injury and the time which intervenes between the first insect puncture and the final separation, since, by means of other experiments, I have found that it is possible to cause the abscission of 100 per cent. of young bolls by means of suitable injury (a transverse cut across the ovary), within 48 hours, and 90 per cent. have been shed within 24 hours in one series. "Squares" (flower-buds) are not so sensitive, shedding 35 to 55 per cent. in 36 hours; 40 to 75 per cent. in 48 hours, and the rest later.

Larger bolls respond only after a longer period, namely, in from 3 to 6 days, or not at all if too large, though they may die without becoming detached. From this we see that a point of development and induration of the tissues of the peduncle may be reached when abscission is not more possible.

Shedding of the very young bolls may also be caused by cutting off the style before pollination, but this, as Fitting found in *Geranium* and *Erodium*, depends on the absence of pollination. In *E. Manescavi*, the petals fall away much sooner after the style was injured than in the uninjured flower. Hannig also found that cutting off the petals, stamens or stigma, from unpollinated flowers, and still more readily by removing the ovary, before or after pollination, caused abscission of the whole flower. Wounding of the peduncle did not do so if a portion of the tissue was left, indicating, as I have above shown, that a reduced amount of vascular tissue was able to carry on the function of the whole.

Much has been said about the effect of the wounding of leaves by cutting off the blade, and it is generally believed that such injury causes abscission. The results thus obtained are, however, very inconstant and uncertain, as I have found in my own experience. Only a single example. I cut off the petiole (in *Ampelopsis*) from one leaf 10 mm. from the base, and allowed the next lower leaf to remain. The latter separated in 24 hours (in a moist chamber), while the stump of the cut petiole remained attached. I have done similar experiments with other species with like results, and I have observed injured leaves in nature, finding them to adhere just as long and firmly as uninjured, in many cases. We must therefor say, as Hannig has, that wounding as such does not induce abscission, but works in a round-about way.

THE EFFECT OF TEMPERATURE UPON ABSCISSION.

The occurrence of abscission at the time of the year when the cold is increasing, and the dropping of leaves in great numbers on frosty mornings, must not be thought to indicate that low temperatures cause abscission. Fitting found that *Geranium pyrenaicum* sheds its petals in a much shorter time (2.5 minutes) only when the temperature is raised to over 40° C. Lower temperatures, but yet as high as 33° to 34° were necessary, for certain other species, and in all cases the rapidity was greatest in a saturated atmosphere. Some species have their reaction time reduced from 25 seconds to 60 seconds (*Linum*, *Verbascum*, etc.). Hannig also found that temperatures higher than the normal laboratory ones caused a more abundant shedding of flowers and that sudden change was more effective than gradual. On the other hand, a lowering of temperatures inhibited it. That the higher, more effective temperatures increased the rate of abscission, and even cause them, as Wiesner (35) has suggested in the case of inner leaves, which may become over-heated does not militate against his explanation of abscission in consequence of frost, which may be procured, according to him, by the macerating (hydrolysing) effect of organic acids escaping from the frozen cells of the abscission layer or by the differences of tension produced at the limits of the dead leaf-stalk tissues and the still living and turgescent cells of the leaf-base. Entire killing of both leaf and abscission layer may be followed by the rotting away of the tissues, and thus ending in separation. High osmotic pressures, held by Wiesner and his pupils to be important in the case of ordinary abscission, have no place in frost defoliation.

THE EFFECT OF CHEMICAL AGENTS.

