

SOME FACTORS INFLUENCING THE ABSCISSION
OF DEBLADED LEAF PETIOLES

BY

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INTRODUCTION

This reasearch was prompted in the first place by some questions which had arisen in the practice of fruit growing. It is generally known that there is some relation between the growth of a tree and its fruitfulness, the highest fruitfulness being obtained at a moderate growth of the tree (see e.g. KOBEL, 1954). Now one of the factors determining fruitfulness is the fall of the young fruits. This fall is said to be stimulated by vigorous growth of the tree.

It is a common practice among fruit growers to bend the branches of too fast growing trees in a horizontal position, which is said to cause a reduced growth and an increased and earlier fruitfulness of the tree. According to some fruit growers this bending not only stimulates flower formation but also reduces the fall of young fruits. However, there is no agreement on the latter point.

It seemed desirable to investigate whether this common orchard practice could have some influence on abscission phenomena. Now experimenting with young fruits, for instance apples, is hardly practicable, as they are available only for a short time of the year and cannot easily been grown in large numbers under controlled conditions. It seemed acceptable, however, that the fall of young apple fruits is controlled by a similar mechanism as governs the fall of leaves. Some arguments for this supposition are the following:

a. The anatomical differentiations, accompanying the fall of apples, namely dissolution of the middle lamella between two layers of cells, either or not preceded by cell divisions (Mc COWN, 1943) do not differ from those observed in leaves (ADDICOT and LYNCH, 1955).

b. Like debladed petioles, pedicels of apples fall after a certain number of days if the young fruit is removed, and falling can be inhibited by the application of growth substances (BARLOW, 1948, 1950).

c. A healthy leaf is supposed to remain attached to the plant as a result of its continuous auxin production. This may also be true for apple fruits: it could be shown (unpublished results) that in young

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apple fruits a considerable auxin production begins immediately after fruit setting, whereas LUCKWILL (1948, 1953) provided evidence that periods of fall coincide with a low auxin content of the seeds.

d. According to EDGERTON (1947) fruits of apples give the same general abscission reactions as do the petioles to various synthetic growth substances.

It seemed justified, therefore, to investigate the problems mentioned, for the present, with leaves. As an experimental plant *Coleus* was chosen, as this plant can easily be cultivated and has already been used in many investigations concerning abscission phenomena. Some of the results have been checked using leaves of apple trees and seedlings.

MATERIAL AND METHODS

For the experiments a clonal stock of *Coleus rhenaltianus* was used. The plants were cultivated in a greenhouse at a constant temperature of 26° C, the experiments were carried out in a greenhouse at a constant temperature of 23° C. In general the deviation from these mean temperatures did not exceed 1° C. In the winter months (beginning November 1 st) the daylight was supplemented with the light of 60 Watt incandescent lamps (about one lamp per m² at a height of 75 cm) until the total length of the light period was 15½ hours. In this way flower formation could largely be prevented. Although no fundamental differences were found between the experiments made in summer and winter, there were indications for quantitative differences (see experimental results).

In general, plants were used which possessed four or five full-grown leaf pairs (i.e. leaf pairs in which the leaf blades had reached or nearly reached their full size). If not stated otherwise, the youngest full-grown leaf pair (called number 1) with its axillary buds was wholly removed, the fall of the petioles of the second and third leaf pair (numbers 2 and 3) was studied. There were usually one or two pairs of unfolded leaves above the first fullgrown leaf pair. Together with the apical bud they will be called the tip of the plant. The length of the experimental petioles was about 1 cm, their axillary buds were removed. The tendency of the petioles to abscise was checked daily by lightly touching them from below with a small stick.

In the experiments with plants placed in a horizontal position a hook was put just behind leaf pair 1 in such a way that this leaf pair lay parallel to the soil surface, while the internode between the second and third leaf pair was supported by a small piece of wood in order to prevent this part from bending down. The axis of the second and the third leaf pair were perpendicular and parallel to the soil surface respectively. After one day the tips of the plants so treated had curved upwards and the operations needed for the experiment could be performed.

