Contributions to the Knowledge of Abscission and Exfoliation of Floral Organs.

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Contents.

I. Introduction.

With regard to the abscission of floral organs, Gärtner, at an early date (1844), made a number of important statements. He made observations on the duration of the corolla and claimed that the pollinated flowers cast their corollas earlier than the unpollinated ones, and he used, to express the duration of the latter, the term

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"absolute duration" (absolute Dauer). The falling and abortion of flowers or young fruits were observed, and he enumerated the following causes as responsible for them : 1. Deficiency of nutriment and water. 2. Injury and diseases of terminations of the finer roots. 3. Lack of sufficient heat during fertilization or during the further development of ovary and seed. 4. Deficiency of light, or changing incidence of the ray of light. The latter has an influence specially on some susceptible plants, when the situation is changed. 5. Injury to the stigma or ovary, immediately before or after fertilization. 6. Prevention of fertilization. 7. Imperfection of pollen. 8. Sterility of female organ.

Some noteworthy studies have been made by MOHL (1860) on the anatomical changes in the leaf-base, in which the separation of tissue occurs. He traced the process of the separation-phenomenon and proposed the expression "separation-layer" (Trennungsschicht) for the special tissue which is situated at the base of the leaf or other organ and consists of secondary meristem. The abscission of an organ is brought about by the separation of cells in this layer. In the case of the leaf, he held the opinion that the formation of the separation-layer depended not only upon the age of the leaf but also upon the environment, above all the climatic conditions. Actually he observed that the abscission of young leaves of several trees could be induced under certain experimental conditions, and that the mode of separation was the same as that normally occurring in autumn. In the case of abscission of the shoot in *Gymnocladus*, *Catalpa*, *Gleditschia*, *Tilia*, *Ailanthus* and *Phyllocladus*, he observed also the same separation-layer of secondary meristem. He stated further that, in the flowers with an incomplete pistil of *Aesculus* and *Pavia* the flower-stalk abscisses from the pseudo-axis of the cyme, and the pseudo-axis separates from the main axis of the inflorescence, and later, also the majority of the more or less developed fruits separates at the articulation, which is present in the fruit-stalk. In a similar way, the male flower of the *Cucurbitaceae* abscisses at the separation-layer which is formed at the top of the flower-stalk. Flowers of *Ricinus communis* separate at the joint formed near the base of the stalk. He indicated also that even the hermaphrodite flowers such as *Hemerocallis flava* and *fulva* fell, if the fruit did not develop. He described the abscission, by means of a separation-layers, of other floral organs giving the following cases :

Sepals. *Papaver somniferum, Liriodendron Tulipifera, Mirabilis Jalapa, Datura Stramonium.*

Corolla. *Rosa canina, Papaver somniferum, Glaucium luteum, Liriodendron, Lonicera Caprifolium, Rhododendron ponticum, Datura Stramonium.*

Stamens. *Lilium bulbiferum, L. Martagon, Dictamnus Fraxinella, Liriodendron.*

Styles. *Lonicera Caprifolium, Mirabilis Jalapa, Lilium Martagon.*

REICHE (1885) investigated the anatomical changes in the perianth during the development of the fruit in the case of forty five families including dicotyledonous and monocotyledonous plants. In conclusion, he gave three modes of defloration which is brought about 1. by the separation of cells in the separation-layer formed at the insertion of the perianth, 2. by withering and disorganization under the influences of atmospheric conditions, and 3. by the mechanical splitting of perianth due to swelling of the fruit. It was remarked that the modes 1 and 3, or 2 and 3 might occur combined together.

HÖHNEL (1878) noticed, when studying the shedding of shoots and twigs of forest trees, that the separation-layer was formed at the base of the catkin-stalk of *Populus* and *Salix.*

MÜLLER-THURGAU (1883, 1908) observed the shedding of flowers in the grape-vine and ascribed it mainly to the climatic conditions and too vigorous vegetative growth.

According to BROWN and ESCOMBE (1902) *Cucurbita, Impatiens, Nicotiana, Fuchsia* and *Begonia* throw off their flower-buds in air containing 0.114 per cent of carbon dioxide.

KUBART (1906) studied the falling of the corolla and classified the separation-layer into the following types : (a) tissue derived from primary meristem and remaining still in an active state ; (b) the secondary meristem ; (c) the primary meristem which remains in the separation-zone. He was of the opinion that the separation of the tissue was brought about by the dissolution of the middle lamella under the action of an organic acid. Connected with this, the increase of cell-turgor in the separation-layer was believed to be a participating factor.

BEQUEREL (1907) reported with regard to the tobacco-plant that the flower, in which the corolla, stamens or style were injured, fell off at the separation-layer, which is formed in the stalk and consists of small cells.

FITTING (1911) reported the sudden fall of petals of *Geranium* induced by different causes such as narcotic vapours, mechanical injuries to the floral organs or sudden rise in temperature etc. He thought that such a sudden separation which was completed in 25–60 seconds after the beginning of exposure to abnormal environment might not be brought about by the dissolution of the middle lamella, but by the sudden increase of turgor and rapid growth of the separation cells. Actually he never observed any sign of swelling of the middle lamellae in this case. And he claimed that the chain of reactions, between the first subjection to the abnormal external conditions and the final physico-chemical process of separation, must be conceived as an irritation phenomenon. He named this type of reaction aitionomic chorism. According to the causes, he classified it into chemo-chorism, thermo-chorism, seismo-chorism and traumato-chorism.

HANNIG (1913) noticed the shedding of floral organs in laboratory air in the case of several species belonging to the following families: *Liliaceae, Nyctaginaceae, Papilionaceae, Begoniaceae, Lythraceae, Oenotheraceae, Labiatae, Solanaceae* and *Caprifoliaceae.* He observed also the shedding of flowers induced by illuminating gas, tobacco-smoke, sudden rise in temperature and mechanical injury to floral organs, and in his conclusions, he agreed with the chorism theory of FITTING. He suggested generally that the abscission of the male, unisexual flower after anthesis might be termed autonomic chorism.

LLOYD (1914a, 1914b, 1916a, 1916b, 1920a, 1920b) described the anatomical changes in detail during the separation of flowers, fruits, buds etc. in species of *Gossypium, Mirabilis, Juglans, Vitis* and *Ampelopsis.* In the case of *Gossypium,* he (1916b, 1920b) stated that high atmospheric temperature and deficiency of water in the soil were the causes responsible for the shedding of the bolls. Regarding the young fruits of *Juglans* he (1920a) expressed the opinion that the abscission was brought about by the repeated too great water deficit in the tissue of growing fruits resulting in competition among them.

From the horticultural standpoint, HEINICKE (1917) studied the factors influencing the abscission of flowers and young fruits of the apple, and noted that the abscission occurred abundantly in the less vigorous spurs, being affected by insufficient supply of water and nutriment to the developing fruits.

KENDALL (1918) reported that the separation-layer in the pedicel of most of the *Solanaceae* agrees with the first type of KUBART. The only exception was *Datura*, in which no visible difference between the separation-layer and other parts of the pedicel could be found previous to abscission. According to him, the separation of cells in *Solanaceae* is accomplished by the hydrolysis and consequent dissolution of the primary cell-membrane or perhaps of both the primary and secondary cell-membranes. He observed an expansion and turgid appearance in the separating cells and conceived that this might be the result of a natural release of pressure caused by the isolation of the cells. In the case of artificially injured flowers or fruits, he noticed that the length of the reaction-time depends more on the age of the flower than on the type of injury, and he thought that the cell-walls must gradually become less subject to hydrolysis with age.

With regard to the premature shedding of *Citrus*-fruits, COIT and HODGSON (1919) stated that the separation was brought about by hydrolytic dissolution of the middle lamellae in the separation-layer, which is at the base of pedicel. They were of opinion that the abundant shedding of young fruits was mainly induced by deficiency of water in the soil.

In the case of premature falling of the apple, the writer (1922) indicated the presence of a preformed separation-zone at the base of the pedicel. According to him the nature of the separation-layer can alter with the age of the pedicel from one type to another. And he cited a similar occurrence in the pedicel of *Lycopersicum*. He observed a sudden accumulation of starch grains, reducing sugar and oil droplets, as well as the rapid increase of osmotic pressure in the separation-cells immediately before the abscission. At that time the osmotic pressure in the flesh of detaching fruit was much lower than that of sound fruit which would not fall till much later. The number of the seeds in the abscissed fruit was always smaller than that of those remaining.

It is intended in this paper to deal with some less investigated problems concerning the abscission and the exfoliation of floral organs. The term exfoliation is to be understood as implying the falling of a certain organ, being preceded by the drying and death of it, and accomplished by mechanical rupture of the dead tissue. So the actual amputation is not directly brought about by living phenomena, but owing the latter a physiological barrier between the

living parent-body and the organ to be thrown off has been constructed. Abscission means on the other hand the amputation of an organ by means of isolation of living cells in a special separation-layer, usually predetermined in a certain part of the organ. Abscission and exfoliation occur often in different organs of one species, and in the same organs of different species closely related. Be that as it may, the type of the defoliation of a given floral organ is nearly constant in a given species. Observations have been made on the anatomical changes before and during the defoliation of floral organs.

The predestinated falling of male unisexual flowers after anthesis is also a problem to be studied. As material for this study, the catkin has been preferred, simply because it is easily obtainable. An anatomical study was made of the male catkin and also, to some extent, of the female catkin for purposes of comparison.

The corollas or perigones show, in spite of their belonging to the same category as foliage leaves (phyllomes), quite different structures and functions. The carbon assimilation is nearly lacking in these organs. Consequently the metabolic changes are far simpler in petals or perigones than in foliage leaves. And these organs absciss or defoliate usually after a relatively short duration of bloom. For this reason, it will be worth attempting to trace some of the physiological changes which precede the abscission or exfoliation of these organs, and to compare the results with those of other writers concerning foliage leaves.

A part of this work has been carried out at the Botanical Institute of Hokkaido Imperial University in Sapporo, Japan, and in part at the Jadrell Laboratory of the Royal Botanic Garden, Kew. Here I hope to express my heartiest thanks to Prof. K. Koriba for his kind direction. And, I am under obligations to the Director of the Royal Botanic Gardens, Kew, for permission to work in the Jadrell Laboratory, and to Mr. L. A. Boodle, who has during my stay in the Jadrell Laboratory given me many valuable suggestions and kind help in several ways.

II. Abscission of Catkins.

1. Alnus japonica.

Alnus japonica is the tree which blooms earliest in the vicinity of Sapporo. Early in April, when the ground is still partially

snowclad, catkins of this tree commence their anthesis. The bloom lasts for about two weeks. The shedding of male catkins occurs usually at the middle of April. In the grounds of Hokkaido Imperial University in 1921 the falling of the male catkins took place from the 9th to the 20th of April continuously, and the majority of them were shed about the 13th.

The inflorescence of the tree is already formed at the top of the shoot before winter. Each ramified branch of the first order bears an amentum. A flower-branch bears 2–6 male catkins on its upper portion, and 1–3 female ones near the base. As is usual in anemophilous plants the number of male catkins always exceeds that of the female ones, and in some flower branches, the latter may often be lacking. After the majority of the anthers in a catkin have burst and withered, the abscission of the catkin follows, being brought about by separation in a layer of tissue at the base of the catkin-stalk.

Some of the amenta, however, which are situated at or near the top, may not be shed. Then, the separation of the main axis takes place in a plane just above the insertion of the uppermost female catkin (Fig. 1). As the result of this separation, the flower branch falls with one to two male catkins still attached to it. When the female is lacking the flower-branch concerned separates at its base. Naturally the female catkin does not fall in normal conditions.

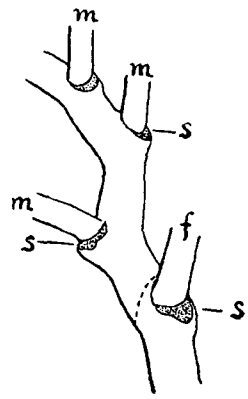

Fig. 1. *Alnus japonica*. A part of the flower-branch. *f*, stalk of the female catkin; *m*, stalk of the male catkin; *s*, scar of the bract. The broken line represents the plane in which the separation takes place. ca. 2/1.

A separation-zone is differentiated at the base of the flower branch and at the insertion of the stalk of each male and female catkin. The differentiated tissue consists of 10–20 tiers of cells. The size of the cells is conspicuously small and the intercellular spaces occur very sparsely in this zone. The cells have rich plasmatic contents and the cell-wall has a more or less thickened appearance. Such a tissue makes up a hollow bowl-shaped layer across the axis (Fig. 2). As the result of the small dimensions of the cells in this zone, a constriction or groove is occasioned on the surface around the zone. The outermost 6–10 tiers of cells in the bottom of this groove, are more or less flattened

parallel to the surface. These cells show the smallest dimensions (5–12) × (20–30)μ among the separation-zone. The cells in the inner cortex and medulla of the zone are generally isodiametric and measure 13–30μ in diameter. On the other hand, the cells of the cortex or medulla above the separation-zone are 20–40μ in diameter. The constriction of the central cylinder at the separation-zone is rather slight. It is evident, therefore, that the formation of the constriction is mainly due to the suppressed growth of the cells in the cortex of this zone. The parenchymatous elements in the vascular bundle show, in this zone, a slight diminution of dimensions in every direction. At every node of the flower-branch a

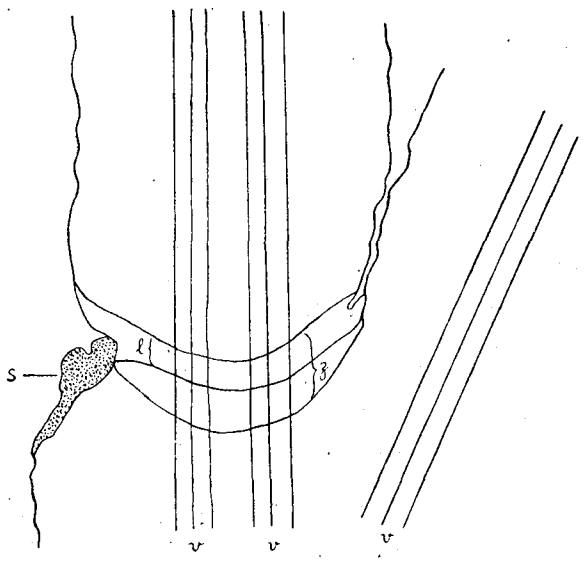

Fig. 2. *Alnus japonica.* Separation-zone at the base of a catkin-stalk. *z*, separation-zone ; 1, separation-layer ; *s*, scar of the bract ; *v*, vascular bundle. ca. 25/1.

slightly differentiated separation-zone is developed across the axis immediately above the insertion of the catkin-stalk. The cells of this layer are a little smaller than the neighbouring tissue, but the superficial constriction is not distinct.

Throughout the whole flower-branch and catkin-stalk the mechanical cells are remarkably reduced. The bast fibres are completely lacking in the axis of the male catkins and very slightly developed in the main axis of the inflorescence-branch, and in the stalk of the

female catkin. The tracheidal elements of the vascular bundle are developed weakly in the flower-branch, and generally they have narrow cell-cavities and thin membranes. The phloem portion shows, on the contrary, a larger cross section than the xylem. The ratio of the area between phloem and xylem in cross section was approximately 13:7 at the base of the flower-branch, 3:2 in the middle part of the same branch, 2:1 in the stalk of the male catkin, 8:7 in the uppermost internode of the flower-bearing shoot, 1:1 in the stalk of the female catkin and 2:3 in the uppermost internode of the non-flowering shoot[1] (Fig. 3). These results may be compared with those of HABERLANDT (1918). He measured the cross-section of the phloem in both vegetative and flower-bearing shoots of *Corylus Avellana*, and found the ratio to be 100:146. He thought that the larger extent of the phloem in the flower-bearing shoot than in the vegetative was due to the abundant supply of organic nutriment required for the development of the sexual organs.

About a week before the anthesis, sparsely distributed starch grains occur throughout the cortex of the axis and in the separation-zone of the male catkins. In every living tissue of the flower-branch in this stage, the occurrence of small oil drops is also observed. These substances are not apparent, however, in the flower-bud in a latent state during the winter, until toward the end of March. During 4–7 days before the anthesis, the axis of the catkin elongates from 2.5–4.5 cm, its previous length, to 4.5–8 cm. Simultaneously the starch-content increases considerably in the cortex of the axis and in the separation-zone. Even in this period, the starch-content in the central cylinder of the axis is rather poor. Such changes arise usually at the beginning of April. In the middle of March, some twigs, with flower-branches in the resting stage, were brought into the laboratory and placed in a bottle with water. The elongation of the axis and the increase of starch-content in the catkin-axis commenced in one day, probably accelerated by the higher temperature of the laboratory than out-of-doors, and, after 2–3 days their anthesis began. The previously accumulated starch in the axis was found to

1) In each case, the figures given, represent the mean value of the measurement from three different axes. At first, a sketch was made on paper of uniform thickness from cross-section of the vascular bundle, using a Camera lucida, and a magnification of about 90 diameters. Then the phloem and xylem of the sketch were cut apart at the border lines and these pieces of paper were weighed separately.