The air and soil of cities and in the neighbourhood of certain kinds of mills and factories is usually more or less contaminated, and, as a result, there is much detriment to the health of vegetation. Among the first symptoms to be noticed is the shedding of leaves, and this is doubtless a sensitive, and perhaps a very sensitive, indication of an abnormal condition. Harvey (36) found, for example, that one part of ethelene in 1,000,000 of air was sufficient to cause abscission of the cotyledons of the castor-oil plant (*Ricinus*), which is perhaps a more delicate reaction than would be observed in trees. It is significant, however, and we may expect to find similar behaviours in many plants. Even the small amount of illuminating gas found in the ordinary air of the laboratory was sufficient, according to Fitting, to produce abnormally quick shedding of petals, this result following dosage with carbon dioxide, tobacco smoke, chloroform, ether, and other agents. Brown and Escombe (40) found that other organs are similarly affected by disturbance of nutritive relations. Hannig got similar results, except in the case of carbon dioxide. 0.00002 vol. per cent. of illuminating gas caused the abscission of flowers (*Mirabilis*, etc.). A high concentration did not cause this directly up to 14 hours exposure, but indirectly after removal from the gas. Carbon dioxide, in concentrations up to 10 per cent., produced no effect, in accord with experiments of Demoussy (1903, 1904, see Hannig). On the other hand, leaves are shed if kept in air free of carbon dioxide (Loewi). It is evident that more work on this point, as indeed on all others, would be welcome.

Light. Light is the source of energy for green plants, so that much disturbance of this relation would be expected, indirectly at least, to lead to abnormal behaviours. It would be expected that changes in light intensity would have less effect on floral parts than on green parts, but Hannig and Fitting came to different results. Wiesner (39) believes that leaf abscission occurs in early summer in the leaves less favourably exposed to light because of the reduction of the absolute available light supply. I may observe that this kind of leaf-fall, as regards the time of occurrence, takes places whether shade is present or not. I have seen it on young plants of *Negundo*, which were completely illuminated, in which it seems more in accord with the appearances to recall Dingler's paper, earlier cited. Leaves shaded by the outermore foliage nevertheless do become yellow and fall (*Vitis*, *Ampelopsis*, *Euonymus*, etc.), and the earliest leaves in the White Birch in the autumn are those on the inner branches, irrespective of their age. In the climate of Quebec the question of high temperature is probably not important, and in such cases it seems quite proper to explain this, in the absence of more exact experimental observation, as due to the reduction of light.

THE TIME REQUIRED FOR THE ACT OF SEPARATION PROPER.

By this is meant the time occupied by the process of separation itself to the exclusion of the period required to institute it (latent period). It would seem on general grounds that when cell division is involved, the process would require more time than otherwise. In some organs (petals) in which no cell-division occurs, the evidence (Fitting) shows that it may be quite brief, less than 30 seconds indeed, but we cannot say in any case exactly what it is.

There can be no doubt, furthermore, that the age of an organ has some influence. In the small cotton boll (8 mm. diam.) no evidence of separation (following injury) can be seen at the end of 16 hours, but at 20 hours the process is practically complete, as shown by the ease of removal of the peduncle. In larger ones cell-divisions in the separation layer can be seen for a day previous. However, the act of cell-division is not necessarily a precursor of separation, since in the young bolls above mentioned no cell divisions are to be seen at the moment of separation of the cells concerned, there being only a slight elongation of them, accompanied by a chemical alteration of the cell walls, causing the loosening. The essential phase of the process of abscission may, even in older as well as younger cotton bolls, be of much shorter duration than above indicated, less, namely, than four hours.

With reference to petals, Fitting found that in the dark, at temperatures of 31°-32°, they are shed earlier than normally, and the older the more quickly. On the other hand, petals of younger flowers were found by Fitting to be less sensitive than older, an apparent reversal of things which may be regarded as a "phenomenon of interference," between increasing adaptability and shortening of reaction time.[13] In petals, however, there is no development of mechanical elements, such as quickly appear in many leaves, to increase the amount of preparation before separation may become effective. Early in the season I have observed that abscission (in a moist chamber) will overtake older leaves frequently more rapidly than younger. The slowness of separation in indurated organs may simply mean interference by tissues or mechanical elements in which separation takes place only passively or not at all, as, *e.g.*, in the non-living or moribund pith in older cotton peduncles.

THE MECHANISMS OF ABSCISSION.