In the experiments with indole acetic acid (IAA) this substance was applied to the plant as a lanolin paste. The pastes were made by adding equal parts of water-free lanolin and an aqueous IAA-

solution and mixing them by vigorous stirring in a waterbath at 45° C and afterwards at room temperature until cooled. In the controls a lanolin-water mixture, prepared in the same way, was used. The pastes were stored in the refrigerator and were never used for more than two weeks after their preparation. In all experiments the fresh cut surfaces of the petioles were covered with a small amount of the lanolin-water emulsion.

The control experiments with apples were made outdoors with shoots of "James Grieve" budded upon the rootstock E.M.IX, or with six months old seedlings from "Keulemans", cultivated in the greenhouse. For the experiments a number of petioles in the middle of the shoots were used.

The experimental results have been presented in time-course graphs, from which the number of petioles used can be read. In order to avoid long descriptions of each experiment the treatment of the plants has been drawn schematically in each graph. Only the full-grown leaf pairs have been drawn separately, the young leaves and the apical bud being taken together. A point marks the place where a full-grown leaf with its axillary bud has been wholly removed. A short line in the axil of the leaves denotes an axillary bud.

RESULTS AND CONCLUSIONS

A. Experiments with plants in a normal position

a. Influence of the tip and axillary buds on the abscission of petioles

Four sets of plants were treated in the following way:

1. Removal of axillary buds in leaf pairs 2 and 3.
2. Removal of the tip.
3. Removal of axillary buds in leaf pairs 2 and 3, and the tip.
4. Control (untreated plants).

In all sets the leaf blades of leaf pairs 2 and 3 were removed and the fall of their petioles checked. The results are presented in Fig.1. The following conclusions can be drawn: the growing tip has a marked fall-accelerating action upon the petioles below (as has also been found by JACOBS (1955)). The influence of axillary buds is negligible unless the tip has been removed. In the latter case the axillary buds probably take over the function of the tip. In order to prevent complications, in all subsequent experiments the axillary buds of leaf pairs 2 and 3 were removed.

The statement of JACOBS (1955) that IAA can fully replace the growing tip could be confirmed. The concentration used in our experiments was 2.10^{-3} g/cm³, the pastes were renewed every other day. As this concentration was considered to be fairly high a lower concentration was tried, namely 2.10^{-6} g/cm³, but in this case no effect could be obtained.

The influence of the growing tip has been checked in *one* experiment with apple leaves. Of twenty growing shoots of 8 years old apple trees ("James Grieve") four leaf blades in the middle of the shoot were removed. In one half of the shoots the tip was taken away.

Fig. 2 shows the result: just as in *Coleus* the growing tip in apples seems to accelerate the fall of the petioles below.

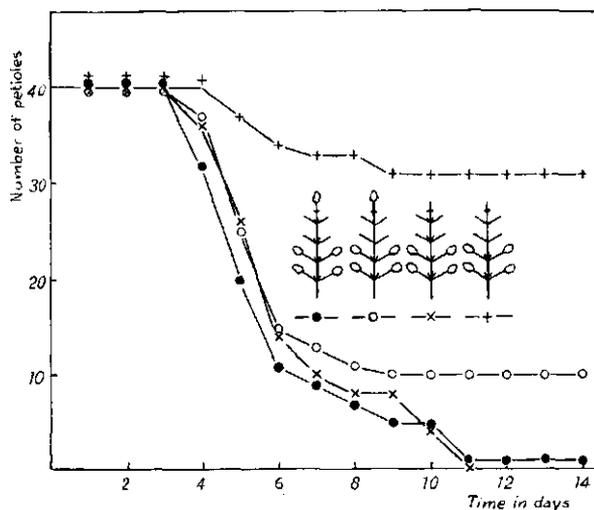


Fig. 1. The influence of the tip and axillary buds on the abscission of petioles in *Coleus*.