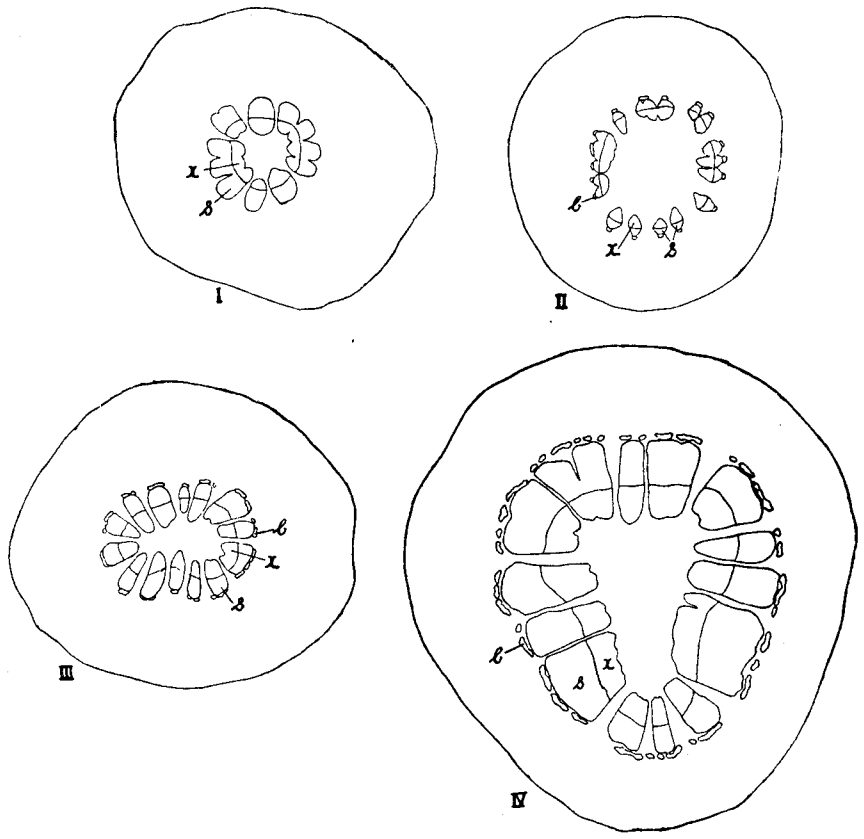

Fig. 3. *Alnus japonica.* Cross-sections through the axis of the inflorescence. I, the stalk of a male catkin ; II, the stalk of a female catkin ; III, the internode at the middle of a flower-branch ; IV, the internode at the base of the same branch ; *b*, bast-fibres ; *s*, phloem ; *x*, xylem. ca. 30/1.

have nearly disappeared at the end of the anthesis. This decrease of starch at the end of anthesis was also proved in the case of the outdoor specimens.

Previous to abscission, however, the starch grains and the oil droplets increase in the separation-zone. The richest accumulation takes place in the upper layer of the separation-zone in 2–4 tiers of cells. This layer is the actual separation-layer (Fig. 2).

The first step toward separation is a swelling of the middle and secondary lamellae of certain somewhat thickened cell-walls in this layer. The swollen lamellae stain easily with ruthenium red. By the later disorganization of these lamellae, the cells in the layer

become more or less isolated. The thin membrane of the isolated cells scarcely absorbs ruthenium red, but it stains dark violet with chlorzinc-iodine. Other microchemical tests show that the membrane of the isolated cells consists of practically pure cellulose. During the process of isolation, the cells concerned grow to (20–40) × (30–60)μ. These isolated cells contain starch grains and oil droplets very sparsely and lose their turgor soon after the isolation and then shrink and degenerate.

Such a process takes place, at first, in the cortex in the separation-layer a few tiers of cells below the epidermis, specially in a tissue lying under the upper end of the bract-scar, which adjoins the insertion of the catkin-stalk externally. In rather rare cases, the first change of separation begins at some other part of the cortex or medulla in the separation-layer. The separation-process then spreads throughout the separation-layer in the cortex, medulla, epidermis and finally in the parenchymatous tissue of the vascular bundle. After the maceration of the separation-layer has proceeded to a certain extent, the inner part of the layer (i.e. the part furthest from the bract) is torn by the weight of the catkin itself. The tracheidal elements which traverse the layer are broken quite mechanically. Eventually, the catkin falls off, leaving a concave scar on the axis.

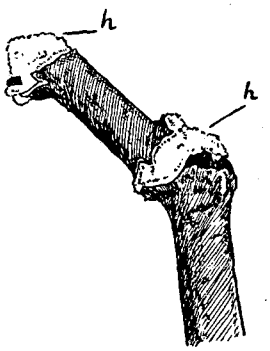

Fig. 4. *Alnus japonica*. The heap of isolated cells appearing on the scar after the separation(*h*). ca. 3/1.

It is noticeable in this plant, that preliminary cell-division in the separation-layer or in the adjacent tissue can not be discerned at all.

The isolation of cells in the scar continues even after the abscission, and, it is specially noticeable in the cortex and the parenchyma of the vascular bundles. Consequently a snowy white heap of partially isolated cells appears on the scar (Fig. 4). The maceration often reaches 2 mm or even deeper from the surface of the scar, so that brush-like tufts representing the finely split vascular bundles can be observed in a longitudinal section through the scar. The loosening of tissue is generally slight in the epidermis, hypoderm and medulla. Also in this case, the size of the isolating cells increases strikingly during the process, but their shape corresponds to their original shape ; namely, the round cells are derived from the isodiametric

cortical cells, and rod or club shaped ones from the sheath or parenchyma of the vascular bundle. In the latter, the top of the cells is generally thicker than the base. Formation of new septa or cell-division could not be observed in these isolated cells.

The occurrence of such a spontaneous maceration of the tissue after the abscission is reported by LOEWI (1906), KÜSTER (1904, 1916) etc., and the loosened tissue is thought to be produced owing to excess of water and is called "hyperhydrisches Gewebe". A mass of the isolated cells is sometimes visible around the separation-zone before the falling of the catkin, in cases in which the connection of the vascular bundle is strong enough to bear the weight of the catkin. If the catkin has been cut off, so as to leave a short stalk (3–5 mm) above the separation-zone, then the stalk, being less loaded, does not fall after the completion of the separation-process. In this case, the heap of loose cells around the separation-zone is usually very well developed. This feature is a good indication that the separation is completed. Under normal conditions in open air, the mass of loosened tissue on the scar remains until the beginning of May, being covered by a thin layer of degenerated cells on its surface. This heap corresponds to the "parenchyme sacrifié" of TISON (1900). Showing a noticeable contrast to the cells first isolated in the separation layer, those subsequently isolated on the scar are long-lived under favourable conditions. In a moist chamber they live for a week or more.

On the 30th of March, some of the isolated cells from the scar, left by the abscission of the catkin under the conditions in the laboratory, were placed on agar medium containing about 10% cane sugar which had been allowed to solidify in Petri-dishes. From time to time, observations were made to ascertain whether the cells were alive or not. Some of the cells were for this purpose taken out with a needle and put into 10% solution of potassium nitrate, in which the living cells plasmolysed. When the isolated cells were placed on the agar medium, their cell-contents were colourless and clear. On the 7th of April, practically all of the cells showed granular cell-contents. These granules or droplets were making an incessant and irregular movement in the cell-sap. Larger drops among them had a slightly greenish tint. They stained yellow or brown with iodine and dissolved very easily in the following solvents; ether, chloroform, benzine, carbon bisulphite, acetic acid, concentrated potassium hydroxide solution, chloral hydrate solution and 5% alcohol. It can

be ascertained from these tests that the droplets consist of the essential oil. On the 20th, about one third of them were found to be dead. On the 25th, the surviving cells were very few. In the dead cell, the plasm had a brown colour, and the cell-wall was a little shrunken. In some of these cells a gum-like substance could be observed either in simple or aggregated drops or a sometimes in an amorphous body. During this experiment which lasts more than three weeks the percentage of cane sugar in the agar medium must have become concentrated to a certain degree by evaporation. The isolated cells on the medium probably showing osmotic regulation accompanying the concentration of sugar in the agar. No growth nor cell-division could be seen in these cells.

I shall mention here some evidence of the general occurrence and transformation of essential oil in this plant. Not only in the isolated cells on the scar but also throughout the epidermis, cortex and medulla of the shoot, minute droplets of essential oil were observed. They occurred more abundantly in the hypodermal layer of the flowering branch and catkin-stalk. When the shoot or flowering branch is wounded, a sudden increase of this substance was noticed near the injured tissue ; and it was generally noticeable in parenchymatous cells. This substance is said, in fact, to play an important rôle in wound protection in plants. In the case of this plant, by subsequent change into a resinous substance, the rôle seems to be successful. During this change, the minute drops of essential oil fuse with each other, or they combine into larger aggregated droplets. The colourless or slightly greenish drops change, probably due to oxidation, into yellow at first, then yellowish brown and finally reddish brown, and the previous liquid state changes into an amorphous and resinous condition. The different grades of this change can be detected in the peripheral tissues of the shoot in normal conditions, and more prevalently in the abscissed flower-branch. While this substance is in a liquid state, the cells concerned are still alive. When it becomes amorphous, the disorganization of protoplasm takes place, and by the loss of turgor, these cells become compressed by adjoining living cells. Such a mode of cell degeneration is commonly found in this plant. In the dead periderm in any part of this plant, the cell-cavity is filled with this resinous substance.

The healing of the abscissed scar on the branch makes very slow

progress. At the middle of May, the heap of loosened tissue on the scar collapses and withers, adhering to the surface of the scar. Beneath this the formation of a protective layer takes place in 5–10 tiers of cells. The cells of this layer are a little stretched longitudinally, and intercellular spaces are very sparsely present. Ligno-suberization of their cell-walls proceeds from the outer part of cortex, then to all the parenchymatous cells in this layer. Simultaneously with this ligno-suberization, the essential oil occurs abundantly in this layer and it changes gradually into a resinous substance. At the end of May, when the ligno-suberization of this protective layer is complete, all the cell-lumina of this tissue are filled up with resinous substance. At that time, the periderm-formation takes place immediately beneath this protective layer.

Also on the catkin-side of the scar a ligno-suberization occurs, a trace of which can be observed at an earlier stage of the separation-process. The degree of this chemical change is, in this case, strong in the hypodermal layer and progressively weaker inwards on surface of the scar. Covering the ligno-suberized tissue 2–3 tiers of cells lie in a partially isolated state.

If the female catkin in bloom is cut off at the upper end of the stalk, the abscission of the remaining stalk occurs in the same manner as the normal separation in the male. This method of inducing the separation artificially is often used for the study of the abscission in the petiole or flower-stalk (KÜSTER 1916a, SAMPSON 1918, NAMIKAWA 1922 etc.) On the 19th of April, some branches with female catkins were collected and placed in bottles with water, and then all the female catkins were cut off. Some of the branches, on which altogether 10 stalks of female catkins were left, were kept in the open air, and the other branches likewise with 10 stalks, in the laboratory. All the stalks were shed between the 23rd and 26th in the laboratory, and between the 25th and 30th in the open air. During the flowering time, plenty of starch grains are present in the cortex of the stalk of the female catkin, but not or only sparsely in the separation-layer. In the stalk, from which the catkin has been removed, the starch grains decrease conspicuously in a day, but on the contrary they increase in the separation-layer and in the adjacent region. At the time of separation, however, the partially isolated and enlarged cells of the separation-layer no longer show rich starch-contents.

The unfertilized female catkin falls usually at the beginning of

May. The method of the separation and the healing of the wound is just the same as in the male catkin, except for some unimportant details, which are not necessary to mention here.

During the summer, a strong development of the wood portion of vascular tissue takes place throughout the catkin axis and the separation-zone in the fertilized female catkins, and the separation-zone itself loses the characters previously distinguishing it from the adjacent tissue. At the end of the season, the whole stalk of fruiting catkin and a certain portion of the shoot beneath it die, due to the stoppage of the wood portion with a resinous substance and the periderm-formation in the bast occurring in a zone, the position of which in the shoot is not constant. The dead catkin remains attached often for a few years and is not actively thrown off.

2, Alnus hirsuta.

The flowering and the abscission of catkins of this plant begin a few days later than in *Alnus japonica*. The abscission-phenomena are identical in most respects with those which occur in *Alnus japonica*. Preliminary cell-division in the separation-layer previous to the abscission can not be observed. The growth of isolated cells on the surface of the scar is a little stronger than in the foregoing species. The cortical cells in the separation-zone grow from 12–13μ to 40–80μ in diameter during their isolation. The fully elongated cells of ellipsoidal shape produced in the central cylinder of the scar often measure 180μ in length. The starch content of the isolated cells is generally poor ; a small number of cells, however, often show very rich starch-contents. The essential oil occurs very commonly in the isolated cells of the scar and in the parenchyma of the fallen flower-branch, and its change into resiniferous substance is also observed. The mode of wound-healing in the scar is just as in the case of *Alnus japonica*.

The lignification of the scar on the fallen catkin is stronger than in the case of *Alnus japonica*. On the surface of the scar, there are 4–7 tiers of partially isolated cells, and beneath these the lignified tissue is formed to a depth of about 1 mm. The lignification is particularly intense in the hypodermal tissue and in the sheath of the vascular bundles.

3. Corylus Sieboldiana.

The abscission of the male catkin takes place at the end of April.

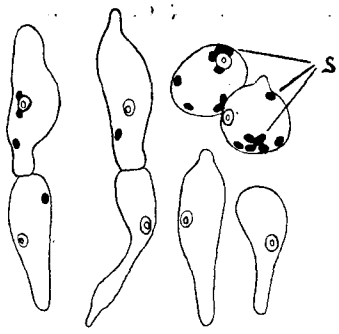

Fig. 5. *Corylus Sieboldiana.* Isolated cells on the scar of the fallen catkin. *s*, starch grains. ca. 200/1.

The base of the catkin-stalk is slightly differentiated as a separation-zone by the smallness of the cells. The constriction in this zone is hardly recognizable. In the flower-branch and catkin-stalk, the occurrence of mechanical cells is, also in this case, quite reduced. In the vascular bundle of the flower-branch, the phloem develops in larger proportion than in the vegetative shoot or in the axis bearing the flower-branch. The following measurements have been made from traverse sections of the axis, and will give a general idea of this relation.

	Number of specimens	Thickness of the axis in mm	Thickness of the phloem in μ	Thickness of the xylem in μ
The internode next below the insertion of the flower-branch.	1	1.7	25–70	115–230
	2	1.6	20–80	110–250
The internode immediately above the insertion of the flower-branch.	3	1.3	10–60	75–155
	4	1.5	15–60	50–170
Base of the flower-branch.	5	1.5	70–170	75–180
	6	1.1	60–120	25–130
Uppermost internode of the non-flower-bearing shoot.	7	1.5	15–60	60–170
	8	1.7	20–70	75–170

The difference in the development of the phloem between the flower-bearing and non-flower-bearing shoot, as shown by the measurements, is not, however, as great as HABERLANDT reported in *Corylus Avellana.*

The position, in which the separation-layer is formed, does not seem to be strictly defined. The separation occurs usually in a layer situated about 1 mm above the insertion. Often it takes place at the very point of the insertion or in a layer situated at some distance, but not exceeding 2 mm above the insertion. If a longitudinal section through the catkin-stalk, which is just about to fall, be examined, it can be seen by the naked eye that the separation-zone shows a little dark colour due to the replacement of air in the intercellular spaces by mucilage derived from the swollen middle lamellae. There is a simultaneous accumulation of starch and oil which can be detected in this zone by microchemical tests. The first

step in the isolation of the cells may take place in any part of the cortical parenchyma of this zone. The isolation spreads then throughout the living elements of the separation-layer very rapidly. In this process of separation the rapid growth of the cells is accompanied by the dissolution of the middle lamella. Also in this case, previous cell-division in the separation-layer could not be found. After the separation of the layer, the catkin-stalk falls in a quite fresh and living state.

Even after the abscission, the isolation and growth of the cells proceed continuously on the scar. Consequently, a conspicuous mass of partially isolated loose tissue is to be seen on the scar, showing, due to abundant intercellular spaces, a snowy white appearance. The maceration of the tissue of the scar proceeds to a very slight longitudinal distance in the peripheral region of the axis, such as epidermis and hypoderm, but towards the centre of the axis this change extends deeper ; at the central cylinder, it reaches usually a longitudinal depth of 2/3–1 mm or sometimes to 2 mm. The tracheidal elements are loosened in a brush-like shape as the result of the maceration of the inner tissues. In this loosened tissue, the substance of the disorganized middle lamellae remains in small irregular masses sticking to the cell-wall. These masses stain with ruthenium red intensely, but the cell-walls of the loosened tissue scarcely stain ; the latter can be stained a dark violet with chlorzinc-iodine. The isolated cell has a diameter 5–8 times larger than its previous size, and in the case of longitudinally elongated cells, the length becomes often 10 times or more enlarged. The relatively less enlarged spherical cells among these contain a considerable amount of starch grains and oil droplets. These substances are, however, scarcely seen in the cells which have grown to a large size. In the longitudinally elongated cell, the diameter of the upper end surpasses generally that of the base, and a nipple-like process appears at the point where the cell has been connected with another cell above or below (Fig. 4).