By "mechanism" is meant that histological behaviour resulting in the separation of one organ, or a part of it, from another organ or part. To the best of our present understanding it may be purely mechanical, either by a break (a) passing directly across the tissue irrespective of the position of the cell wall (rhexolysis, according to Correns 1, 372, *e.g.*, *Dicranum scoparium*), or (b) passing along the middle lamella, causing separation of entire cells (schizolysis, Correns). In the latter alternative the separation is believed by some to result from a marked increase in turgor, the pressures causing the cells to

[13]The character of the behaviour of petals under various stimulants has led Fitting to insist on a conception of abscission as an active separation of an entirely living organ in response to stimulation, quite analogous to movements, etc. He proposes the term "chorism" for this phenomenon.

become spherical and thus reducing their contact surfaces to nearly nil (Loewi, Fitting, Hannig). Or it may be a result of chemical alteration (a) of a part or (b) of the whole of the cell wall. The middle lamella may be dissolved, in this way loosening the secondary walls from each other; or the whole or part of the secondary membrane may be altered (Tison). Such chemical alteration may or may not be preceded by cell-division in the cells directly involved. Even in species in which this usually takes place, it may be omitted (Tison, Loewi) either entirely or in a part of the separation layer, as I have myself observed. When cell-division does occur, it is an expression of a resumption of growth (secondary meristem of previous authors), but as cell growth obviously does not necessarily lead to cell-division, this may be absent. The amount of growth may vary with external conditions, and it is usually much more marked under water or when high relative humidity prevails, and may lead to callus hypertrophy (Kuster, 40, p. 289). And in species where growth is usually omitted (*e.g.*, *Ampelopsis*, *Impatiens*) cell-division accompanying separation is still occasionally observable.

Rhexolysis, while frequent in the mosses, is, so far as I know, generally quite rare, and its precise nature and the causes leading up to it need investigation. Tison believes it to occur in *Aristolochia Sipho* (leaf), but Loewi questions the accuracy of Tison's observations, basing his criticism on the similarity of Tison's description and drawings to appearances seen by him (*Laurus*, etc.), and leading to separation by the joint action of chemical alteration in the cell-wall and turgor. In view of my own work, Loewi's criticism is justified.

An apparently true case of rhexolysis, however, occurs in the style of *Gossypium*. Several minute transverse fissures appear at different levels somewhat above the apex of the ovary. These deepen and gape. Microscopically, they are seen to pass transversely through the tissues without relation to the position of the cell-walls, and without any evidence of separation of entire cells. The protoplasts, with their inclusions, are found *in situ* and the protoplasm torn through. Experiments indicate that external mechanical relations (pull or pressure of the staminal tube) are not factors. The fissures are not to be discovered before the latter half of the second day of anthesis.

Schizolysis is, on the other hand, general, but presents widely divergent appearances. The simplest cases (primary meristem) are those in which, by the solution of the primary membrane (middle lamella), the involved cells—usually occupying an ill-defined and irregular zone—can fall apart. Loewi, assigning to alteration of the membranes a very minor rôle, believes that separation, as exemplified in *Ampelopsis*, is accomplished chiefly by turgor increase, the greater surface curvatures reducing the contact areas and so setting the cells free. Kubart ascribes to chemical alteration a larger share in the process, still attributing, however, the chief place to turgor, *e.g.*, *Syringa*. Fitting excludes such alteration in the case of petals studied by him and sees, in a general sudden increase in volume of the cells, the active cause. I find in *Ampelopsis* and in *Impatiens* positive evidence against Loewi's view of the matter, separation not being found to involve any change in the shape of the cells, while evidence of chemical alteration, involving both primary and secondary membranes, has been clearly seen. Similarly, abscission of the corolla in *Gossypium* is without doubt accompanied by a decrease in turgor, being otherwise similar in operation to *Ampelopsis* (leaf, tendril, internode). But in this form the primary membrane dissolves first, and this is not preceded, at any rate to an appreciable extent, by alteration of the secondary membrane. Hannig's explanation of the process in *Salvia*, etc., and Kubart's in part of that in *Nicotiana* accord with my own, the latter finding in the organic acid released from the cells involved the agent of dissolution.

Different are, *e.g.*, *Lonicera*, *Syringa*, *Hydrangea*, and a number of others, chiefly, however, in that the secondary membranes are also attached, but more vigorously, and showing marked and measureable swelling. The collenchyma behaves peculiarly—the thickened walls resisting attack and lying free in the mucilaginous matrix. Aside from the last mentioned observation[14] Tison recognizes, in essence, this type of abscission. Kubart would designate it as "maceration."

