

# THE EFFECT OF FLOWERING ON ADVENTITIOUS ROOT-FORMATION

## PROEFSCHRIFT

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H. H. A. SELIM



H. VEENMAN & ZONEN - WAGENINGEN - 1956

# THE EFFECT OF FLOWERING ON ADVENTITIOUS ROOT-FORMATION

THESIS

IN PARTIAL FULFILMENT OF THE REQUIREMENTS  
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BY

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BORN AT MIT KENANA (EGYPT), THE 13TH OF NOVEMBER 1922

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## THEOREMS

### I

Flowering-stimulus cannot always be transported from a donor branch to a receptor one in a branched plant.

### II

A co-operation between the Netherlands and Egypt in the field of horticulture would be beneficial to both countries.

### III

The basical translocation of the flowering-stimulus cannot only take place through the phloem, but also through the xylem.

### IV

The fruit yield of naval orange trees is not effected by pollination.

### V

Manuring late sown cotton with nitrates has a harmful effect on the crop, while the reverse is true for the early sown one.

### VI

The way by which the perennial irrigation was applied in Egypt, was disastrous to the agricultural production and the soil properties.

### VII

The Egyptian agricultural expansion has to begin with increasing the area of cultivated lands.

### VIII

The need of an easy and accurate method for determining the virus infection before the appearance of the symptoms, is urgent.

### IX

For soils heavily infested with flag smut spores, the sowing method so called "aaffir" is to be used to control the disease in Egypt.

### X

LYSENKO's experiments on transformation winter wheat into spring one and vice versa can be explained on the basis of Mendelism.

SKRIPTSCHINSKY, W. W. (1955) - STUBBE, H. VON (1955)

### XI

Sex determination in dioecious plants before flowering is possible by morphological and chemical methods.

## FOREWORD

At first, I should like to express my thanks and acknowledgments to all those who have helped directly or indirectly in carrying out this study. As I feel myself unable to record my thanks to all those who had offered me a hand during my study and my stay in the Netherlands, I hope that will be forgiven.

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## I. INTRODUCTION

Since long ago, it is well known among plant propagators and mentioned in nearly all horticultural text books that one has to avoid branches carrying flower buds when selecting cutting material. Although the depressing effect of flower buds or flowers on root formation was observed, yet the cause has not been investigated. The part played by the presence of the flower bud itself or the flower stimulus on adventitious root-formation is still obscure.

Plants in the juvenile phase root readily, even those which are difficult to root in later stages. If one considers that by definition a plant in the juvenile phase does not flower at all even under the most favourable conditions, this may throw some light on the relation between flowering and rooting. As a matter of fact, in most cases pronounced morphological differences exist between plants in the juvenile phase and those in the adult phases, i.e. the shape of the leaves and the growth pattern. The differences between the vegetative adult phase (non-flowering, but able to form flower buds) and the generative adult one (flowering) are not pronounced at all, except those related to the change of growth from vegetative to generative phase, such as bolting, stopping of the vegetative growth... etc. The difference in adventitious root-formation in such a case, if any would be found, is considered to be due to the conditions leading to flowering or to the flowering process itself.

It is in the leaves that the rhizocaline, which has been suggested to be responsible for root-formation, is formed. The presence of the leaves during root-formation is a prerequisite for successful rooting in many cases. Also, it has been shown that the leaves act as perceptors of the light in the photoperiodic reaction of the flowering process. From this one can see that leaves play a part in affecting both processes and thus may give some indication as to how a correlation between these two processes comes about.

The internal conditions leading to flower formation are not yet clear. Whether or not the concentration of auxins within the plant has any role in the process of flower formation has not been clarified. Most of the work done in that field was to study the effect of applied auxins on flower initiation, although recently some investigators have tried to obtain extracts of flowering plants and to study their chemical structure and properties. The internal conditions of an intact plant cannot easily be studied, but the role played by auxins and other internal factors on rooting has been well studied. Hence it was thought that by trying to find a relation between flowering and rooting, one might be able to get some knowledge of the internal factors leading to or at least related to flower initiation.

After a literature review (II), the experimental part of this study will be treated (III, IV, V). As experimental plants, representatives of the day neutral, the short day (= S.D.) and the long day (= L.D.) plants, namely tomato, *Perilla crispa* and red clover respectively were chosen. In tomato the process of flower initiation cannot be inhibited, while in *Perilla* and red clover it can be completely controlled by regulating the day length, so that these three plants offered a suitable material for studying the relation between flowering and rooting. In VI the experimental results will be discussed as a whole and a general conclusion will be drawn.

## II. GENERAL REVIEW OF LITERATURE

As one of the most important links between flowering and adventitious root formation seems to be the auxin content of the plant, we shall first discuss the part which auxins play in flowering. These follows a discussion of the part played by auxins in adventitious root-formation, while the relation between flowering and root-formation completes the review.

## 1. THE ROLE OF AUXINS IN THE MECHANISM OF FLOWERING

The physiology of flowering received much attention from investigators during the last few years. In spite of the enormous amount of work carried out in different parts of the world, it is still impossible to draw a clear-cut conclusion about the mechanism of the process. Several reviews have been published recently, summarizing the work done on the subject, to which reference may be made for detailed information: HAMNER (33, 1948)\*, LANG (35, 1952), BONNER and BANDURSKI (5, 1952), LEOPOLD (40, 1952), BONNER and LIVERMAN (6, 1953) and LIVERMAN (46, 1955).