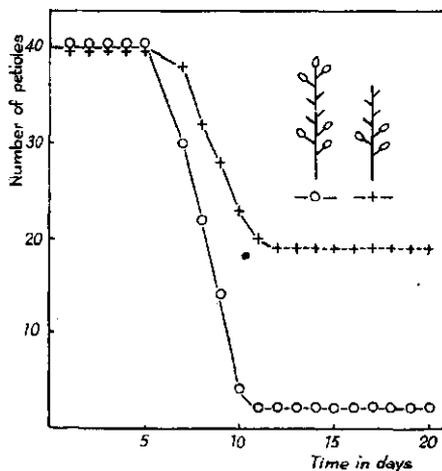


Fig. 2. The influence of the tip on the abscission of petioles in apple.

b. Influence of leaves and roots on the abscission of petioles

ROSETTER and JACOBS (1953) and JACOBS (1955) found that, in addition to the tip, full-grown leaves above and below the debled leaves can accelerate the fall of their petioles. This could be confirmed. JACOBS (1955) stated, that the fall-accelerating influence of leaves

below the petioles tested is almost entirely due to the stimulating effect they have on the compensatory growth of the young leaves in the tip ("A-leaves"). However, JACOBS did not test the influence of the lower leaves in the absence of the apical bud. In the following experiments the influence of the lower leaves (together with their axillary branches) was studied both in the presence and absence of the tip. In order to increase the effect of the remaining parts, the plants were left for two days after cutting off leaves and tips with the leaf blades still on leaf pairs 2 and 3. After this interval these leaf blades were removed and the fall of their petioles was checked. The results are shown in Fig. 3. It can be seen from this figure that,

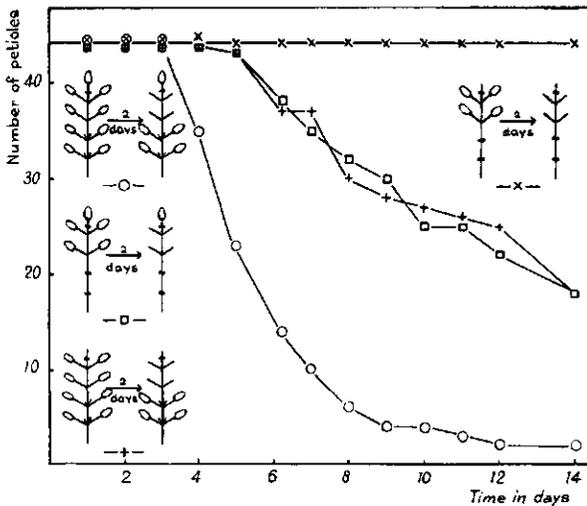


Fig. 3. The fall-accelerating action of the lower leaves on petioles in plants with and without tips.

also in the absence of the tip, there is a marked fall-accelerating influence of the lower leaves together with their axillary branches on the petioles tested. (The influence of the leaves alone have not yet been investigated). It was a somewhat striking result that the petioles of the wholly debladed plants did not or nearly not abscise. Since the publication of ADDICOT *et al.* (1949) leaf abscission is often studied by working with explants, in which case no leaves but only the petioles to be tested are present. In these experiments a rapid fall of the petioles was observed. It was supposed that the presence of the roots in our experiments might have some influence. Therefore, in a set of plants, both leaves and roots were cut off, the remaining stalks were put with their lower ends in vials containing about 50 cm³ tap water. The water was renewed every other day. The plants remained quite healthy in appearance. Again there were two days between the deblading and derooting of the plants and the deblading

of the leaf pairs 2 and 3 to be tested. The results of such an experiment are given in Fig. 4. It can be seen that, at least in the beginning, there actually was an acceleration of the fall in the derooted plants.