Finally, abscission may be accompanied by growth, usually longitudinal, but, as regards the axis of the organ, may be more or less oblique. The growth (under special conditions very limited in amount) may or may not be accompanied by cell divisions, the occurrence of which has impelled earlier observers to regard the separation tissue as a secondary meristem. Before growth sets in, however, the cell walls are altered chemically (but only slightly) often in a restricted transverse zone about the cell, and the elongation of the wall takes place here (Loewi). But this chemical alteration may not be so restricted, but may rather be very general, as in the collenchymatic region of the leaf of *Populus* and of *Euonymus*, producing a condition directly comparable with that in the leaf of *Lonicera*, above cited, so that we may agree with Loewi in saying that there is no sharp line of demarkation to be drawn between these processes, the one

[14]Hannig (12, p. 428) appears not to have observed this peculiar behaviour, and no one else, so far as I can determine, has done so.

being supplanted by the other even in the same organ. Thus, in *Gossypium* (the flower-peduncle), normally one to three divisions occur, previous to separation, but they may be quite absent in the peripheral tissues; and when rapid abscission follows a suitable stimulus, none at all are to be observed.

The cells of the abscission layer may separate from their secondary walls at their distal extremities, and, in addition, the outer daughter cells may separate also from each other, one clinging to the distal rejected wall, but from which it is usually free, and one (or more) remaining permanently incorporated with the proximal wall. The separation in younger or thin-walled tissues may follow the plane of the middle lamella, but more frequently it occurs between a very thin innermost membrane (*i.e.*, that which immediately surrounds the lumen) and the earlier formed secondary membranes; or this membrane may have been laid down anew, during growth, against, but not incorporated with, the earlier formed secondary membranes. The evidence favours the former alternative; but this I cannot at present decide.

The crux of the problem of abscission lies in the manner of separation. It is conceivable that the mere increase of turgor is sufficient to cause separation along the place of the middle lamella. The smaller the cells, the more efficient can the energy at the disposal of the cell be applied; and small cells are found to characterize the abscission layer in many cases. Fitting favours this view in the light of the rapidity of reaction which, he believes, allows too short a time for swelling of the membranes, and because he could not see any such change in them. Renewed growth in these and increased turgor he regards as the responsible factors. (Fitting 21, p. 244-5). Strasburger (41), Tison (except in cases of rhexolysis) Lee (42) and others have taken a quite different position, seeing in the chemical alteration of the membranes a factor of primary importance. Tison calls the product of this change a pecto-cellulosic mucilage. The membrane lining the cell lumen does not take part in this. Growth contributes a relatively small part to the process. Hannig, too, takes the same position, except in the case of the peduncle of *Mirabilis*, in which occurs what he considers to be an undescribed method—a lysigenous one, involving the total destruction of the membranes. The appearances seen by him could, I believe, be reconciled with a method already known. This will, however, be discussed elsewhere.

Between these extreme views lie those of Wiesner, Kubart and Loewi, who, without denying a rôle to chemical alteration (by the excretion of organic acids, or perhaps enzymes), see in turgor changes the more important factor. They believe, indeed, that in some instances chemical change is absent.

The study of about 30 odd species leads me to the conclusion that chemical change is always present to some extent whether growth and turgor changes intervene or not. I found that under the influence of a hydrolysing agent (5% KOH) the walls of the abscission cells break down more readily than those of the neighbouring tissues above and below (*Cheiranthus*), and may be so treated as to stimulate advanced autolysis, both in the swollen condition of their walls and in their behaviour toward stains.

Concerning turgor effects it may be said that in such forms as *Ampelopsis* and *Impatiens*, which present ideal material for study, the abscission cells show a no higher osmotic equivalent at the time of abscission (of floral parts, peduncles, leaves) than others. In the case of the axis, the cells of the cortex and epidermis are pulled apart, apparently by elongation of the central tissues, since in partially wilted peduncles the faces of the abscission-wound remain juxtaposed, although abscission actually takes place.