The healing of the scar commences about a week after the abscission. Beneath the loosened tissue, there occurs a protecting layer consisting of a few tiers of cells, in which a slight lignosuberization of the cell-walls is visible. Immediately below this layer, cell-division takes place in 2–3 tiers of cells, and a phellogenous cambium is formed. Any sign of resin-formation, as just described

for species of *Alnus*, could not be recognized in this case.

4. Betula japonica.

The anthesis of this tree begins in the middle of May, and by the end of the month all the catkins fall off in a fresh condition bearing withered anthers on them. The period from the beginning of the anthesis to the abscission in an individual catkin is about a week. The separation-zone is previously formed at the insertion of the catkin-stalk and at the base of flower-branch. The zone can just be distinguished by the smallness of the cells and the sparseness of intercellular spaces. These characteristics disappear gradually on both sides of this zone. Obvious constriction is not present in this zone. The mechanical elements such as bast-fibres or stone-cells, are completely lacking in the flower-branch and its separation-zone.

Before the separation, the plasmatic contents in the separation-zone increase obviously and become granular. By microchemical tests, the sudden increase of starch grains and oil droplets can be detected in this tissue. A preliminary cell-division before the separation in this zone can not be observed at all.

The actual cell-separation takes place in 3–5 tiers of cells situating in the upper half of the separation-zone. The lower layer of the zone does not participate in the separation itself, but in the healing wound.

The separation is brought about by the isolation and growth of cells in the separation-layer. Isolation of cells may first take place in any part of the cortex in this layer, and then it proceeds throughout the layer. The isolated cells no longer have rich contents of starch or oil, and usually degenerate very soon after the separation. The maceration of a few tiers of cells beneath the separation-layer follows, but it does not make a large enough heap of loosened cells to be seen with the naked eye. Cells in the lower part of the separation-zone still have their rich plasmatic contents after the abscission ; then they commence cell-division and growth. The cell-walls of the uppermost 2–3 tiers of cells of this newly formed tissue become slightly suberized, and immediately beneath this layer, the ligno-suberization of the membrane occurs in 5–10 tiers of cells. Beneath this protecting layer the formation of phellogenous cambium akes place.

5. Salix jessoensis.

The catkin of species of *Salix* is a short, non-ramified shoot in itself and each catkin bears a crowded group of 4–6 small foliage leaves at its base. After the anthesis of this species the catkin may either fall or remain attached, its point of detachment being at the base of the stalk below the group of leaves. The separation-zone, which is present at the base of the catkin, can be slightly distinguished by the smallness of the cells. This difference does not extend to the central cylinder, but is limited only to the epidermis and cortex. Previous to separation, the starch-content increases a little in the separation-layer, which lies in the upper half of the zone. The separation-process takes place mainly in the cortex of this layer, being brought about by the dissolution of the middle lamellae and the growth of the cells. The isolation of cells is often to be seen also in the medulla, but it proceeds only to a slight degree in the central cylinder. So that the separation is generally incomplete, and some withered catkins will be found still attached to the twig after the flowering season.

After the separation, a slight loosening of the tissue on the scar is to be seen in about 10 tiers of cells. At the same time as the separation process occurs or a little later, cell-division takes place in a layer 7–10 tiers of cells beneath the actual separation-layer, at first in the parenchymatous elements of the vascular bundles, then in the cortex and finally in the medulla. A protecting layer with ligno-suberized walls is derived from this newly divided tissue and consists of 3–5 rows of cells, which are a little elongated in the longitudinal direction. Below this protecting layer, a phellogenous cambium of 3–6 tiers of cells occurs. In the scar on the fallen catkin-stalk, lignification of cell-walls is to be seen, strongly in cortex, rather slightly in the medulla, and scarcely in the vascular boundles.

It is peculiar, that those catkins, which bear relatively well developed leaves at their base, do not absciss after the flowering. In this case, a periderm layer is formed, traversing the axis above the insertion of the uppermost leaf on the stalk ; consequently, the upper part above the periderm withers and dries. By meteorological actions, this dried part can be thrown off quite mechanically. The remaining portion of the axis with its leaves, however, often continues to function as an assimilatory shoot during the summer.

6. Salix rorida and other species.

The axis of the male catkin of *Salix rorida* is more than twice as thick as in the foregoing species. It measures about 2.5–3 mm in diameter. This difference depends upon the larger thickness of the medulla, which measures 2–2.5 mm in diameter. The leaves at the base of the catkin are less developed than those of *Salix jessoensis*. The base of the catkin-stalk shows a slight constriction, in the plane of which the dimensions of cells of the epidermis, cortex and medulla are a little smaller than in the neighbouring tissue. The length of every element in the vascular system is shorter in this zone, also a constriction of the central cylinder can be barely seen. The cell-walls of the cortical cells are somewhat thickened in this zone. Thus the separation-zone in this case is more differentiated than in the foregoing species. Mechanical elements, such as bast-fibres or stone-cells, are not developed in the catkin-stalk nor in the separation-zone at all.

Previous to the separation, sudden increase of starch, oil and essential oil can be detected by microchemical tests in the separation-zone. The separation takes place in the upper layer of the separation-zone throughout the living elements. Eventually the catkin falls in a fresh and living condition. In the scar on the fallen catkin, no sign of lignification could be seen. The other sequence of events in the mode of abscission and wound-healing is on the whole very similar to that of *Salix jessoensis*.

Further, in male as well as female catkins of *Salix Miyabeana* and *Salix sachalinensis*, the process of abscission is identical in most respects with that which occurs in *Salix rorida*.

7. Populus Maximowiczii.

The shedding of male catkins takes place usually from the end of April to the beginning of May. The separation-zone is easily recognized at the insertion of the catkin-stalk by the presence of a constriction. The tissue consists of small cells with rich plasmatic contents ; and intercellular spaces occur sparsely in this zone. Crystal-cells with aggregated crystals of calcium oxalate are dispersed abundantly in the parenchymatous tissue of the shoot, catkin-stalk and separation-zone. Bast-fibres and stone-cells are not generally to be seen in the separation-zone or in the catkin-stalk. They are,

however, well developed in the vegetative shoot. Some weakly developed bast fibres are rarely present in the basal portion of the catkin-stalk, but they never penetrate the separation-zone.

Before the abscission, a sudden accumulation of starch grains can be detected in the separation-zone. Also aggregated droplets of essential oil arise in some cells of this tissue (Fig. 6). Preliminary cell-division in the zone could not be observed. Abscission takes place as the result of growth of cells and disorganization of middle lamellae in the upper layer of the separation-zone. After the abscission, the scar is covered with cells some of which are rounded and entirely isolated, others partially separated from one another and protruding in club-shaped form. The elongated cells often show

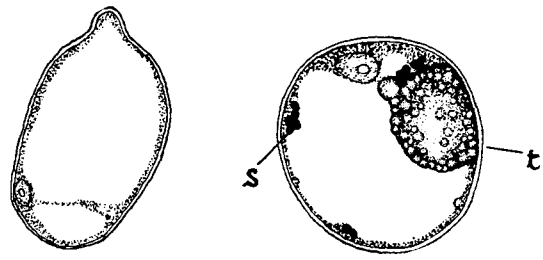

Fig. 6. *Populus Maximowiczii.* Isolated cells on the scar.
s, starch grains ; *t*, aggregated droplet of essential oil. ca. 625/1.

at their free end a nipple like process (Fig. 6). Some of these partially isolated cells contain a small amount of starch grains or droplets of essential oil. A light suberization of the membranes occurs in 1–2 tiers of cells in the scar. Later, a periderm is formed beneath the suberized layer.

After the ripening of the fruit, the female catkin falls in the early part of July. The mode of the abscission and wound-healing is generally the same as that of the male catkin.

8. Castanea pubinervis.

At the insertion of the catkin-stalk, a normal separation-zone is formed, showing a slight constriction. In the separation-zone, the cells are small, isodiametric and have rich plasmatic contents ; their cell-walls are somewhat thickened and intercellular spaces are present sparsely. In the catkin-stalk, bast-fibres with thick lignified walls are well developed ; moreover, the cell-walls of the medulla and

hypoderm are thickened and lignified. In the case of the medulla, pits occur on the cell-walls in considerable numbers. In the separation-zone, however, lignified elements are strikingly diminished in number. The medulla in this region consists of parenchymatous tissue with thin walls, containing only a few groups of cells with thickened and pitted walls. In the cortex and pericycle, no lignified elements can be observed.

Cell-division takes place, previously to the separation, in some cells of separation-layer, but not as a whole. At the same time, starch grains and oil droplets increase in this zone. And the swel-

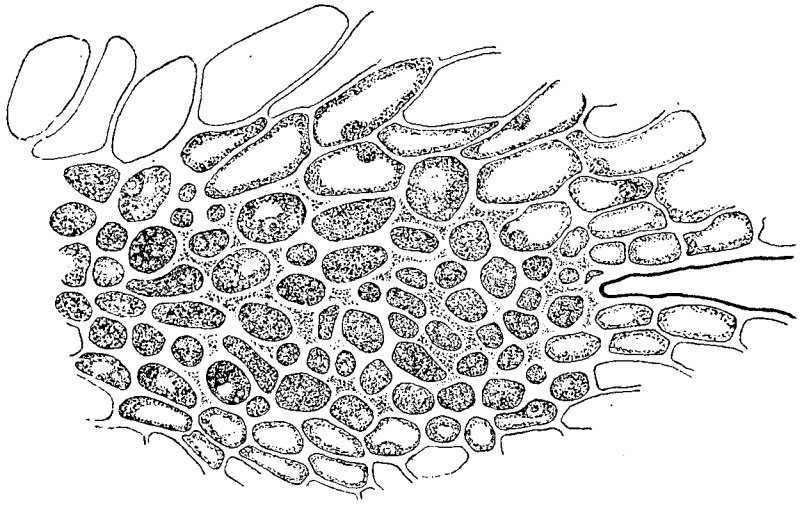

Fig. 7. *Castanea pubinervis*. A part of median longitudinal section of the separation layer; the disorganization of middle lamellae is taking place. ca. 560/1.

ling of the middle and secondary lamellae of the cell-walls succeeds these changes (Fig. 7). The separation of the tissue is brought about by the dissolution of these lamellae and the rapid growth of the cells concerned. The isolated cells keep their turgid condition only for a short while, and soon their cell-contents degenerate and their walls shrink. Further isolation of cells on the scar can not be found in this case. A periderm-layer arises at the depth of a few tiers of cells from the plane of separation.

Mohl (1860) observed cell-divisions in the separation-layer previous to or during the separation-process in every case of abscission

examined by him, and supposed them to be a necessary characteristic of the separation-zone. A number of examples by later writers, however, disproved the universal occurrence of the cell-division in the separation-zone. As described in *Salix* and *Castanea*, cell-divisions were observed in the separation-layer of the catkin-stalk accompanying the separation. In the case of *Salix*, cell-division took place at the same time as the separation or when the process was nearly complete. Moreover, the cells which undergo division were not in the actual separation-layer, but in a layer beneath it. In *Castanea*, the cell-division occurred previous to or at the same time as the separation-process and in the actual separation-layer, though not throughout the layer. In *Betula*, the cell-division was observed after the separation, dividing cells were in the lower part of the separation-zone and finally gave rise to the protecting layer (ligno-suberized layer). In *Alnus*, *Corylus* and *Populus*, no cell-division could be observed in the separation-zone at all. Though it may be necessary that the tissue in the separation-layer should be capable of growth and resemble young tissue, the meristematic nature does not seem to be always indispensable. Cell-divisions are conceived as a sign of the renewal of the tissue (LLOYD 1914b, 1916b ; NAMIKAWA 1922). HÖNEL (1880) noted cell-divisions, which occurred often in the parenchyma entirely outside of the actual separation-layer. Thus, occasionally the cell-division is concerned only with the formation of the protecting tissue in the scar.

Rich plasmatic contents of the separation-zone are reported as a characteristic feature by several writers. In the cases examined by me, the same character could be observed in well differentiated separation-zones. The feature was, however, not very noticeable when the differentiation of the separation-zone was slight. The relative amount of plasmatic contents is in inverse proportion to the intensity of growth which has been made in the tissue, because, in usual cases, the protoplasm does not increase proportionally with the increase of the volume of a growing cell.

The rapid increase of the plasmatic content, starch and oil in the separation-layer has been seen previous to the abscission. Such a change seems to be a sign of the rejuvenation of the tissue and to be important for the subsequent cellular growth and the separation-process. The accumulation of the substances mentioned must be interpreted in such a non-reserve-organ, as an indication of the

strengthened cellular activity (HANNIG 1913, KENDALL 1918, NAMIKAWA 1922).

The lack or the reduced development of the mechanical elements, such as bast-fibres or stone-cells, is favourable to the separation-phenomena. As has been seen in the fertilized catkin of *Alnus japonica*, it is noticeable that, if mechanical tissues develop strongly, the usual separation-process can not take place in the separation-zone.

III. Exfoliation of Floral Organs.

1. A few cases of Liliaceae,

REICHE (1885) observed that the perianth of *Gagea* and *Ornithogalum* withered gradually and that they were cast off eventually by atmospheric influences. In the case of *Ornithogalum* he found an intense lignification in a layer of parenchyma at the base of perianth. In *Gagea* he could not find any anatomical change in the perianth during the withering. According to my observations on *Gages lutea*, the perigones do not wither until the fruit ripens, but they grow a little and function as an assimilatory organ. After the flowering, the chlorophyll content increases in the perigone and the yellow colouring matter on the upper surface of it decreases. These perigones share the same fate as the stem, their withering being simultaneous. According to WACKER (1911) the mode of defloration in *Liliaceae* can be classified under three types, namely : 1. falling of the perigones at the end of flowering ; 2. slow death and drying of the perigones on the ovary ; 3. greening of the perigones. *Gagea lutea* must belong to the third category of his enumeration. The tissue at the base of the perigones of this plant is slightly differentiated by the smallness of the cells, but no anatomical change takes place in this region even after the flowering. After the fruit ripens the stem becomes, together with the leaves and perigones on it, faded and withered. At that time, a strong ligno-suberization is taking place in a few tiers of cells traversing the base of the stem in the bulb.

Trillium kamtschaticum is also one of those plants in which the petals are not shed. The tissue at the base of the petals is slightly differentiated by the smallness of the cells, but no sign of separation nor exfoliation can be found at all. In the summer, the stem withers together with the petals, sepals, leaves and the fruit on it. The change of the tissue at the base of the stem occurs in the same way as in *Gagea*.

In the case of *Hosta japonica*, the tissue in a zone at the base of the full grown perigone is scarcely differentiated except that the size of its cells is a little smaller than in the neighbouring tissues. At the end of the flowering, the cells in a layer of 3–7 tiers of cells in this tissue become somewhat enlarged, then the lignification of the walls proceeds in the same cells (Fig. 8). The situation of this

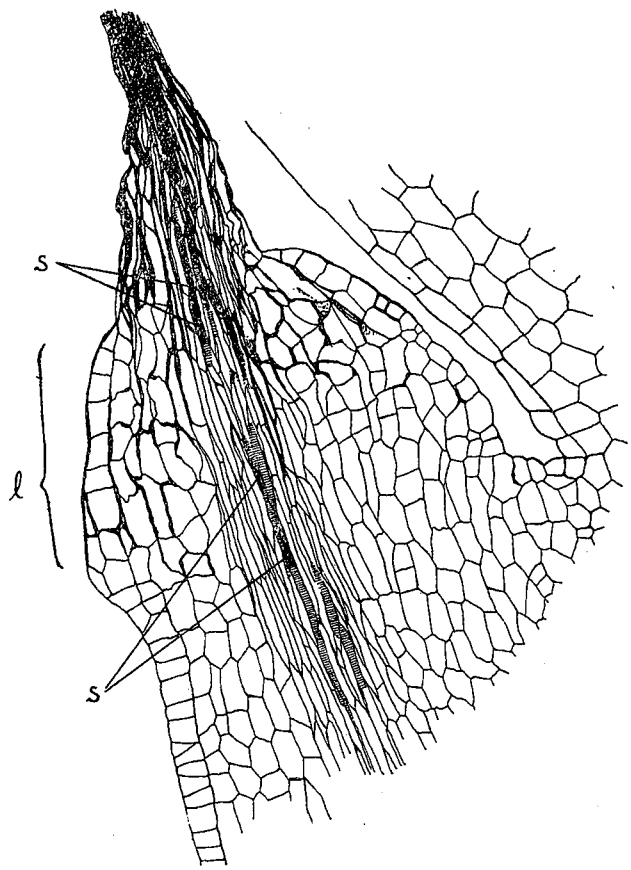

Fig. 8. *Hosta japonica*. Basal part of the perigone. *l*, lignified layer. *s*, stopper in the tracheids. ca. 120/1.

lignified layer does not seem to be strictly determined. It arises either at the base of the perigone or above it at a distance not exceeding 2 mm. The tracheidal elements of the vascular bundle which penetrate the lignified layer have their cavities filled with a gum-like substance which shows the same reactions as lignified walls.