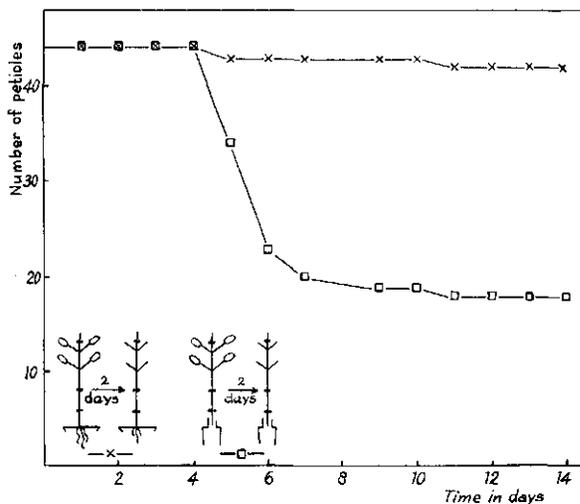


Fig. 4. The influence of derooting on abscission of petioles.

It was tried whether in the plants with roots but without leaves the fall of the petioles could be induced afterwards by putting IAA ($2 \cdot 10^{-3}$ g/cm³) on the cut surface of the decapitated plant. For this purpose in two sets of plants the tip and all the leaves and axillary

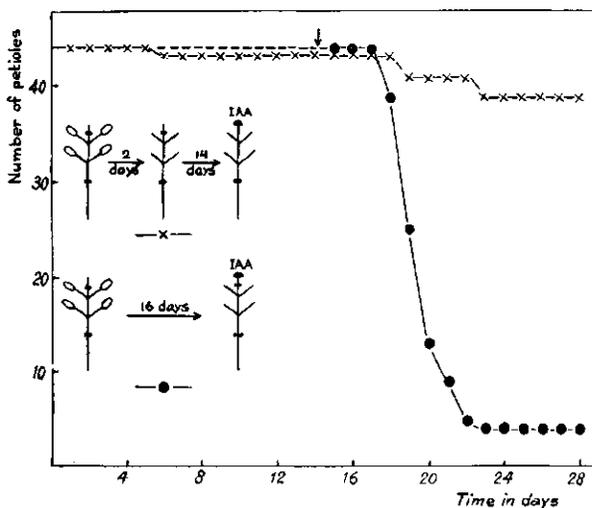


Fig. 5. The influence of IAA, applied proximal of the abscission zone, on the fall of petioles in wholly debladed plants. *a.* Application of IAA at the moment at which the petioles tested are debladed. (●) *b.* Application of IAA 14 days after deblading the petioles tested. (×)

buds were removed except the leaf pairs 2 and 3. After two days the leaf blades of leafpairs 2 and 3 of one set of plants were cut off. At the end of 14 days all plants received a treatment with IAA paste and at the same time the leaf blades of the leaf pairs 2 and 3 of the second set of plants were taken away. As can be seen from Fig. 5

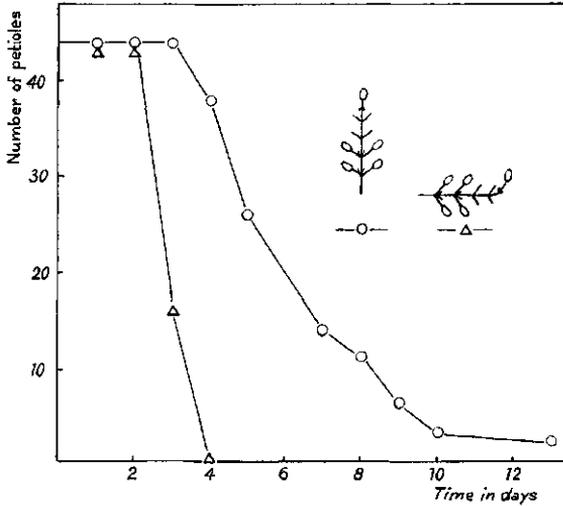


Fig. 6. The accelerated abscission of petioles in plants placed horizontally.

the IAA on the top had only a clear effect if the leaf blades were removed at the same time, it could only induce to a slight degree the fall of the petioles that had previously been deblated. These experiments will be discussed below.