Before, during or after abscission, secondary changes in neighbouring tissues take place. They consist of suberization, sclerification and lignification in various degrees, and all are either extensions of periderm or are of the nature of wound responses. This phase of the subject, beyond this very general statement, lies beyond the present purpose. Numerous details have been worked out by Tison and by Lee. It is, however, pertinent to indicate that, on the abscission of decurrent peduncles in *Gossypium* there may follow an extensive sacrifice of tissues, including all the living element of the stem, resulting in the formation of a wound-cavity of sometimes large extent, and not unlike gum pockets in appearance. Some of these phenomena recall the abnormal behaviours seen by Loewi, which, however, may readily occur in other species* (Ash, Poplar, etc.) under special conditions.

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DEPARTMENT OF BOTANY,

McGILL UNIVERSITY.

GALL MIDGES AS FOREST INSECTS.

By E. P. FELT, Albany, N.Y.

The minute gall midges or Itonididae have been practically ignored by the forester and, taken as a group, little is known of their economic importance under average woodland conditions. The larger, frequently abundant deformations produced by the gall-making wasps, Cynipidae, and the sawflies, Tenthredinidae, are relatively much better known, though it is probable that they are of less economic importance.

Numerous gall midges, referable to the Lestreminae and Heteropezinae, live as larvae in decaying woody tissues and materially hasten the process of disintegration. Species of *Miastor* and *Oligarces* inhabit the inner bark of various trees in incipient stages of decay, while some species of *Monardia*, such as *M. lignivora* Felt have been reared from the fungous affected heart-wood of pine and undoubtedly hasten decay. Some Epidosariae inhabit dead, mostly dry, woody tissues.

All of the foregoing species are of less importance than the gall-making forms infesting living trees. The deformations of the latter may be conveniently classified according to the part affected.

Seed of fruit-inhabiting midges, such as *Dasyneura canadensis* Felt, may destroy a considerable proportion of seed in spruce cones. The same is true of *Oligotrophus betulae* Winn. and birch seed, while *Itonida catalpae* Comst. infests Catalpa pods and is a pest of some importance. Whitish, flower-shaped, fungoid galls, probably a bud and possibly a fruit deformation, are numerous in some parts of the South on Bald Cypress, *Taxodium distichum*, and are caused by *Itonida anthici* Felt. The extent to which fruit infestation may go in this group is shown by the rearing of seven species from the fruit of various wild cherries.

Bud galls are produced by many species and usually mean the death of the affected part, or at least a resultant deformation. The Catalpa midge, mentioned above, not only infests the seed pods but destroys the greenish tips and produces stunted, comparatively worthless trees. *Phytophaga ulmi* Beutm. and *Dasyneura ulmea* Felt infest lateral and terminal buds of elm sprouts and occur somewhat abundantly, though their injuries have not as yet been considered of much practical importance. The Box Elder in the West suffers from the attack of two gall midges, namely, *Cecidomyia negundinis* Gill., a bud-inhabiting form, and *Contarinia negundifolia* Felt, a species which attacks the leaves while still within the bud. *Contarinia coloradensis* Felt infests and destroys the terminal buds of *Pinus scopulorum* in Colorado and occasionally appears to be somewhat abundant. Spruce buds are destroyed in Canada and probably in the Adirondacks by *Phytophaga tsugae* Felt and the terminal ones in part by *Rhabdophaga swanei* n. sp.

RHABDOPHAGA SWAINEI n. sp.

The midges described below were reared by Mr. J. M. Swaine, Ottawa, Canada, the latter part of May, 1914, from spruce bud galls. This species apparently confines its attack to the terminal bud. It is easily differentiated from other known species of *Rhabdophaga* by the characters given below.

Gall. The enlarged bud has a length of about 7 mm. and a diameter of 4 mm., the lateral scales being somewhat reflexed and the apical portion of the gall loose and open. It contains a central, oval cell about 1.5 mm. long.