All the tissues lying above the lignified layer become withered and dry. When the ovary has grown to 1 cm or a little more in length, lignification takes place at the base of the style in 2–4 tiers of cells. Then the withering of the style proceeds gradually from the top to the base of the style.

2. Amaryllidaceae.

It is well known that the perigone, style and bract of some species of *Amaryllidaceae* are not cast off but become withered and

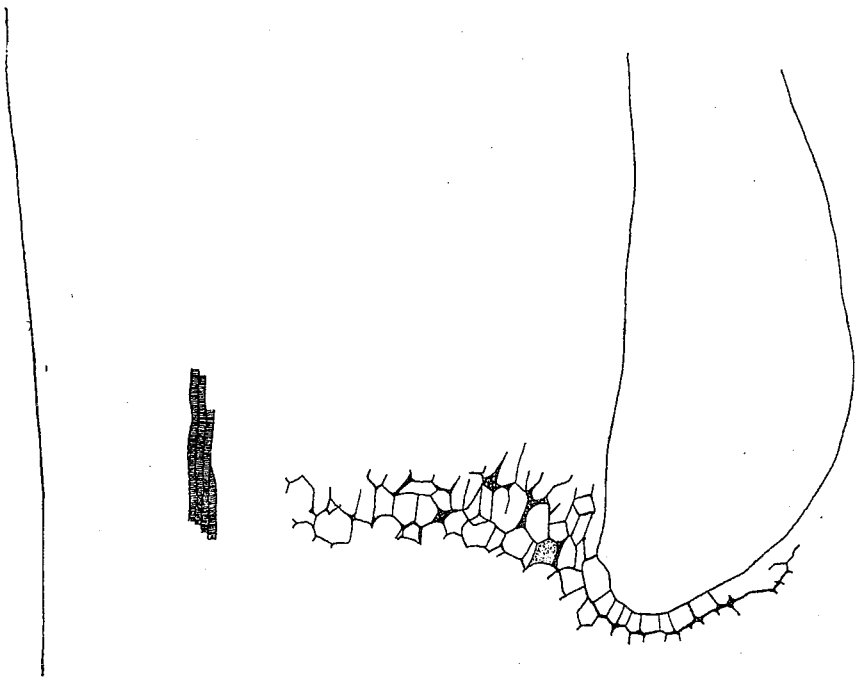

Fig. 9. *Narcissus Pseudo-Narcissus.* Basal part of the petal immediately before the withering. The material is treated with phloroglucin and conc. HCl, and shows the lignified cell-walls only. ca. 110/1.

dry after flowering. In *Leucojum*, REICHE has mentioned the formation of a cork layer, which arises at the base of the perigone at the same time as the latter withers. Further details on the anatomical changes at the insertion of floral organs in *Narcissus* and *Lycoris* will be described here.

Narcissus Pseudo-Narcissus. At the base of the perigone a zone of the tissue can be distinguished by the smallness of its cells, but

no other difference in its structure can be found. A few days before the withering, a ligno-suberization of the cell-walls takes place in 2–4 tiers of cells in the upper layer of this zone. Such a ligno-suberization can be traced, at first, in the inner (or morphologically upper) part reaching from the epidermis to the vascular bundles, then in the epidermal and hypodermal tissue of the outer (or morphologically under) surface (Fig. 9). In a later stage, the lignifica-

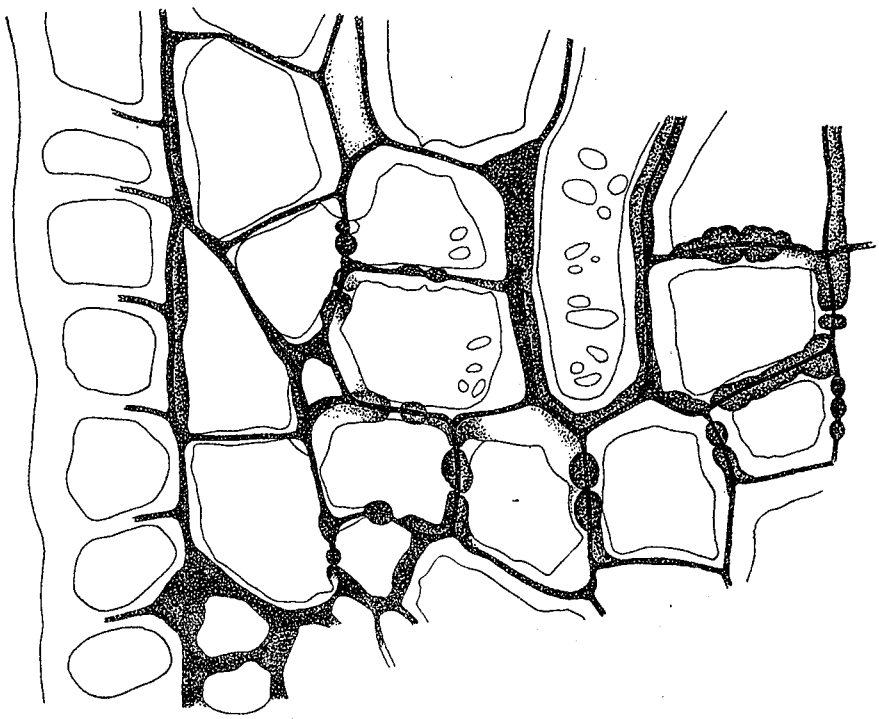

Fig. 10. *Narcissus Pseudo-Narcissus.* Lignified layer at the base of the withered petal. The material is treated with phloroglucin and conc. HCl, and the dotted part represents the lignified lamellae. ca. 560/1.

tion can be detected throughout the living elements of the layer. The ligno-suberized cells are more or less elongated in the longitudinal direction. The changed wall is considerably thickened and abundantly pitted, and its thickening is generally noticeable at the corners of the cells (Fig. 10). The ligno-suberization takes place in the vascular bundles a little later.

In the flower, in which the ovary is swollen to a thickness of

about 5 mm in diameter, bearing the withered perigone on it, the ligno-suberization is to be seen in a layer traversing the bases of the perigone and style. At this stage, cell-division is taking place immediately below the ligno-suberized layer. Afterwards a periderm occurs in this rejuvenated tissue. The tracheids in the ligno-suberized layer are filled with gum-like substance, which shows the same reaction as the lignified membrane, and losing their firmness, they become crushed (Fig. 11). The wood-gum also occurs in some lignified cells of the parenchyma in the form of drops or irregular lumps adhering to the inner surface of the cell-wall.

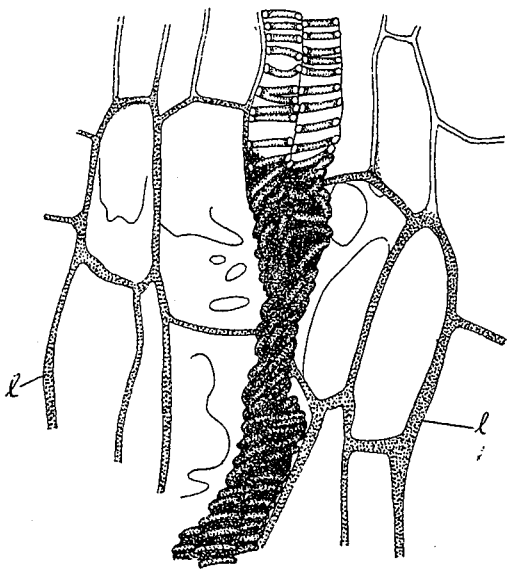

Fig. 11. *Narcissus Pseudo-Narcissus.* Crushed tracheids in the lignified layer of the bract. A gum-like substance fills the cavity of the tracheids. *l*, lignified cell-wall. ca. 560/1.

The withering of the perigone in the unfertilized flower takes place in consequence of ligno-suberization similar to that just described. Then, the whole flower withers as a result of the periderm-formation at the base of the peduncle. The tissue of this region consists of small cells not elongated in the longitudinal direction. Before the withering of the flower a ligno-suberization takes place traversing the axis in 2–4 tiers of cells, some of which show preliminary elongation in some degree in a longitudinal direction. The intensity of ligno-suberization is, in this case, not so

strong as in the base of the perigone. In some of the cells, however, the wall is noticeably thickened and pitted. Wood-gum rarely occurs in this layer. Beneath this ligno-suberized layer, a secondary meristem is formed, showing granular plasmatic contents, in which a considerable amount of minute oil drops can be detected by microchemical tests. This layer develops into a periderm, later. While this layer is still in a meristematic condition, there can be observed, sometimes, a sign of incomplete separation. In this case, the newly divided cells or the cells lying immediately below the dividing layer pursue a rapid growth and simultaneous isolation. As they lose their turgidity and shrink soon after their isolation, this schizogenous

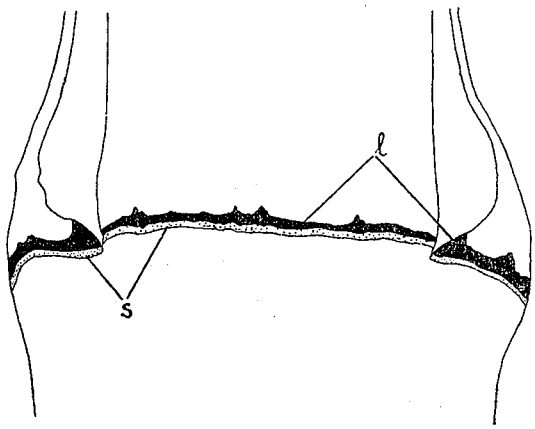

Fig. 12. Double flowered variety of *Narcissus Pseudo-Narcissus*. Basal part of the peduncle and the bract. *l*, ligno-suberized layer; *s*, suberized layer.

separation may be mistaken for a lysigenous one. This change does not prevail throughout the layer, but is limited to a group of a few cells, and the withered peduncle is not cast off. The stoppage of tracheids with wood-gum in this layer can be observed after the whole flower has withered. It is noticeable that, in the unfertilized flower, the ligno-suberization at the base of the style does not occur even after the whole flower has withered.

The double flowered variety of this species is sterile. The ovary is remarkably stunted, and after the flowering it withers together with the perigones. The formation of a ligno-suberized layer and periderm, as well as the stoppage of tracheids proceeds at the base of the peduncle in the same way as in the unfertilized of the single flowered form (Fig. 12). No noticeable anatomical changes can be

discerned at the insertion of the perigones. The separation of cells in or below the dividing layer is, though incomplete, more frequently observed than in the previous case.

In the bract, the withering takes place far earlier than in the petals. The preformed small-celled layer is also present at the base of the bract. Before the opening of the flower, ligno-siberization at the insertion of the bract takes place in 2–5 or sometimes even in

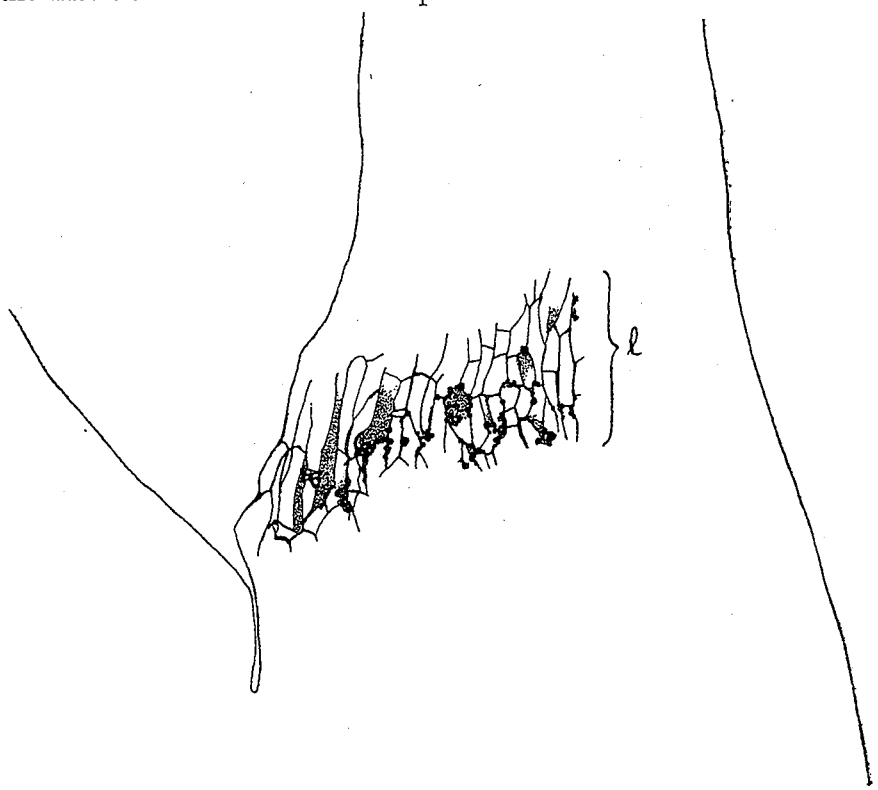

Fig. 13. *Narcissus Pseudo-Narcissus.* Basal part of the bract. *l*, ligno-suberized layer. ca. 120/1.

10 tiers of cells, which have recently become a little elongated in the longitudinal direction. The simple pits, which are round, elliptical or often irregular in their form, and not uniform in their size, occur on the walls of these cells. Wood-gum of drop-like or amorphous form occurs in the ligno-suberized cells, adhering to the inner surface of the walls (Figs. 13 and 14). All these changes proceed at first in the epidermis and mesophyll of the inner (or

morphologically under) side, (Fig. 13) and finally in all the living elements of the vascular bundle. The tracheids become stopped with wood-gum. At the end of the flowering, slowly continued cell-division takes place beneath the ligno-suberized layer. This secondary meristem develops finally into a cork layer 4–7 tiers of cells in thickness.

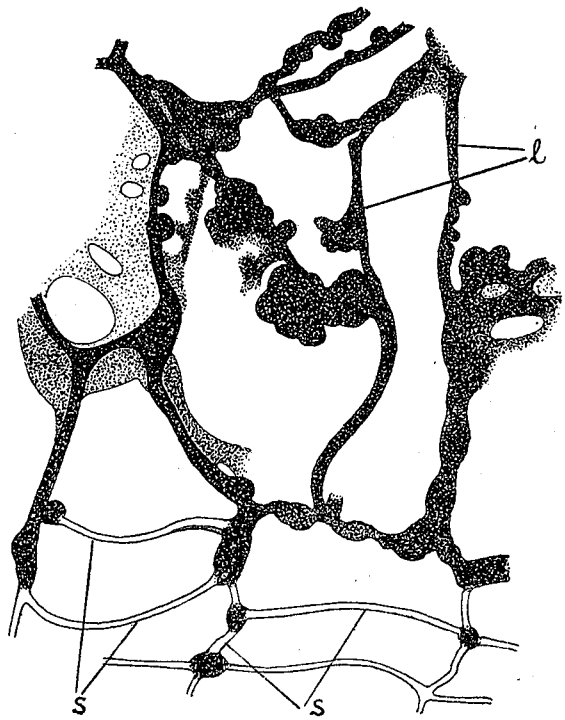

Fig. 14. *Narcissus Pseudo-Narcissus.* A part of the ligno-suberized layer in the base of the bract. *l*, ligno-suberized membrane ; *s*, suberized membrane. ca. 560/1.

Lycoris sp. The tissue at the base of the perigone is slightly distinguished from the neighbouring tissue by the smallness of the cells. At the end of the flowering, cell-division takes place in a traverse layer throughout this region. The place in which the cell-division appears is not strictly determined ; it may be at the very base of the perigone, or 1–2 mm above the base or between these two portions. The cells of this meristem grow a little in longitudinal direction, and then their walls become ligno-suberized. The ligno-

suberization occurs in 3–5 tiers of cells and is generally more intense at the upper part of the layer. Many simple pits appear in the thickened part of the ligno-suberized wall. Wood-gum in drop-form also occurs in the upper layer. The cavities of tracheids in this layer are stopped up with wood-gum. Moreover, it is often to be seen that the tracheid is crushed and torn by the expansion of the newly divided and growing cells adjacent to it. In the tissue in which such a destruction has taken place, the occurrence of wood-gum is generally abundant. After this process, all the tissues above this ligno-suberized layer become withered, and their cell-walls show a slight mucilaginous change. The whole perigone afterwards becomes dry.

In the case of *Hippeastrum hybridum*, the process of ligno-suberization at the base of the perigone and the mode of defoliation are identically the same as in *Lycoris*.

3. Iris setosa.

As regards the perigones of *Iris*, REICHE described that at the end of flowering, the withering proceeded from the top to the base of them, and that they remained in a dried condition attached to the top of the ovary for a fairly long time. Some of my observations in *Iris setosa* will be added here.