B. Experiments with plants in a horizontal position

a. Influence of the position of a plant on the abscission of petioles

The findings, reported in the foregoing section, which indicate that the presence of a growing tip accelerates the fall of deblated petioles seem to fit the experience of fruit growers that a rapid growth of a tree results in an increased fall of young fruits. As in practice bending the branch in a horizontal position is done with the object of reducing the growth of that branch it was expected that putting a *Coleus* plant in a horizontal position might have a retarding influence, if any, on abscission of deblated petioles. However, the experiments showed that the reverse was true. The fall of petioles was compared in normal vertical plants and plants that one day before the experiment had been placed in a horizontal position, only allowing the tip to grow upwards. There proved to be a marked acceleration of the fall in the horizontal plants (Fig. 6). It was thought that the horizontal position of the roots might influence the results. Experiments with bent plants, where the pot remained in a normal position gave, however, the same results. It was tried whether the acceleration

effect could be obtained with decapitated plants. This proved to be the case, provided decapitation and deblading of the test-petioles took place at the same time. If, however, there was an interval of two days between decapitation and deblading of the test-petioles, the effect was much less marked or had disappeared. (Fig. 7).

The results obtained with plants with apical buds could be reproduced with plants in which the tip had been substituted immediately

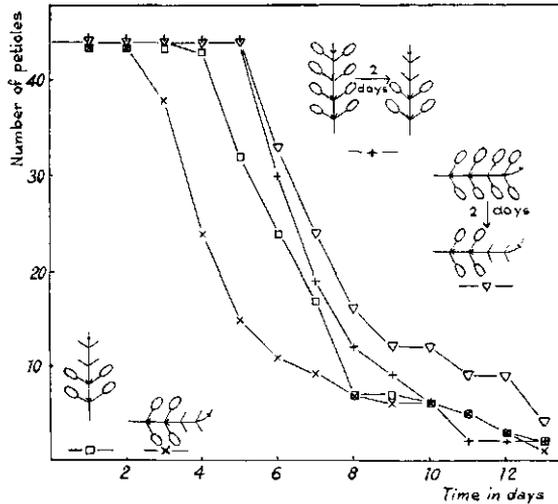


Fig. 7. The effect of decapitation on the abscission of petioles in horizontal plants. *a.* Deblading of the test petioles and decapitation at the same time (□, ×) *b.* Deblading of the test petioles two days after decapitation. (+, ▽)

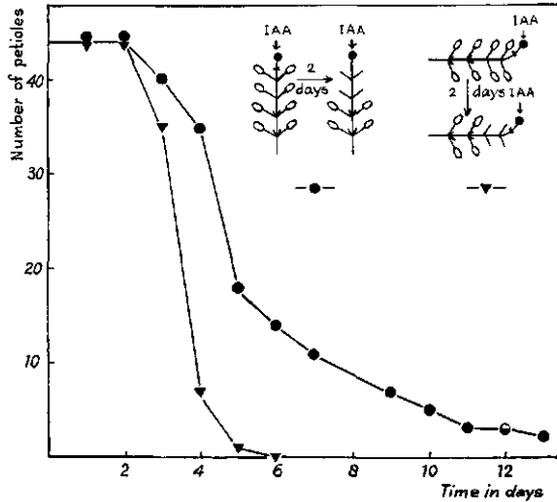


Fig. 8. The accelerated abscission of petioles in horizontal plants in which the tip has been substituted by IAA.

after decapitation by IAA (2.10^{-3} g/cm³). (Fig. 8). In a preliminary experiment it was tried whether the effect in plants that had been decapitated some days in advance, could be restored by means of putting IAA on the cut surface of the tip. To this end a set of plants was laid horizontally and decapitated after one day (at the same time the axillary buds of the leaf pairs 2 and 3 and the first leaf pair with its axillary buds were cut off). After 8 days the lanolin-water emulsion, which had been applied to the cut surface of the tip, was replaced by IAA (2.10^{-3} g/cm³) and the leaf pairs 2 and 3 were debladed. Vertical plants, treated in the same way, served as controls. There was a clearly accelerated abscission in the horizontal plants.