Male.—Length 2.25 mm. Antennae probably nearly as long as the body, dark reddish brown, presumably with 14, and possibly with more, segments, the fifth with a stem about ½ the length of the basal enlargement, which latter has a length 2½ times its diameter. Palpi: first segment ovoid, the second ½ longer than the first, moderately stout, the third ½ longer than the second, more slender, the fourth ⅓ longer than the third, slender. Mesonotum shining dark brown, the submedian lines sparsely gray-haired. Scutellum, postscutellum and abdomen dark brown, the latter sparsely haired. Genitalia reddish brown. Halteres, coxae and femora basally reddish brown, the distal portion of femora, tibiae and tarsi mostly dark brown; claws moderately stout, curved, minutely unidentate, the pulvilli ½ longer than the claws. Genitalia: basal clasp segment moderately stout; terminal clasp segment rather short, swollen near the middle; dorsal plate deeply and triangularly emarginate, the lobes divergent, the outer margin tapering roundly to a narrowly rounded setose apex; ventral plate rather long, broad, deeply and roundly emarginate, the lobes short, stout, sparsely setose. Harpes broad, broadly rounded and thickly setose apically; style short, tapering, narrowly rounded distally.

Female.—Length 2.25 mm. Antennae probably extending to the second abdominal segment, sparsely haired, light brown. Mesonotum dull dark brown, the submedian lines sparsely fuscous haired. Scutellum dark brown, postscutellum a variable yellowish and dark brown. Abdomen dark brown, the margins and ovipositor reddish orange, the venter reddish brown. Halteres yellowish orange. Coxae yellowish brown; femora and tibiae dark yellowish brown, the tarsi darker, almost black. Ovipositor moderately stout, as long as the body; terminal lobes broad, the length thrice the width and thickly setose. Other characters practically as in the male. Type Cecid a2520.

LEAF GALLS. The primary infestation, as we have shown elsewhere, frequently begins in the bud. Deformations belonging in this class are not very important, though *Thecodiplosis liriodendri* O. S. is responsible for serious disfiguration, and probably some weakening of tulip leaves, particularly in the latitude of North Carolina. The recently established box leaf miner, *Monarthropalpus buxi* Lab. of Europe, appears to be a serious pest of the highly prized ornamental Box. The young leaves of the Black Locust, *Robinia*, may be seriously deformed by the larvae of *Dasyneura pseudacaciae* Fitch, or the margins rolled by those of *Obolodiplosis robiniae* Hald. *Contarinia canadensis* Felt, the probable producer of the midrib gall on ash, is so abundant locally in the Hudson valley as to seriously affect the foliage of saplings. The extent to which leaf infestation may go is shown by the fact that some 22 species of gall midges are known to infest the leaves of hickory and about 20 those of oak. Most of these, as well as numerous other leaf-inhabiting forms, are of comparatively little importance.

STEM GALLS. Irregular, subcortical galls are produced in living tissues by species of *Rhabdophaga* and *Lasioptera*, the former being confined mostly to willow. The European *Rhabdophaga salicis* Schr. has become established in some localities where basket willows are grown and causes considerable loss by ruining the shoots for both basket work and the binding of bundles of nursery trees. Willow twigs are attacked by 21 American species of gall midges. *Lasioptera querciperda* Felt lives in the subcortical tissues of white oak twigs, producing gnarly areas and, presumably, defects in the wood. Several species of *Itonida*, *I. resinicola* O. S. and *I. resinicoloides* Wlms. attack the inner bark of young pines, and in some instances considerable pitch exudes and rather serious injury may result in the case of individual trees. *Itonida inopis* O. S. is a subcortical form, the larvae producing a swollen, gouty condition of the twigs and a marked lowering in the vigor of badly infested trees.

Root galls are known in only a very few cases, probably because of the difficulty of discovering them, and, so far as forest trees are concerned, none of importance have been recorded.

A general survey of the gall midges known to infest forest trees, shows that the hickories, the oaks and the willows, and to a less extent the poplars, all representing genera with a number of closely allied species, are subject to attack by numerous gall midges, indicating an extremely close relation between the infested plant and the insect dependent thereupon. The bud-inhabiting gall midges are potentially the most destructive, and, owing to the known prolificacy of certain gall midges, it is to be expected that injuries by species referable to this group will become more, rather than less, apparent with the advance of time.