The tissue in a layer at the base of the perigone is slightly differentiated by the smallness of the cells. Some elongated mucilage-cells with raphides are present scattered in this tissue. At the end of the flowering, cell-walls of the parenchymatous cells near each of the mucilage-cells undergo a mucilaginous change. These cell-walls begin, at first, to swell and become readily stained with dyes. They can be stained with ruthenium red very intensely, and also absorb many other stains such as safranin, methylene blue, methylgreen, congo red etc. Finally, the entire cell-walls change into a mucilaginous state and the cells disorganize. This process spreads gradually throughout the layer. During this change, all the tissues which lie above this layer also undergo a mucilaginous change and shrink. The shrunken perigones afterwards become dry and their free ends may be cast off mechanically, while the basal part remains covering the surface of the scar.

A slight ligno-suberization takes place in the walls of the living cells immediately below the disorganized tissue ; there arises, how-

ever, no cell-division nor periderm formation (Fig. 15). After the whole flower has withered, tracheidal elements in the scar become stopped with a gum-like substance.

4. Cucumis sativus.

REICHE noted that in the female flower of *Cucurbita Pepo* and *Ecballium agreste*, the corolla withered and became disorganized after

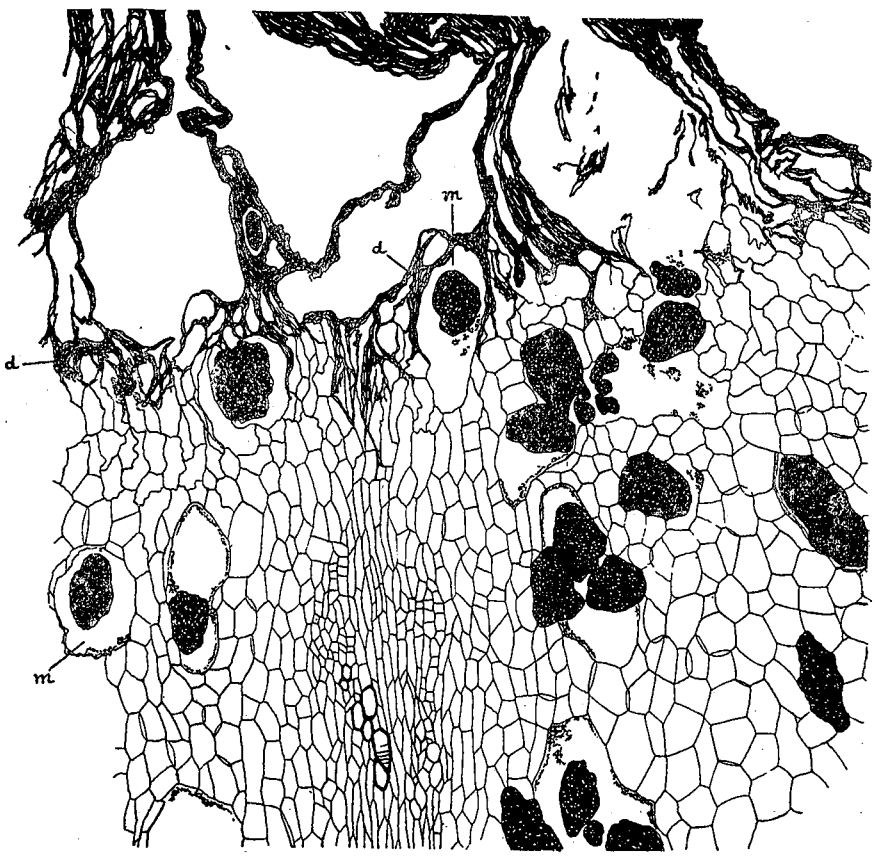

Fig. 15. *Iris setosa*. Basal part of the perigone. *d*, disorganized tissue; *m*, mucilage-cell. ca. 120/1.

the flowering, and that the dead tissues formed a structureless layer, "the pseudo-epidermis", adhering to the top of the fruit. In the case of the male flower he observed a normal separation-process at the joint between the upper end of the stalk and the receptacle.

The writer's observations on *Cucumis sativus* agree generally with the results of REICHE.

In the connecting region between the male flower and the flower stalk, a differentiated separation-zone consisting of small cells is present. After anthesis, a sudden increase of plasmatic contents and starch grains arises in this zone. The separation of the tissue is then carried out, being brought about by the rapid enlargement of the cells and the dissolution of the middle lamellae. It can be observed for a while after the separation that the wholly or partially isolated cells on both side of the separation-plane are still in a turgid state. In most of these cells, the starch content is scanty. On the scar of the stalk, cells in 2–3 tiers shrink afterwards, and in 1–2 tiers of cells immediately below them, the cell-walls become lignified. After the fall of the flower, the flower-stalk, which persists, shows a gradual withering proceeding from the top toward the base. The tissue at the insertion of the flower-stalk is also slightly distinguishable by the smallness of the cells. There are, however, no other evident differences from the neighbouring tissue. Afterwards, ligno-suberization of the cell-walls occurs in 2–3 tiers of cells traversing the base of the stalk throughout all the elements of this zone. The tracheidal elements become, in most of the cases, stopped up with a gum-like substance. The formation of thyloses can be observed only occasionally. All the tissue above this ligno-suberized layer becomes dry, but the stalk never falls off. The situation, in which the ligno-suberization occurs, differs in different specimens. It is usually quite at the base of the stalk, but sometimes in a layer 1–3 mm above the insertion. Such a difference may be due to the fact that the tissue is not highly differentiated and not strictly localized.

The female flower of this plant withers and dries after the flowering, and remains on the top of the ovary even after the fruit reaches its full-grown size. In the part in which the epigynous flower is attached to the ovary, a layer of small cells is formed. Before the perianth begins to wither, the cells in 3–6 tiers become slightly enlarged in this layer. Then the thickening and ligno-suberization of their cell-walls follows, and wood-gum occurs in the tracheids. The formation of thyloses can not be observed in this case. Immediately below this ligno-suberized layer, cell-division takes place and eventually a periderm-layer develops. In the parenchymatous tissue beneath the periderm, some cells in groups change

into stone-cells ; the number of cells in a group is rather variable, 5–40 being counted in optical sections of these groups. Their walls become thick, lignified and richly pitted. These groups of stone-cells are scattered in the fruit flesh at a distance of only 2–4 mm below the periderm.

5. Menyanthes trifoliata.

At the base of the corolla, the tissue consists of small cells of isodiametric shape. Before the withering of the corolla, the plasmatic

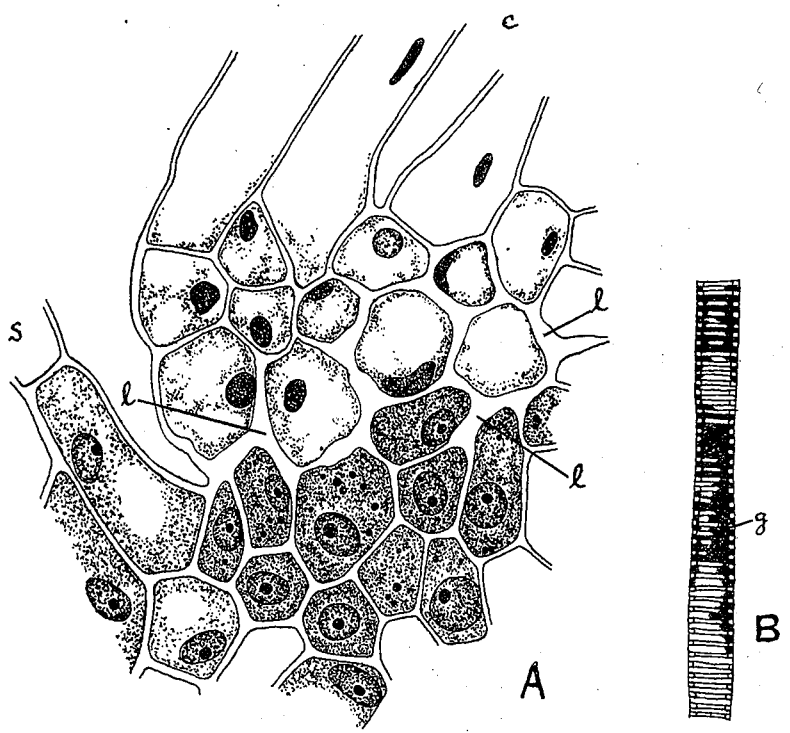

Fig. 16. *Menyanthes trifoliata.* A. Basal part of the petal. *l*, lignified cell-wall; *s*, sepal ; *c*, Corolla. B. A piece of the tracheid in the lignified layer. *g*, gum-like substance in the cavity. ca. 625/1.

contents increase in this tissue, and in a few tiers of cells, which are situated at the upper portion of this tissue, the cells become slightly enlarged, and their walls become thick and lignified. These lignified walls often show a slight suberization. The plasmatic contents of these lignified cells diminish gradually and finally disorganize (Fig. 16). All the living cells in this layer undergo this

change. The thickness of the layer of lignified tissue is found, in the region of the vascular bundles, in which all the elements have an elongated shape, to be larger than in the ordinary parenchymatous tissue. Wood-gum stops the cavities of the tracheids in the lignified layer, and also occurs in some lignified cells of the parenchyma. During the process of lignification no change can be observed in the layer with rich plasmatic contents lying immediately below this lignified layer.

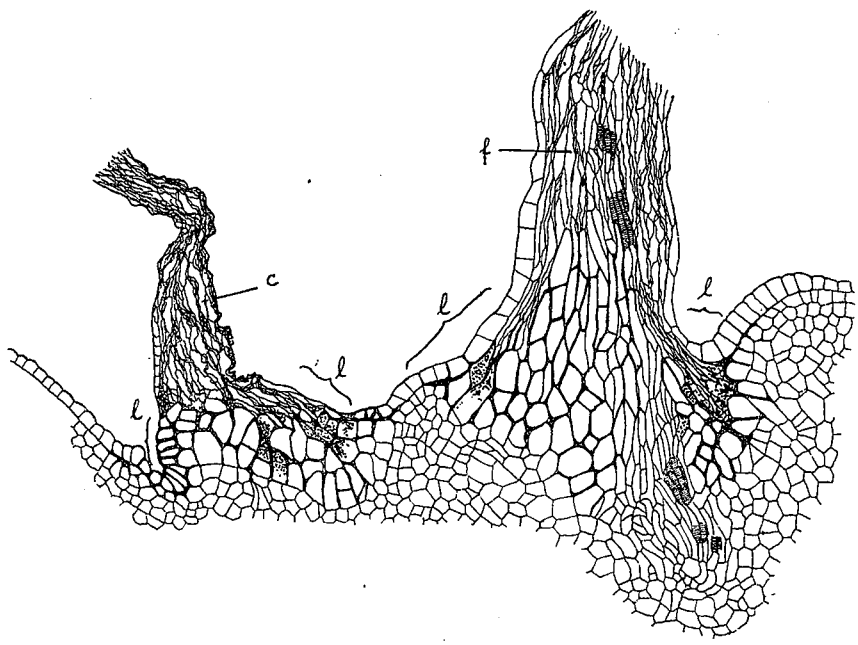

Fig. 17. *Platycodon grandiflorum.* Lignified layer at the receptacle. *l*, lignified layer ; *f*, filament ; *c*, corolla. ca. 110/1.

6. Platycodon grandiflorum.

At the base of the petal, filament and style, no special differentiation of the tissue can be observed. The elongated shape of the parenchymatous cells in these organs changes gradually to isodiametric form at the insertion. The size of these cells in this region is, on the whole, identical with that of the ovary-wall and of the receptacle. The withering of the petal, filament and style is brought about by the lignification of the tissue at the insertion of these organs. The thickness of the lignified layer is, according to circumstances, rather variable e. g. from 3–10 tiers of cells (Fig. 17).

The lignification occurs throughout all the living cells of this layer, and their cell-walls become thick and irregularly pitted. Wood-gum stops up the cavities of the tracheids and often occurs also in some parenchymatous cells of this layer in the form of drops. Afterwards the lignification takes place over the whole surface of the receptacle in the epidermis and in 1–2 rows of the parenchymatous cells beneath it. The thickening of the membrane is, in this case, specially noticeable in the tangential wall between the epidermis and the inner fundamental tissue. By microchemical tests a slight suberization can generally be detected in the lignified membrane.

The features observed in this plant agree on the whole with the results of REICHE in *Campanula, Specularia* and *Jasione.* He reported that the corolla of these plants withered after the flowering and that the connecting tissue between the ovary and corolla assumed a woody character.

7. Ribes Grossularia.

In the cases of *Ribes Grossularia, R. oxycanthoides, R. rubrum* and *R. nigrum,* the process of the anatomical change at the perianth takes place, on the whole, in the same way, and the following description applies to *Ribes Grossularia.*

The tissue at the base of the corolla and style is not differentiated as a separation-layer, but the cells in it are smaller than those in the neighbouring tissue. After the flowering, the ligno-suberization of the cell-walls takes place in a layer of 3–5 tiers of cells at the base of the perigone. The ligno-suberized layer has the form of a convex plane which slopes downwards towards the axil of the perigone, so that the layer meets the outer surface at a height of 1/2–1/3 mm above the insertion. In this layer, wood-gum occurs in the tracheids stopping up their cavities. The perianth above this layer withers and dries but is never cast off. The style withers gradually from the top and assumes a dark colour. The withering, however, usually does not reach to the base until the fruit ripens. Between the dead and living tissue we can observe no sign of ligno-suberization nor any other changes of the cell-membrane.

As is evident in these examples, the tissue, in which the lignification or ligno-suberization occurs, consists of smaller cells than those of the corresponding tissue outside this region. With regard

to the separation-zone, this peculiarity has been noticed by practically every worker on abscission problems. Besides this, judging from the course of the development of this tissue, as traced by KENDALL (1918), NAMIKAWA (1922) and others, it is doubtless that this tissue has remained without expansion during the intercalary growth on one or both sides of it. To keep the characters of young tissue in this region may be a convenient arrangement for the accomplishment of the sudden change of separation or ligno-suberization etc.

As seen in the cases of the catkin-stalk of *Corylus,* the perigone of *Hosta* and the stalk of the male flower of *Cucumis,* where the tissue is not definitely differentiated at the base of an organ, the situation in which the separation or ligno-suberization takes place, is not strictly determined. Such a case as KENDALL reported in *Datura,* that no peculiarity of morphological differentiation was present at the pedicel-base, in which the abscission was to be carried out, may be regarded as an extreme example. He noticed in this case "that cell-separation is possible in several different types of living cells" and "that separation takes place more readily in small cells than in large ones and more readily in isodiametric cells than in elongated ones". He made a remark, applying the statement of LLOYD and LOEWI "that the separation-layer is not a morphologically differentiated structure, but represents a physiological condition". It can be ascertained that the more strictly localized and differentiated the tissue is, the more precisely determined is the situation of the change. It is interesting to see that, even in the same individual, the mode of shedding becomes modified corresponding to the differentiation of the organs, as may be seen by comparing the female with the male flowers and with the stalk of the latter in *Cucumis.*

It has been thought that the shedding of an organ being brought about by a lysigenous process in the tissue is rare in higher plants. In *Aristolochia* a mode of abscission which was accomplished by a passive breaking of the tissue at the base of the leaf, was reported by TISON (1900). But the evidence is doubted by LOEWI (1907). HANNIG (1913) observed the abscission of the flower in *Mirabilis Jalapa* and *Oxybaphus viscosus* and stated that the abscission was brought about by the disorganization and dissolution of the tissue in the separation-layer. LLOYD repeated an anatomical study in *Mirabilis Jalapa* and claimed that the separation was accomplished by the

usual separation of the cells in the tissue. The case of *Iris*, in which the perigone is shed by the disorganization of the tissue at the insertion, may be cited as a noteworthy example.

IV. Osmotic Pressure in Catkins.

The osmotic pressure has been measured in the separation-zone and at the lower part of the catkin-stalk at different stages, and some measurements also have been made, for comparison with these, in some other floral organs. The plasmolytic method was applied for this purpose, using potassium nitrate solutions in different concentrations, which are indicated in the following tables by numbers representing 1/100 molar concentrations; thus 10 means 10/100 M. Fresh sections of the material were put into the solution and after immersion for 20 minutes they were taken out and observed. The grade of plasmolysis has been indicated in the following way: very slightly + ; slightly or less than half way round the plasmatic membrane ++ ; half +++ ; more than half $\overset{+}{+++}$; completely plasmolysed $\overset{++}{+++}$. As the osmotic pressure of individual cells always differs to some extent, so the measurement refers to the grade of plasmolysis shown by the great majority of the cells in the tissue in a solution of the concentration noted in the tables.

1. Alnus japonica.

To see the variation and the fluctuation of the osmotic pressure in different tissues of the catkin at different stages, determinations were made for the catkin-stalk, catkin-axis, separation-zone, some floral organs and the separation-cells in their operation, in the case of both male and female catkins. The results are given in Tables I-XII.

TABLE I.

Alnus japonica. March 13. Material: Young male catkins, at the stage before the elongation of the catkin-axis.