It is clear from these experiments that for the acceleration of petiole abscission in a horizontal position the presence of some substance, coming from the tip, is necessary. This substance can be replaced by IAA and so it is very likely that the growth substance, produced by the tip, is needed for producing the effect. The acceleration of abscission in horizontal decapitated plants that have been debladed immediately after decapitation may be ascribed to the presence of some residual growth substance, the amount of which diminishes gradually. In later experiments, made in the middle of the winter, the interval of two days after decapitation did not suffice to prevent the accelerating effect and a five days interval was used. Probably this has to be ascribed to the reduced light intensity in the greenhouse.

The results obtained with *Coleus* were checked with leaves of apple seedlings. From two sets of six seedlings, as nearly as possible in identical pairs, six leaf blades per plant were removed, leaving about four leaves at the tip. One set was placed horizontally. The experiments were made at 26° C. The results (Fig. 9) show, that the fall-accelerating effect in horizontal plants could also be observed in apple seedlings.

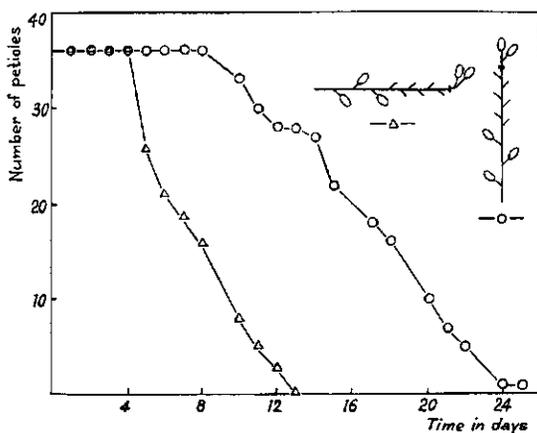


Fig. 9. The accelerated abscission of petioles in horizontal apple seedlings, compared to vertical ones.

As to the auxin gradient theory, it seems desirable to modify this theory to some degree, for instance as follows: For abscission to occur at least two conditions have to be fulfilled: 1. A reduced auxin production on the distal side of the abscission zone. 2. A sufficient amount of auxin (or auxin induced growth) on the proximal side of the abscission zone.

In many experiments it can be seen that some of the petioles do abscise very slowly or not at all within the experimental time (*cf.* e.g. Fig. 1), which has the consequence that the curve has not the normal S-shape that might be expected. In connection with the foregoing this may be explained by supposing that at the moment at which the leaf blade is removed the supply of auxin or the growth activity of other organs on the proximal side of the abscission zone is not sufficient to induce abscission, thus retarding or preventing this process.

Attempts were made to explain the results obtained with horizontal plants with the hypothesis mentioned above. In order to explain the accelerated fall of leaf petioles an increased production of auxin on the proximal side of the abscission side should be supposed. It might be possible that the tips of horizontal plants produce more auxin. However, if the tips of vertical and horizontal plants are replaced by the same amount of IAA, the fall-accelerating effect is still present, while the auxin "production" of the artificial tips in both sets of plants must be the same.

Another supposition might be that there is an increased growth of the tip in horizontal plants in reaction to the geotropic stimulation. In this case the tip could attract an increased amount of nutrients, thus withdrawing them from the petioles to be tested. However, it was shown by CHOLODNY (1929) that during the time the geotropic reaction takes place the position of the growing stem has no influence on its growth, nor on its production of growth substance.