EXCURSIONS.

The second excursion of the season was held on the afternoon of Saturday, May 9th, the locality visited being the north shore of the Ottawa River above the Chaudiere Falls. The rock formations were rich in fossils; the trees and general vegetation, at this season, were assuming their spring verdure, and the pools by the banks of the river contained a variety of forms of life. A large attendance of members was present and much interesting material was examined and collected. The President, Mr. Arthur Gibson, was in charge of the party. At the close of the outing addresses were delivered at the side of a grassy knoll close to the river, and the first leader called upon to speak was Mr. Halkett, of the zoological branch. Specimens of two kinds of small crustaceans—one an amphipod (*Gammarus*) and the other an isopod (*Asellus aquaticus*), as well as several kinds of fresh water pulmonate gastropod mollusks were passed around and points explained regarding their life-habits.

Miss Fyles spoke of the plants which had been observed or collected. Several specimens of *Geaster hygrometricus* were found. It was pointed out that the Geasters were distinguished from the puffballs by the outer coat, which breaks and spreads out in the form of a star, whence the name Earth-star. This odd and interesting fungus is very sensitive of moisture, spreading out its star-like coat in wet weather and folding in its points when the atmosphere is dry. Miss Fyles also gave an interesting account of the life-history of the Horse-tails (*Equisetum* spp.)and of many other plants which were handed to her to name.

A very interesting account of the herbs used by the Iroquois medicine men was given by Mr. Waugh, a leader of the archæological branch, the substance of which he has since supplied in manuscript notes, which, given in his own words, are as follows:—

"A large number of animal and vegetable materials are used in the Iroquois medicines. Although many of the herbal or vegetable preparations are most effective from a therapeutic standpoint, a great deal of reliance is placed in sympathetic magic or the idea that like cures like. For instance, bloodroot is used to purify the blood because the juice is red. This idea is at the bottom of a large percentage of Iroquois remedies. A decoction of stoneroot is given to children in the belief that it will make them hardy. Quite a number of effective laxatives and emetics are known where barks are used. These are scraped up or down according to the action required. Among the laxatives are mandrake root, also a decoction of butternut bark. A hunting medicine is made of the early leaves of *Prenanthes* or lion's foot, from a fancied resemblance of these to the heads of a buck and a doe. A decoction is made and the rifle-barrel washed with it inside and out. The small spherical bulb found attached to the dwarf ginseng is crushed and tied to fishing tackle to give luck in fishing. A selling medicine is obtained by chewing a small wood anemone (*Anemone quinquefolia*) and rubbing the juice on the hands when about to offer anything for sale. The person to whom the articles are offered will not be able to resist buying. A medicine to give speed in running is derived from the toad rush (*Juncus bufonius*). A decoction is made and the body and limbs washed with it, the idea being that, as the plant grows beside the runner's pathway, it will assist him in running. Love medicines are very common. Every native medical practitioner has several. These are also usually based on sympathetic magic. For instance, two leaves of *Aster cordifolia*, which lean one upon the other, are taken, and a decoction made and rubbed upon the face and hands. A remedy for snake-bite is obtained by finding a root of the white ash which sticks up like a snake's head. This must be kicked off with the foot. A decoction is made of this and applied to the bite. Among the most important medicines are a couple of secret preparations belonging to medical societies. These are found to consist largely of a number of fanciful or mythical ingredients. These medicines are considered the most effective of any and their administration is connected with a series of ceremonies."

The next speaker, Dr. Williams, spoke of the birds, observed, viz.—the herring gull, the spotted sandpiper, the ruffed grouse, the northern flicker, the American crow, and the tree swallow.

This last-mentioned useful little bird is very common in the vicinity of Ottawa this spring, and it is to be hoped that some may take possession of the nesting boxes either at Rockcliffe or at the Experimental Farm.

In addition to the above, brief addresses were also delivered by the President and the Rev. Seymour Bullock.

A.H.

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