Example 1.

Concentration of the solution.	10	15	20	25	30	35
Separation-zone.	−	+	+++	++ +++	++ +++	++ +++
Cortex of the catkin-stalk.	−	−	−to++	+++	++ +++	++ +++
Epidermis of the catkin-stalk.	−	−	−	−	+	+

Example 2.

Concentration of the solution.	10	15	20	25	30	35
Separation-zone.	−	+	+++	+ +++	++ +++	....
Cortex of the catkin-stalk.	−	−	−to++	−to + ++	+ +++	++ +++
Epidermis of the catkin-stalk.	−	−	−	−	−	++

Example 3.

Concentration of the solution.	10	15	20	25	30	35
Separation-zone.	−	−	+++	+ +++	++ +++	....
Cortex of the catkin-stalk.	−	−	++	+++	++ +++	....
Epidermis of the catkin-stalk.	−	−	−	−	−	++

TABLE II.

Alnus japonica. March 13. Material : Same as Table I.

Example 1.

Concentration of the solution.	11	12	13	14	15	16	17	18	19	20
Separation-zone.	−	−	−	+	+	+	++	++	++	+++
Cortex of the catkin-stalk.	−	−	−	−	−	−	+	+	++	++
Epidermis of the catkin-stalk.	−	−	−	−	−	−	−	−	−	−

Example 2.

Concentration of the solution.	11	12	13	14	15	16	17	18	19	20
Separation-zone.	−	−	+	+	+	++	++	+++	+++	+++
Cortex of the catkin-stalk.	−	−	−	−	−	−	−	+	+	++
Epidermis of the catkin-stalk.	−	−	−	−	−	−	−	−	−	−

Example 3.

Concentration of the solution.	11	12	13	14	15	16	17	18	19	20
Separation-zone.	−	−	+	+	+	+	++	++	+++	+++
Cortex of the catkin-stalk.	−	−	−	−	−	−	−	+	+	++
Epidermis of the catkin-stalk.	−	−	−	−	−	−	−	−	−	−

TABLE III.

Alnus japonica. March 17. Material: Newly collected male catkins in the similar conditions as above.

Example 1.

Concentration of the solution.	10	15	20	25	30	35
Outer cortex of the separation-zone.	−	+	++	+++	+ +++	++ +++
Inner cortex of the separation-zone.	−	+	++	+ +++	++ +++	....
Outer cortex of the catkin-stalk.	−	−	+	++	+++	++ +++
Inner cortex of the catkin-stalk.	−	−	++	+ +++	++ +++	.. .
Sheath of the vascular bundle.	+	+++	++ +++	....	....	....
Epidermis of the catkin-stalk.	−	−	−	−	+	++

Example 2.

Concentration of the solution.	10	15	20	25	30	35
Outer cortex of the separation-zone.	−	+	++	+++	+ +++	++ +++
Inner cortex of the separation-zone.	−	+	+++	++ +++	....	....
Outer cortex of the catkin-stalk.	−	−	+	++	+ +++	++ +++
Inner cortex of the catkin-stalk.	−	+	++	+++	++ +++	....
Sheath of the vascular bundle.	+	++	+ +++	++ +++	....	....
Epidermis of the catkin-stalk.	−	−	−	−	−	++

TABLE IV.

Alnus japonica. March 17. Material: Same as above.

Example 1.

Concentration of the solution.	10	11	12	13	14	15	16	17	18	19	20
Outer cortex of the catkin-stalk.	−	−	−	−	−	−	−	−	−	+	+
Inner cortex of the catkin-stalk.	−	−	−	+	+	+	++	++	++	+++	+++
Outer cortex of the separation-zone.	−	−	−	−	−	+	+	+	++	++	+++
Inner cortex of the separation-zone.	−	−	+	+	+	+	++	++	+++	+++	+++
Sheath of the vascular bundle.	++	++	++	+++	+++	+++	+ +++	+ +++	+ +++	++ +++	....

Example 2.

Concentration of the solution.	10	11	12	13	14	15	16	17	18	19	20
Outer cortex of the catkin-stalk.	−	−	−	−	−	−	−	−	−	−	+
Inner cortex of the catkin-stalk.	−	−	−	−	−	−	+	+	+	++	++
Outer cortex of the separation-zone.	−	−	−	−	−	−	+	+	+	++	++
Inner cortex of the separation-zone.	−	−	+	+	+	++	++	++	+++	+++	+++
Sheath of the vascular bundle.	+	+	++	++	++	+++	+++	+ +++	+ +++	+ +++	++ +++

Example 3.

Concentration of the solution.	10	11	12	13	14	15	16	17	18	19	20
Outer cortex of the catkin-stalk.	−	−	−	−	−	−	−	−	−	+	+
Inner cortex of the catkin-stalk.	−	−	−	−	−	+	+	+	++	++	++
Outer cortex of the separation-zone.	−	−	−	−	−	+	+	+	++	++	++
Inner cortex of the separation-zone.	−	−	−	+	+	+	++	++	++	+++	+++
Sheath of the vascular bundle.	+	++	++	++	+++	+++	+++	+ +++	+ +++	+ +++	++ +++

TABLE V.

Alnus japonica. April 1. Material: Male catkins collected on the 30th of March and kept in the laboratory. In most of the catkins anthesis is occurring.

Example 1.

Concentration of the solution.	19	20	21	22	23	24	25
Outer cortex of the catkin-stalk.	−	−	−	−	−	−	+
Innermost cortical cells of the catkin-stalk.	−	+	++	++	++	+++	+++
Outer cortex of the separation-zone.	−	−	−	−	−	+	+
Inner cortex of the separation-zone.	−	−	−	+	+	++	++

From these tables the following results may be abstracted.

1. The osmotic pressure in the catkin-stalk and the separation-zone of young male catkins of *Alnus japonica* increases until towards the flowering time.

2. The osmotic pressure in the cortex of the separation-zone is lower than in the corresponding part of the cortex of the catkin-stalk.

Example 2.

Concentration of the solution.	19	20	21	22	23	24	25
Outer cortex of the catkin-stalk.	−	−	−	−	−	−	+
Innermost cortical cells of the catkin-stalk.	−	+	++	....	....	....	....
Outer cortex of the separation-zone.	−	−	−	−	+	++	++
Inner cortex of the separation-zone.	−	−	+	+	++	....	....
Sheath of the vascular bundle.	++	+++	+++	+ +++	....	....	....

3. Both in the catkin-stalk and in the separation-zone, the inner tissue shows a lower osmotic pressure than the outer tissue. The parenchymatous cells of elongated shape surrounding the vascular bundles show the lowest value of osmotic pressure.

Table VI.

Alnus japonica. April 4. Material: In early (further advanced) catkins, some cells in the separation-layer are enlarged and have begun to separate.

Example 1.

Concentration of the solution.	20	25	30	35	40	45
Outer cortex of the catkin-stalk.	−	−	−	++	+++	....
Inner cortex of the catkin-stalk.	−	−	+	+++	....	....
Outer cortex of the separation-zone.	−	+	++	....	....	....
Inner cortex of the separation-zone.	−	+	++	....	....	....
Enlarged cells in the separation-layer.	−	−	−	−	+	++

Example 2.

Concentration of the solution.	20	25	30	35	40	45
Outer cortex of the catkin-stalk.	−	−	−	−	++	....
Inner cortex of the catkin-stalk.	−	−	+	+++	....	....
Outer cortex of the separation-zone.	−	+	++	....	....	....
Inner cortex of the separation-zone.	−	+	++	....	....	....
Enlarged cells in the separation-layer.	−	−	−	−	+	++

Example 3.

Concentration of the solution.	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Outer cortex of the catkin-stalk.	..	..	..	..	..	..	..	−	−	−	−	+	+	++	++	..	..	..	..
Inner cortex of the catkin-stalk.	..	..	−	−	−	+	+	+	++	..	..	..	..	..	..	..	..	..	..
Outer cotex of the separation-zone.	−	−	+	+	++	++	..	..	..	..	..	..	..	..	..	..	..	..	..
Inner cortex of the separation-zone.	−	+	+	++	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Separation-cells.	..	..	..	..	..	..	..	..	..	..	..	..	−	−	−	−	+	+	++

Example 4.

Concentration of the solution.	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Outer cortex of the catkin-stalk.	..	..	..	..	..	..	..	−	−	−	−	+	+	++	++	..	..	..	..
Inner cortex of the catkin-stalk.	..	..	−	−	−	−	+	+	+	++	..	..	..	..	..	..	..	..	..
Outer cortex of the separation-zone.	−	−	+	+	+	++	..	..	..	..	..	..	..	..	..	..	..	..	..
Inner cortex of the separation-zone.	−	+	+	+	++	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Separation-cells.	..	..	..	..	..	..	..	..	..	..	..	..	−	−	−	+	+	..	..

Example 5.

Concentration of the solution.	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Outer cortex of the catkin-stalk.		..	..	..	..	..	..	−	−	+	+	++	++	..	..	..	..	..	..
Inner cortex of the catkin-stalk.	..	..	..	−	−	+	+	+	++	..	..	..	..	..	..	..	..	..	..
Outer cortex of the separation-zone.	−	−	+	+	+	++	..	..	..	..	..	..	..	..	..	..	..	..	..
Inner cortex of the separation-zone.	−	+	+	+	++	++	..	..	..	..	..	..	..	..	..	..	..	..	..
Separation-cells.	..	..	..	..	..	..	..	..	..	..	..	..	−	−	−	−	+	+	++

From these measurements the following results are obtained.

1. The osmotic pressure in the cortex of the catkin-stalk and separation-zone becomes higher in this stage than in the previous cases.

2. Both in the catkin-stalk and in the separation-zone, the outer cortex has higher osmotic pressure than the inner. The osmotic pressure of the unchanged cells in the separation-zone is lower than in the stalk.

3. The cells, which have become enlarged as a first step in the process of separation, show the highest pressure among the investigated tissues.

The osmotic pressure of some other floral organs situated in the middle region of the catkin was measured at the time of the anthesis and the separation. The results are as follows.

TABLE VII.

Alnus japonica. April 1. Material: Same material as in Table V. Anthesis is just beginning.

Example 1.

Concentration of the solution.	20	25	30	35	40	45	50	55	60
Cortex of the catkin-axis.[1]	−	+	+++	++ +++	....	....	....	....	....
Epidermis of the axis.	−	−	++	+++	++ +++	....	....	....	....
Epidermis of the bract.[2]	−	−	−	−	−	−	−	−	+
Upper surface of the perigone.	−	−	−	−	−	++	+++	++ +++	....
Under surface of the perigone.	−	−	−	−	−	−	+	+++	+ +++
Filament.	−	−	−	++	+ +++	++ +++	....	....	....

Example 2.

Concentration of the solution.	20	25	30	35	40	45	50	55	60
Cortex of the catkin-axis.[1]	−	+	+++	++ +++	....	....	....	....	....
Epidermis of the axis.	−	−	+	++	+ +++	....	....	....	....
Epidermis of the bract.[2]	−	−	−	−	−	−	−	+	+++
Upper surface of the perigone.	−	−	−	−	+	+++	+ +++	++ +++	....
Under surface of the perigone.	−	−	−	−	−	−	+	+++	+ +++
Filament.	−	−	−	+	++	+ +++	++ +++	....	....

1) In this case, no evident difference of osmotic pressure could be found between the inner and outer cortex.

2) Observations were made in those cells which are situated on the outer or morphological under surface of the bract.

TABLE VIII.

Alnus japonica. April 4. Material: Same material as in Table VI. The separation is taking place in the separation-layer.

Example 1.

Concentration of the solution.	10	15	20	25	30	35
Cortex of the catkin-axis.	−	+	+++	+ +++	++ +++	....
Epidermis of the axis.	−	−	++	+++	+ +++	++ +++
Epidermis of the bract.	−	−	−	+	++	+++
Upper surface of the perigone.	−	−	++	+++	+ +++	++ +++
Under surface of the perigone.	−	−	+	++	+ +++	++ +++
Filament.	−	−	+	++	+ +++	++ +++

Example 2.

Concentration of the solution.	10	15	20	25	30	35
Cortex of the catkin-axis.	−	+	+++	+ +++	++ +++	....
Epidermis of the axis.	−	−	++	+++	+ +++	++ +++
Epidermis of the bract.	−	−	+	++	+++	+ +++
Upper surface of the perigone.	−	+	++	+ +++	++ +++	....
Under surface of the perigone.	−	−	+	++	+ +++	++ +++
Filament.	−	−	+	++	+ +++	++ +++

At the time of the anthesis, the osmotic pressure in the tissues of the floral organs examined (Table VII) is higher than in the catkin-axis (Table VII) and catkin-stalk (Table V), and the pressure in the cortex of the catkin-axis is generally higher than in the cortex of the catkin-stalk (Table V). At the time of separation, the pressure in the cortex of the catkin-axis has become, as represented in Table VIII, far lower than in the cortical tissue of the catkin-stalk in the same stage (Table VI) and in the corresponding tissue of the catkin-axis in the previous stage (Table VII). As can be seen by comparing Tables VII and VIII, the osmotic pressure in the tissues of all the organs examined decreases noticeably during the time from anthesis to the separation. It is interesting to note that, between the stages of anthesis and separation, the changes in osmotic

pressure in the flowering part of the catkin are in reverse direction to those taking place in the catkin-stalk and separation-zone, the pressure decreasing in the former case and increasing in the latter (compare Tables VII and VIII with V and VI).

For comparison with the result for male catkins, the osmotic conditions were also observed in the female catkin at the stage preceding and of anthesis, and at the time of separation, which is induced by the artificial removal of the head of the catkin.

TABLE IX.

Alnus japonica. March 17. Material: Newly collected young female catkins before their anthesis. Measurements were made in the basal portion of the catkin-stalk.

Example 1.

Concentration of the solution.	7	8	9	10	11	12	13	14	15
Outer cortex of the stalk.	−	−	−	−	−	−	−	+	+
Inner cortex of the stalk.	−	−	−	−	−	+	+	++	++
Outer cortex of the separation-zone.	−	−	−	−	+	+	++	++	+++
Inner cortex of the separation-zone.	−	−	−	+	+	++	++	+++	+++

Example 2.

Concentration of the solution.	7	8	9	10	11	12	13	14	15
Outer cortex of the stalk.	−	−	−	−	−	−	+	+	++
Inner cortex of the stalk.	−	−	−	−	+	+	++	++	....
Outer cortex of the separation-zone.	−	−	−	+	+	++	++	....	....
Inner cortex of the separation-zone.	−	−	+	+	++	++	+++	....	....

Example 3.

Concentration of the solution.	7	8	9	10	11	12	13	14	15
Outer cortex of the stalk.	−	−	−	−	−	−	−	+	+
Inner cortex of the stalk.	−	−	−	+	+	++	++	....	....
Outer cortex of the separation-zone.	−	−	−	+	+	++	....	....	....
Inner cortex of the separation-zone.	−	+	+	++	++	+++	....	....	....

It is seen that in the female catkin, as in the male, the outer cortex of the stalk and of the separation-zone has a higher osmotic

pressure than the inner cortex. The pressure in the cortex of the separation-zone is lower than in the corresponding tissue of the stalk. The osmotic pressure of the innermost cortical cells in the stalk is far lower than the value given above in Table IX for the inner cortex. Though not included in Table IX, osmotic determinations were made for the innermost cortical cells and 5 was found to be the average value of the isotonic concentration.

TABLE X.

Alnus japonica. April 4. Material: Female catkins in receptive condition.

Example 1.

Concentration of the solution.	10	15	20	25	30	35	40
Outer cortex of the stalk.	−	−	−	−	+++	+ +++	++ +++
Inner cortex of the stalk.	−	−	++	+++	+ +++	++ +++	....
Outer cortex of the separation-zone.	−	−	++	+++	+ +++	++ +++	....
Inner cortex of the separation-zone.	−	+	++	+ +++	++ +++	....	....
Epidermis of the stalk.	−	−	−	−	++	+++	+ +++

Example 2.

Concentration of the solution.	10	15	20	25	30	35	40
Outer cortex of the stalk.	−	−	−	−	−	+	++
Inner cortex of the stalk.	−	−	−	−	−	++	+ +++
Outer cortex of the separation-zone.	−	+	++	+ +++	++ +++	....	....
Inner cortex of the separation-zone.	−	++	+++	++ +++	....	....	....
Medulla in the stalk.	−	−	−	+	++	+ +++	++ +++

Example 3.

Concentration of the solution.	10	15	20	25	30	35	40
Outer cortex of the stalk.	−	−	−	−	+	+++	+ +++
Inner cortex of the stalk.	−	−	−	−	++	+++	++ +++
Outer cortex of the separation-zone.	−	−	+	++	+ +++	++ +++	....
Inner cortex of the separation-zone.	−	+	++	+++	++ +++	....	....
Medulla in the stalk.	−	−	−	+	++	+++	++ +++

In a similar manner as in the male catkin, the osmotic pressure in the separation-zone and catkin-stalk of the female catkin increases at the time of anthesis. Also at this stage the separation-zone shows a lower osmotic pressure than the epidermis, cortex and medulla of the base of the stalk.