It is generally accepted in practice that in the long run the growth in horizontal branches diminishes; this phenomenon was described by MÜNCH (1940). In literature only very little additional information could be found about the influence of the position of an organ on its growth in length. NOLL (1900) mentions a growth inhibition of horizontally growing roots from *Lupinus*, *Pisum*, *Vicia* and *Phaseolus*, compared with vertically growing ones. BENNET-CLARK and BALL (1950) find indications that rhizomes of *Aegopodium podagraria* grow faster in a vertical downward position than in a horizontal position, the latter again growing faster than rhizomes in a vertical upward position. They suppose this to be caused by the action of the longitudinal component of gravity. CHOLODNY (1932) does not find any effect of the position of roots upon their growth. Except the experiments mentioned of CHOLODNY (1929) no further information on the growth in length of horizontal stems could be found. However, some other growth phenomena in horizontal branches are known. Firstly, it is often observed that axillary buds grow out if branches of fruit trees are bent horizontally (GARDNER, 1925). Secondly, HOFMEISTER

(1867) already pointed out that there is an increased growth in thickness on the upper side of the horizontal branch in a large number of trees. The effect was studied extensively by MÜNCH (1938). PRIESTLY and TONG (1927) described the phenomenon for apple trees; in our experiments it was also noticed in the horizontal apple seedlings in which we had observed the accelerated fall of petioles. PRIESTLY and TONG ascribe this effect to an influence of gravity on cambial activity. As has been shown in the experimental part, in our experiments with *Coleus* there was also an increased growth in thickness in horizontal plants, though in this case on the lower side. It may be supposed that this growth induces an increased auxin production or that certain nutrients are attracted during the increased growth and are thus withdrawn from the abscission zone. Anatomical investigations about this increased growth have not yet been performed.

The experiments with plants on a clinostat suggest that the accelerated abscission in horizontal plants is induced, at least for the greater part, by the action of the transversal component of gravity. It remains to be investigated whether the small fall-accelerating effect, observed in some experiments with plants rotated on a clinostat with horizontal axis, is a real one or will have to be ascribed to technical imperfections. The mechanism of the action of gravity causing increased growth in thickness and, probably via this phenomenon, accelerated fall of petioles, remains obscure.

In the introduction it was pointed out that these experiments were the consequence of practical problems in fruit growing. In the light of the results of these and other investigations, an increased fruit fall in fast growing trees may be explicable, as in these trees a high auxin production or a strong attraction of nutrients by the growing organs may be expected. As regards the bending of branches in a horizontal position, one will have to reckon with the possibility that this treatment influences the fall of fruits. Yet it seems risky, at least for the present, to apply the results of these experiments directly to apple fruits. It should be kept in mind that the apple fruits are normally situated on short side shoots of the branch that is bent downwards and the influence of bending these branches on abscission of the fruits cannot yet be predicted. Further experimentation seems highly desirable.

ADDICOR and LYNCH (1955) point to the relation of abscission phenomena to other ones, for instance the growth of lateral buds. This may be extended to the whole problem of correlative inhibition (bending of branches causes the lateral buds to grow out) and even of flower formation (bending of branched is generally accepted to induce flowerbud formation in fruit trees). Progress made in one of these fields may directly be applicable to the other ones.

SUMMARY

1. Experiments with various deblading patterns in *Coleus* do not confirm in all respects the auxin gradient theory about abscission. Indications are obtained that in order to render abscission possible there should be a sufficient auxin production (or auxin induced growth) on the proximal side of the abscission zone.
2. Placing the plants in a horizontal position induces an accelerated fall of

debladed petioles. This effect is only clear if a certain quantity of auxin (or auxin induced growth) is present at the proximal side of the abscission zone. Some preliminary experiments on the clinostat suggest that the accelerated fall is induced, at least for the greater part, by the transversal component of gravity. The effect is supposed to be connected with an increased growth in thickness in horizontal stems.

The consequences of the results for practical fruit growing are discussed.

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