At the same stage of anthesis as that represented in Table X, the osmotic pressure in some floral organs was measured. The results are as follows:—

TABLE XI.

Alnus japonica. April 4. Material: Same as Table X.

Example 1.

Concentration of the solution.	10	15	20	25	30	35	40	45	50	55	60
Cortex of the catkin-axis.	−	+	++	+++	+ +++	++ +++	....	....	....	....	....
Medulla of the catkin-axis.	−	++	+++	+ +++	++ +++	....	....	....	....	....	....
Parenchyma at the base of the ovary.	−	−	−	−	−	+	++	+++	++ +++	....	....
Parenchyma in the ovary-wall.	−	−	−	−	−	−	−	−	+	+++	+ +++
Stigma.	−	−	−	−	−	−	−	−	−	−	++

Example 2.

Concentration of the solution.	10	15	20	25	30	35	40	45	50	55	60
Cortex of the catkin-axis.	−	−	+	++	+++	++ +++	....	....	....	....	....
Medulla of the catkin-axis.	−	+	++	+++	+ +++	++ +++	....	....	....	....	....
Parenchyma at the base of the ovary.	−	−	−	−	−	−	+	++	+ +++	++ +++	....
Parenchyma in the ovary-wall.	−	−	−	−	−	−	−	−	+	++	+++
Stigma.	−	−	−	−	−	−	−	−	−	−	+

The osmotic pressure in the catkin-axis is lower than in the stalk of the same stage. It is noteworthy that the tissue of the floral organs show a noticeable high pressure, especially in the case of the stigma.

On the 19th April, some branches with female catkins on them were collected and kept in the open air placed in a bottle with water, and all the catkins were removed leaving their stalks on the branch. On the 25th April this material was examined, and osmotic

determinations were made in the stalk and the separation-zone. In the latter the process of separation was just beginning.

TABLE XII.

Alnus japonica. April 25. Material: Stalk of the female catkin at the beginning of the separation.

Example 1.

Concentration of the solution.	20	25	30	35	40	45	50	55
Outer cortex of the stalk.	−	−	−	+	+++	+ +++	++ +++	....
Inner cortex of the stalk.	−	−	+	++	+ +++	++ +++	....	....
Outer cortex of the separation-zone.	−	−	−	++	+++	+ +++	++ +++	....
Inner cortex of the separation-zone.	−	+	++	+ +++	++ +++	....	....	....
Medulla in the stalk.	−	−	−	−	++	+ +++	++ +++	....
Enlarged separation-cells.	−	−	−	−	−	−−	++	+ +++

Example 2.

Concentration of the solution.	20	25	30	35	40	45	50	55
Outer cortex of the stalk.	−	−	−	++	+++	+ +++	++ +++	....
Inner cortex of the stalk.	−	−	+	+++	+ +++	++ +++	....	....
Outer cortex of the separation-zone.	−	+	++	+++	++ +++	....	....	....
Inner cortex of the separation-zone.	+	++	+ +++	++ +++	....	....	....	....
Medulla in the stalk.	−	−	−	+	+++	+ +++	++ +++	....
Enlarged separation-cells.	−	−	−	−	−	−	−	+

Example 3.

Concentration of the solution.	20	25	30	35	40	45	50	55
Outer cortex of the stalk.	−	−	−	+	++	+ +++	++ +++	....
Inner cortex of the stalk.	−	−	+	++	+ +++	++ +++	....	....
Outer cortex of the separation-zone.	−	−	+	++	+ +++	++ +++	....	....
Inner cortex of the separation-zone.	−	+	++	+++	++ +++	....	....	....
Medulla in the stalk.	−	−	−	+	++	+++	++ +++	....
Enlarged separation-cells.	−	−	−	−	−	−	−	+

In this case, the cortex and medulla in the stalk, and the cortex in the separation-zone show a higher osmotic pressure than that in the normal female catkin at the time of anthesis as represented in Table X. Among all the tissues examined enlarged separation-cells in the separation-layer show the highest pressure, and the medulla in the stalk comes next as regards pressure. The osmotic pressure of unchanged cortical tissue of the separation-zone is lower than in the corresponding tissue in the stalk. In the stalk as well as in the separation-zone, the outer cortex shows a higher osmotic pressure than the inner.

2. Alnus hirsuta.

In some male catkins newly collected on the 15th April, enlargement of the separation-cells was taking place in the separation-layer. The osmotic pressure of different tissues in the base of the stalk was measured at this stage, and the following results were obtained.

TABLE XIII.

Alnus hirsuta. April 15. Material: Male catkins, separation process just commencing.

Example 1.

Concentration of the solution.	15	20	25	30	35	40	45
Outer cortex of the stalk.	−	−	+	+++	+ +++	++ +++	....
Inner cortex of the stalk.	−	−	+	+++	++ +++	....	....
Outer cortex of the separation-zone.	−	+	++	+ +++	++ +++	....	....
Inner cortex of the separation-zone.	−	+	+++	++ +++	....	....	....
Enlarged separation-cells.	−	−	−	−	−	++	+ +++

Example 2.

Concentration of the solution.	15	20	25	30	35	40	45
Outer cortex of the stalk.	−	−	−	+	+++	+ +++	++ +++
Inner cortex of the stalk.	−	−	+	++	+ +++	++ +++	....
Outer cortex of the separation-zone.	−	−	+	++	+ +++	++ +++	....
Inner cortex of the separation-zone.	−	+	++	+++	++ +++	....	....
Enlarged separation-cells.	−	−	−	−	−	−	++

The isotonic value of the osmotic pressure in the enlarged separation-cells is rather variable. Twenty measurements were made for these cells and the results were found as follows.

38,39,39,40,40,40,40,41,41,41,
41,41,41,41,41,41,41,42,42,43.

The isolated cells appearing in a heap on the scar after the abscission show far lower osmotic pressure as represented below :

20,20,21,21,22,23,23,23,23,24,
24,24,24,24,24,24,24,25,25,26.

3. Corylus Sieboldiana.

On the 19th April, osmotic determinations were made for the tissues in the base of the stalk of the male catkin at its anthesis. The separation-zone is not obviously differentiated in this case and also differences in the osmotic pressure between different zones at the base of the stalk could not be found. The average isotonic value of the osmotic pressure out of five examples was 18 in the outer cortex and 12 in the inner cortex. On the 25th of April, when the separation of cells was taking place in the separation-layer, the isotonic concentration taking an average of five examples of each case, became 24 in the outer cortex and 19 in the inner cortex. The separation-cells showed a far higher pressure than these, and 44 was found to be average value for ten measurements.

4. Salix rorida.

In some male catkins collected on the 21st of April, the separation process was beginning. The osmotic pressure at the base of the catkin-stalk was very low. The average isotonic concentration was, for five examples of each, 6 in the cortex of the stalk and 5 in the separation-zone. All the cells of the medulla at the base of the stalk plasmolysed in the solution of 5/100M. This condition is quite different from the case of the female catkin of *Alnus japonica,* in which the medulla showed a higher osmotic pressure than the cortex. Enlarged separation-cells in the separation-layer showed a very high osmotic pressure, measuring 49 on a average of 20 examples. The osmotic pressure of the isolated cells on the separation-plane after the abscission was noticeably variable, and measured 11–38.

It is noticeable in the separation process that the separation-cells

showed in every case a higher osmotic pressure, which seems to perform an important rôle in the process. With regard to the mechanism of the cell-separation in the separation-layer, several statements have been made by different writers. FITTING (1911) noted that the rapid isolation of cells in the separation layer was due mainly to the rapid increase of turgidity in the cells. According to TISON (1900), LEE (1911), HANNIG (1913), STRASBURGER (1913), LLOYD (1916a, 1916b), SAMPSON (1918), KENDALL (1918), HODGSON (1918) etc. the separation of the cells was brought about principally by the dissolution of the middle lamellae of the cell-walls. LOEWI (1906) classified six methods of separation viz. (1) rounding off of the cells, (2) dissolution of the middle lamellae, (3) maceration, (4) increase of turgidity, (5) cell-elongation (Schlauchzell-mechanismus) and (6) hard-cell-mechanism. He also remarked that some of these methods might act in combination. He also noted that by changing the external conditions such as temperature, humidity etc. one can produce modifications of the method of cell-separation. WIESNER (1871, 1905), KUBART (1906), MOLISCH (1922 p. 202) etc. conceived that the increase of turgidity in cells and the dissolution of the middle lamellae were important processes occurring together. NAMIKAWA (1922) observed that the increase of osmotic pressure and turgidity, the dissolution of the middle lamellae and the enlargement of the cells participated in the separation process. Also in all the cases of abscission examined in the present work the same processes were found to be concerned in the separation.

REICHE (1885) and KUBART (1906) reported that an acid reaction could be obtained on the newly exposed surfaces after the abscission of an organ, and suggest that the disorganization of the middle lamellae might have been brought about by the action of the acid occurring there. WIESNER also was of the same opinion. Moreover, it can be anticipated that the action of acid or enzymes will help the hydrolysis of the membrane-substance. To explain this process precisely, further studies are necessary.

V. Osmotic Conditions of Floral Leaves.

For the measurement of the osmotic pressure in floral leaves, only the epidermal tissue was tested. In the mesophyll, observation is difficult or sometimes almost impossible owing to the abundant occurrence of intercellular spaces which contain air bubbles and

make the object indistinct. In most of the cases, however, the osmotic pressure of the mesophyll seems to be somewhat lower than that of epidermis. Differences of the osmotic pressure in individual plants can be seen even at the same stage of development and in the corresponding portion of the floral leaves of a species. The following measurements show, for instance, the individual variation of the isotonic concentration of petals of newly opened flowers.

Plants	Isotonic concentrations
Lilium elegans	25–30
Lilium cernuum	35–40
Pharbitis Nil	37–45
Prunus serrulata	35–43
Adonis amurensis	54–65

Such a variation might depend upon the internal or external conditions of the plants. In *Pogonia japonica* and *Prunus avium* (Black Tartarian) the variation was very small ranging from zero to 3. In practically every case, the variation of the osmotic pressure in individual cells in a section of a petal was generally very slight. The average value obtained from measurements at different stages of the development of floral leaves are represented in Table XIV, and the same results are also shown in a graph (Fig. 18).

TABLE XIV.

		Flower-bud	Beginning of the flower-opening	Full-bloom	At a later stage	Beginning of the defloration
Adonis amurensis	Isotonic concentration	70	54	62	50	35
	Lapse of time	0	3 days	1 day	3.5 days	10 days
Bougainvillaea glabra (bract)	Isotonic concentration	58	55	58	45	—
	Lapse of time	0	3 days	1 day	4 days	—
Corydalis ambigua	Isotonic concentration	57	48	48	45	—
	Lapse of time	0	2 days	1 day	3 days	—
Gagea lutea	Isotonic concentration	55	48	54	40	—
	Lapse of time	0	1 day	6 hours	4 days	—

Pharbitis Nil	Isotonic concentration	55	49	43	35	—	30
	Lapse of time	0	9 hours	3 hours	6 hours	—	9 hours
Prunus serrulata	Isotonic concentration	50		33	40	—	31
	Lapse of time	0		3 days	1 day	—	3 days
Prunus Mume	Isotonic concentration	48		31	41	—	24
	Lapse of time	0		2 days	15 hours	—	5 days
Prunus subhirtella var. autumnalis	Isotonic concentration	45		41	45	44	—
	Lapse of time	0		1 day	1 day	1 day	—
Prunus avium	Isotonic concentration	41		33	38	35	—
	Lapse of time	0		1 day	1 day	3 days	—
Lilium concolor	Isotonic concentration	40		36	40	38	—
	Lapse of time	0		9 hours	3 hours	3 days	—
Lilium cernuum	Isotonic concentration	35		29	38	35	—
	Lapse of time	0		9 hours	12 hours	3 days	—
Hosta japonica	Isotonic concentration	30		26	25	23	20
	Lapse of time	0		6 hours	5 hours	1.5 days	3 days
Lilium elegans	Isotonic concentration	28		24	28	28	27	20
	Lapse of time	0		9 hours	3 hours	1 day	1 day	4 days
Pogonia japonica	Isotonic concentration	18		15	16	16		14
	Lapse of time	0		1 day	1 day	5 days		2 days

As is evident in these results, there are two types of the change of the osmotic pressure in the petals and perigones: 1) the pressure becomes simply lower during the development of the floral leaves, and 2) the pressure decreases before the flowering, becomes increased rapidly at the time of the first opening and then shows a final decrease. Generally speaking in both of these cases, the floral leaf in the flower-bud shows a higher osmotic pressure than that of

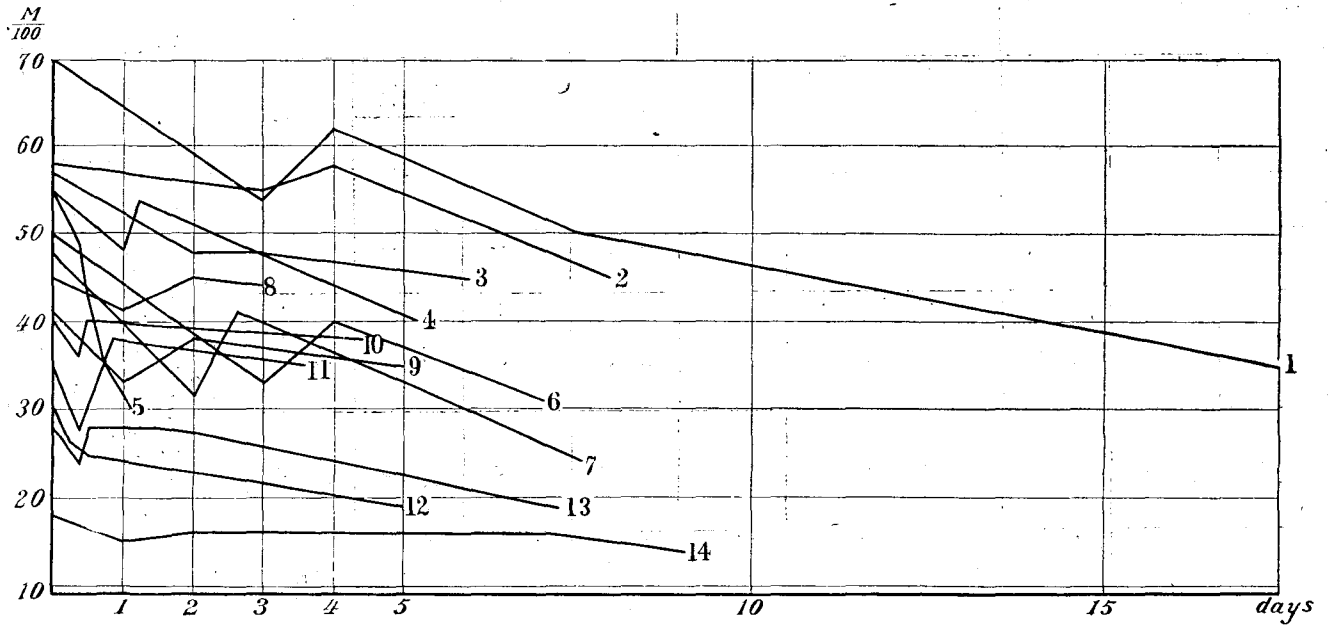

Fig. 18. The osmotic fluctuation in floral leaves. 1, *Adonis amurensis* ; 2, *Bougainvillaea glabra* ; 3, *Corydalis ambigua* ; 4, *Gagea lutea* ; 5, *Pharbitis Nil* ; 6, *Prunus serrulata* ; 7, *Prunus Mume* ; 8, *Prunus subhirtella var. autumnalis* ; 9, *Prunus avium* ; 10, *Lilium concolor* ; 11, *Lilium cernuum* ; 12, *Hosta japonica* ; 13, *Lilium elegans* ; 14, *Pogonia japonica*.

the floral leaves at later stages. *Corydalis, Pharbitis* and *Hosta* undergo the change of the first type and the other specimens show the fluctuation belonging to the second type. It is interesting that the bract of *Bougainvillaea glabra* also shows an osmotic change of the second type in a similar way to the petal or perigone.

The fluctuation of the osmotic pressure during the development of an organ is seen not only in the floral leaves, but also in some other organs. For comparison with the results obtained with floral leaves, other osmotic determinations were made for the foliage leaves of *Rhoeo discolor*. The osmotic pressure was measured in the epidermal tissue of the mid-rib of the under surface in the middle part of the leaf. The results were as follows :

Numbering of the leaves from below upwards.	Isotonic concentrations		
	Example 1	Example 2	Example 3
1	13	13	12
2	—	—	12
3	13	—	12
4	—	13	13
5	14	14	14
6	14	14	14
7	13	13	12
8	13	13	—
9	14	14	—
10	15	—	15
11	15	15	—

Also in this case, the osmotic pressure, which is higher in young leaves, decreases once, then increases and decreases again when the leaves are getting old.

Besides the osmotic pressure, the length and the weight of the floral leaf are the other characters which undergo a certain change during the process of flowering. It will be interesting to ascertain the relationship which might be found between these three characters. Changes of the average dry weight for a petal in species of Lilium have been traced, and the results are represented in grammes in Table XV.

TABLE XV.

stage of the flower	flower bud	do	flower just going to open	later stage	do	do	before the flower-fall
Hours between successive tests	0	5	10	10	5	25	30
Lilium speciosum	0.0821	—	0.0892	—	0.1059	0.0962	0.0851gr.
L. tigrinum	0.0732	—	0.0773	—	0.0937	0.0765	0.0569gr.
L. speciosum var. Tametomo	—	0.0560	0.0563	0.0591	—	—	0.0487gr.

The length, the dry weight and the osmotic pressure of the petals were measured simultaneously at different stages of flowering in *Adonis amurensis* and in *Prunus Mume*. The results are represented in Tables XVI, XVII, Figs. 19 and 20.

TABLE XVI.

Adonis amurensis.

Lapse of days.	0	3	1	3.5	6	4
Isotonic concentration.	70	54	62	50	—	35
Average length of a petal (cm.)	0.88	1.02	1.70	1.81	2.00	—
Average dry weight of a petal (mgr.)	0.73	0.92	1.46	1.73	1.80	1.63

TABLE XVII.

Prunus Mume.

Lapse of time (hours)	0	20	10	15	35	40
Isotonic concentration.	41	—	30	41	—	30
Average length of a petal (cm.)	0.93	1.22	1.47	1.85	1.90	—
Average dry weight of a petal (mgr.)	0.80	1.10	1.20	1.72	1.63	—

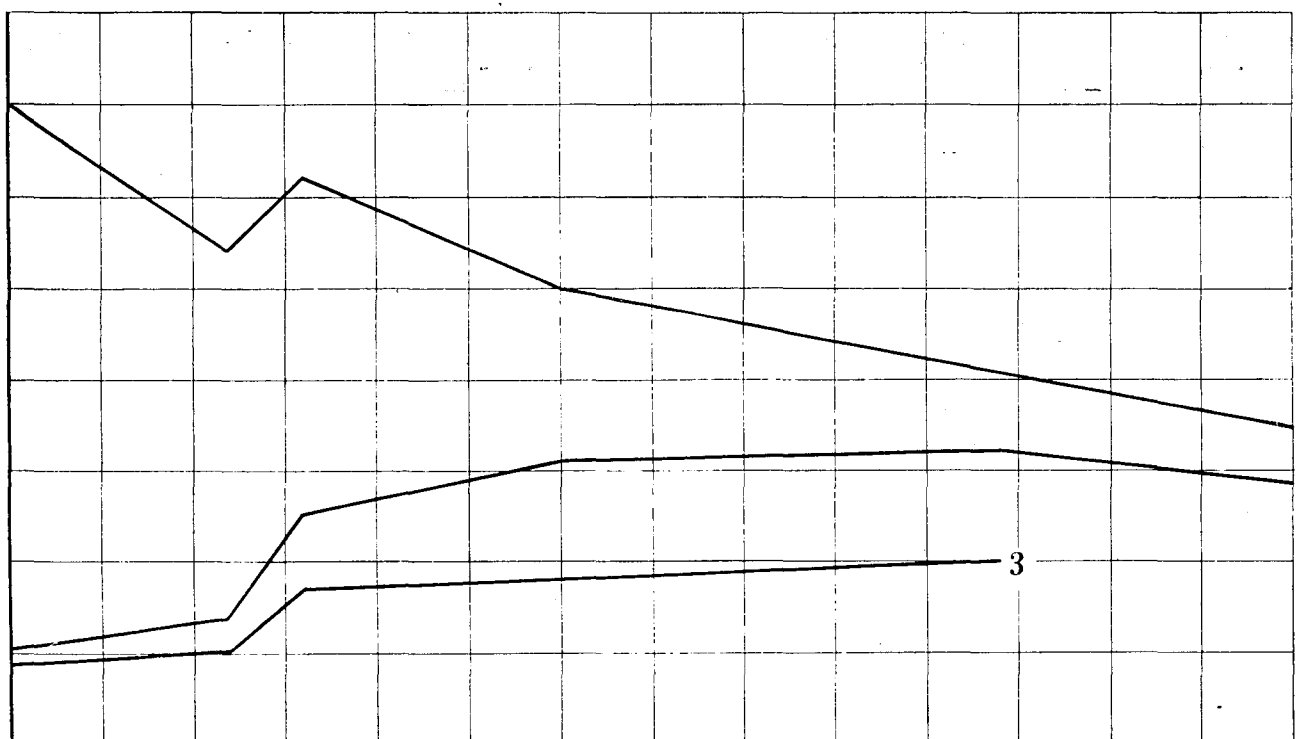

Fig. 19. *Adonis amurensis*. 1, the fluctuation of osmotic pressure; 2, the fluctuation of dry weight of a petal; 3, increase of average length of a petal.

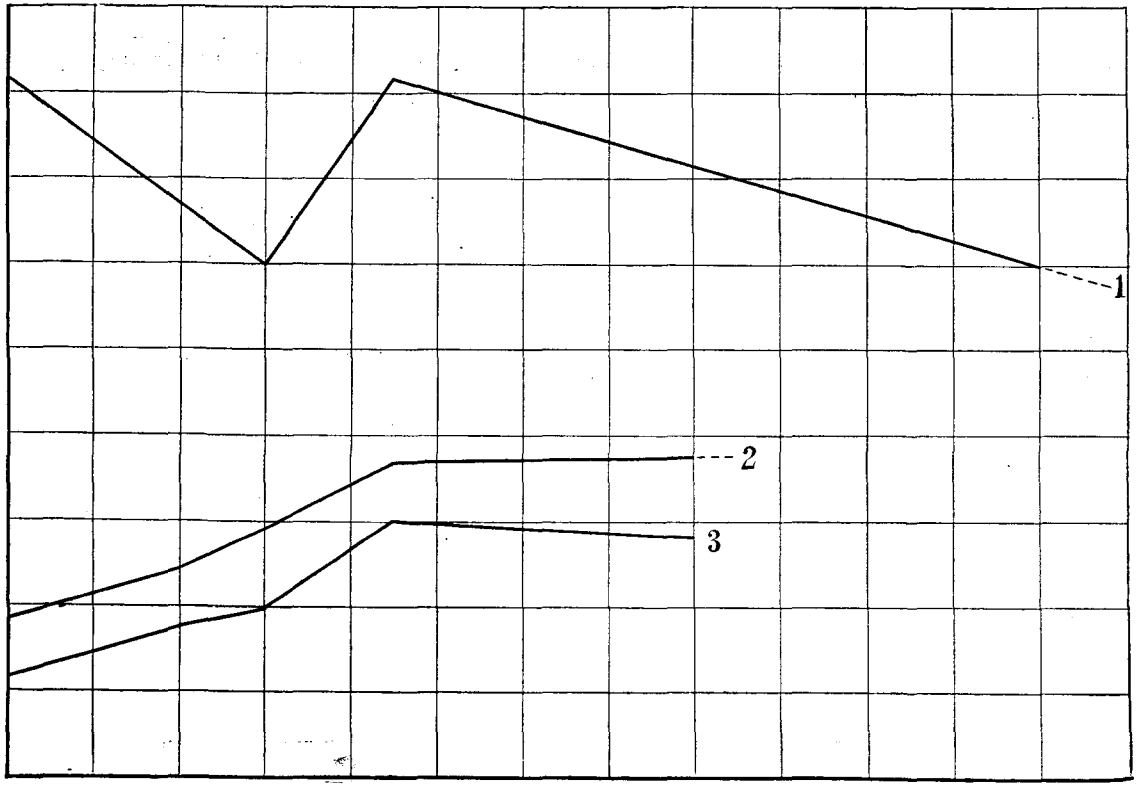

Fig. 20. *Prunus Mume.* 1, the fluctuation of osmotic pressure ; 2, average length of a petal ; 3, the fluctuation of dry weight of a petal.

From these results, it can be seen that the osmotic fluctuation is in close relation with the degree of growth and the change of the dry weight of the same organ. The period of the rapid rise of the osmotic pressure during the first opening of the flower coincides with the period of rapid increase of dry weight and the most vigorous growth of the petal. The growth of the petal becomes very slow after the flower has opened. In all cases, the dry weight decreases together with the osmotic pressure before defloration.

During the measurement of the osmotic pressure, it was found in the case of *Gagea lutea* and species of *Lilium*, in which the petals showed basipetal growth, that the pressure in the basal part of the petal was usually higher than in the apical part. In the case of petals which grow acropetally as in *Corydalis ambigua* and *Portulaca grandiflora* the osmotic pressure at the base was lower than that of the other parts. This relation depends probably upon the fact, that the osmotic pressure in the older tissue of the petal is always lower than that of younger tissue, or higher for a very short interval only. The evidence, that the younger tissue generally has higher osmotic pressure than the older one in different plants, is also observed by PRINGSHEIM (1906), HANNIG (1912), LUTMAN (1919) etc. URSPRUNG and BLUM (1916, a) reported that in the root, stem, leaf and leaf-stalk the osmotic pressure was generally higher at their base than at the top or end of these organs, and that the cells in the same layer of a tissue at the same height above the soil surface showed contiguous osmotic pressure. In the cells in different layers, however, the osmotic strength differed even in the same height. As a rule, the epidermis showed lower osmotic pressure than inner tissues. In young leaves the osmotic pressure was lower than in older ones. These results do not always agree with my present cases probably due to the difference of functions of the organ.

Low temperature retards the growth of the petal and has an influence on osmotic conditions. On cool autumn days, the petal of *Pharbitis Nil* opens very slowly, keeps fresh twice as long as in the summer time, and shows very slow decrease of osmotic pressure. Even twenty four hours after opening, the petal or an autumn flower, which is just going to wither, shows the isotonic concentration of its osmotic pressure 4–8 higher than the pressure measured 15 hours after the opening in the withering petal in summer time. The same influences can be brought about by a mechanical obstruction to the

growth of the petal. For this test, a few buds were covered with wet japanese paper before their opening. After 12 hours, the paper still wrapping the flower tightly becomes dry. The petal thus wrapped up is very much hindered in its growth and shows an osmotic pressure 4–6 higher than untreated control specimens. This result agrees with the observation of REED (1921) in the shoot of apricot and orange trees in which the osmotic pressure and the growth have a tendency to vary in opposite directions. Besides the influence of light, wind and soil moisture on the daily and annual variation in the osmotic pressure, URSPRUNG and BLUM (1916, b) noted that the strength of the osmotic pressure varied accompanying the temperature curve. They (1916, c) observed again that a rise in temperature over zero point up to ca. 10°C brought a lowering of osmotic pressure. The further rise in temperature, however, caused an increase of the pressure. This result might be compared with the case of *Pharbitis* which shows the variation influenced indirectly by the temperature.

DIXON and ATKINS (1910) reported in the leaf of *Syringa vulgaris* etc., that considerable variations in osmotic pressure were found under varying conditions specially of illumination and humidity as affecting evaporation and that the variations are probably due principally to fluctuations in the carbohydrate contents of the cells. They noticed the highest osmotic pressure in matured leaves. They noted with regard to *Syringa vulgaris* (in the later report, 1912), that after the final rise of osmotic pressure in the late summer a diminution in the pressure was registered in the sap from leaves just about to fall, and they thought that this diminution may be attributed to the transport of certain materials from the leaves. In another report by them (1916), it is described that the osmotic pressure of *Syringa vulgaris*, reached its maximum in August, rising irregularly after the opening of the buds. They observed no very pronounced diminution of osmotic pressure before the fall of the leaf. In this case, the concentration of carbohydrates in falling leaves is considerable. These results seem to contradict those of their former report (1912). URSPRUNG and BLUM (1918, a and b) observed that the absorbing power in epidermis and mesophyll tissue distant from vascular bundles is higher than in the tissue close to the latter. In another place (1921) they described that the absorbing power of the tissue in a root was lowest in the absorption-zone ; it became higher from the epidermis

through the cortex up to endodermis, and then lower again in pericycle and wood-parenchyma. LUTMAN (1919) observed that, in very old potato plant, the soluble materials are removed to a considerable extent and the osmotic pressure of the sap drops as a consequence. According to NAMIKAWA (1922), the osmotic pressure in the fruit flesh of apples, which are about to fall prematurely, showed a noticeable decrease. He suggested that the diminution of the osmotic pressure in the fruit-flesh would cause the decrease of the power lifting a supply of water and have certain influences on the abscission process. It is noteworthy that in all the cases of catkins and floral leaves examined in this work, the osmotic pressure in the organ obviously decreases before the abscission.

VI. Summary.

1. The type of the shedding of floral organs can be classified as follows :

(1). abscission.
(2). exfoliation.
  a. ligno-suberization of a more or less differentiated cell-layer at the base of the floral organ.
  b. lignification at the base of the floral organ.
  c. mucilaginous change at the base of the floral organ.
(3). no change in the floral organ, which is eventually shed together with the shoot from the base or some portion of the latter.

2. In every case in the catkins examined, a more or less differentiated separation-zone is observed at the base of the stalk, though in *Corylus* the differentiation is very slight. The cells in any well differentiated separation-zone are small and isodiametric and they show rich plasmatic contents. Mechanical cells such as bast-fibres or stone-cells are nearly or completely lacking in this zone. In *Alnus*, *Salix*, *Populus* and *Castanea*, a constriction is seen in this zone.

3. Measurements in *Alnus* and *Corylus* show that in the vascular bundles of the flower-branch and catkin-axis, the phloem develops in larger proportion than in the vegetative shoot or in the axis bearing the flower-branch.

4. A separation process takes place in a separation-layer, which

is formed in the separation-zone. The separation is brought about by the dissolution of the middle lamellae or of middle and secondary lamellae of cell-walls, rapid enlargemant of separation-cells and an increase in their osmotic pressure. The mechanical cells in the vascular bundles are broken quite mechanically after the separation process has proceeded to a certain degree.

5. Plasmatic contents, starch grains and oil droplets usually increase in the separation-layer before the separation process.

6. Cell-division can be observed in the case of *Salix* and *Castanea* in the separation-zone accompanying the separation process in the stalk of the catkin. No such cell-division takes place in the catkins of other genera studied.

7. Abscission takes place in all the catkins examined, except the fertilized female catkin of *Alnus*. The male flower of *Cucumis sativus* is shed by the normal separation process, while the female flower and the stalk of the male flower in the same plant are not shed in this way.

8. The mode of exfoliation of the floral organs in *Narcissus, Lycoris, Menyanthes* and *Ribes* belongs to the type a. The female flower and the stalk of the male flower in *Cucumis sativus* also exfoliate by this method. The perigone and style of *Hosta japonica,* and the corolla, filament and style of *Platycodon grandiflorum* show exfoliation of type b. Also in these cases, a slight suberization was observed occasionally in the lignified cell-walls. The only example of type c met with was the perigone of *Iris setosa.*

9. After the abscission or exfoliation, the tracheidal elements in the scar or in the tissue which undergoes the change, are stopped with a gum-like substance. Formation of tylosis is scarcely seen.

10. The floral organs of *Gagea, Trillium* and the fertilized female catkin of *Alnus* show the mode 3.

11. The osmotic pressure of the catkin-stalk and separation-zone of young catkins in *Alnus japonica* increases until towards the flowering time. In young catkins of species of *Alnus,* the osmotic pressure in the cortex of the separation-zone is lower than in the corresponding part of the cortex of the catkin-stalk.

12. Generally speaking, the outer tissue of the catkin-axis shows higher osmotic pressure than the inner tissue. In the case of *Salix rorida,* however, the medulla showed a higher osmotic pressure than the cortex.

13. Osmotic pressure in the floral organs on the young catkins is higher than in the catkin-axis. At the time of separation, the pressure in the floral organs as well as in the catkin-axis decreases conspicuously.

14. In the case of all the catkins examined, the osmotic pressure in the separation-zone and separation-cells becomes remarkably high before the separation.

15. Two types of osmotic fluctuation are seen in the petals and perigones : 1) the pressure becomes simply lower during the development of the floral leaves, and 2) the pressure decreases before flowering, becomes increased rapidly at the time of the first opening of the flowers and then shows a final decrease. In both of these cases, the floral leaf in the flower bud shows higher osmotic pressure than that of the floral leaves at later stages.

16. *Corydalis, Pharbitis* and *Hosta* undergo the change of the first type, and *Adonis, Gagea, Prunus, Lilium* and *Pogonia* show the fluctuation belonging to the second type. The bract of *Bougainvillaea* also shows an osmotic fluctuation of the second type.

17. The osmotic fluctuation is in close relation with the degree of the growth and the change of the dry weight of the floral leaf. The period of the rapid rise of the osmotic pressure during the first opening of the flower coincides with the period of rapid increase of dry weight and of the most vigorous growth of the petal. The growth of the petal becomes very slow after the flower has opened. The dry weight decreases together with the osmotic pressure before defloration.

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