Whether auxins have a role in flowering has not yet been determined. The cases in which the positive effect of an auxin on flowering is found are scarce. The outstanding example is the flowering of the pineapple, in which auxin application to stimulate flowering has become a regular practice: VAN OVERBEEK (58, 1946). Many investigators, CLARK and KERNS (14, 1942), COOPER (18, 1942), VAN OVERBEEK (56, 1945), VAN OVERBEEK et al. (59, 1947), VAN OVERBEEK et al. (60, 1948) found that not only phytohormones could induce the pineapple plants to flower, but also that some hydrocarbonic gases resulted in the same effect.

In most other plants the effect of auxin on flowering is less pronounced. HAMNER and BONNER (34, 1938) found that the substance stimulating flowering was not identical with any of the known auxins. CAJLACHJAN and ZDANOVA (10, 1938) concluded that the growth hormone plays no decisive part in flower initiation.

CHOLODNY (13, 1939) however suggested that the flower initiation was determined by a certain complex of phytohormones. The production of a flower-forming substance, in his opinion, is probably connected with a certain chemical transformation of auxin in the leaves.

The application of auxins and anti-auxins to plants received much attention in the last few years. THURLOW and BONNER (77, 1947) proved that auxins (i.e. IAA and NAA), inhibit floral induction when applied to S.D. plants during the inductive period. GREEN and FULLER (28, 1948) also showed a retarding effect of indole-3-acetic acid on the flowering of *Petunia* and Lincoln soybeans, when applied by immersion of their roots in a solution. Higher concentrations of the hormone were found to retard the development of flower buds of snapdragons, annual larkspur, blue salvia and Iris.

LEOPOLD and THIMANN (41, 1948) were able to increase the number of flower primordia in the L.D. wintex barley by infiltrating through the cut leaf tips indole acetic or naphthalene acetic acid in low concentration. LEOPOLD and THIMANN (42, 1949) showed that as both flowering and growth were reacting in the same manner to different concentrations of growth hormones, it was not necessary to assume that the growth hormone is opposed to the functioning of the proposed flowering hormone, but rather influences it in a qualitative manner similar to its influence on growth.

RESENDE (65, 1949) suggested as a working hypothesis that the stimulus for flowering is determined by realization in the vegetative bud of a particular level between auxin and anti-auxin which once attained determines floral differentiation.

BONNER (3, 1949), BONNER and THURLOW (4, 1949) suggested that in *Xan-*

\*) First number refers to "Literature" on page 35, second number is the year of publication.



*thium*, flowering might be caused by a decrease of the effective auxin level in the plant, which might be brought about by short photoperiods or by applying anti-auxins (2-4 dichloroisole and triiodobenzoic acid). The application of anti-auxins during induction was found to hasten flowering.

LEOPOLD (39, 1951) believed that the growth hormone and the flowering hormone are antagonistic systems.

BONNER and BANDURSKI (5, 1952) suggested that auxins might be limiting in the flowering of S.D. plants and perhaps also of indeterminate plants.

LANG (35, 1952) in his review summarized the effect of auxins on flowering. He came to the conclusion that the role of auxins was easily determined in the flowering of S.D. plants, while this was not clear for L.D. plants. In S.D. plants he thought that low concentration of auxin is a prerequisite for flowering. As a proof, he pointed out that treatment with synthetic growth-regulating substances under S.D. conditions suppressed flower formation, while flowering can be induced under noninductive conditions by treating with auxin antagonists. Moreover, the auxin treated leaves of a S.D. plant during its inductive period are not effective as donors to receptor plants maintained under L.D. conditions. Regarding the fact that in *Xanthium* the anti-auxin induced primordia may fail to develop unless the plants are treated with auxin, he suggested that the later stages of flower development seemed to require an increase in the auxin supply.

GUSTAFSON (31, 1953) studied the effect of different photoperiodical treatments on the contents of thiamin, riboflavin and niacin in tissues of Alaska pea, black valentina and tomato. He found that the thiamin content decreased as the plants were exposed to longer photoperiods, while the reverse was true for plants exposed to shorter photoperiods. With the other two substances the effect was the reverse.

LEOPOLD and GUERNSEY (43, 44, 45, 1953, 1954) carried out three investigations on the effect of auxin treatments on flowering. They demonstrated that if the auxin is applied to S.D. plants at a relatively high temperature, it has an inhibiting effect, but when it is followed by a brief exposure to 10°C it promotes flowering. They found that the promotive effect is the same in plants that are sensitive to the photoperiod, or to vernalization, or that are indeterminate in their behaviour. This led them to suggest that the physiological mechanism which controls flowering has close biochemical similarities in all plants. Besides the high temperature shading also brought out the inhibiting effect.

FISHER and LOOMIS (22, 1954) showed that spraying S.D. plants with anti-auxins (2, 3, 5 triiodobenzoic acid) caused the production of abundant flowers in a noninductive environment. This treatment was found to reduce the ratio of mature leaves to expanding ones, to the S.D. level. They concluded that the flowering hormone is some anti-auxin, and that the growth hormone is an antiflowering hormone when present in more than suitable concentration. They also added that at still lower concentrations, auxin may limit flowering indirectly, because it is present in insufficient concentration to support the essential growth of flowering parts.

WELLENSIEK, DOORENBOS and DE ZEEUW (82, 1954) suggested that there is no specific flower forming hormone arising as a direct result of photoperiodism, but that the flower formation is determined by a certain balance between products of photosynthesis and auxin.

COOKE (15, 1954) showed a fluctuation in the auxin content of the S.D. plant

tissue while induced to flowering. He proved that the auxin content decreased with the appearance of the flower primordia. This is the only reference dealing with the contents of the tissues themselves, and not using applied auxins.

Recently, LIVERMAN (46, 1955) in his review mentioned that the data at hand, indicate that the auxin level drops during the dark period in both L.D. and S.D. plants. He believes that in S.D. plants the dark period allows the concentration of auxin to fall to a level where florigen synthesis can occur, but for L.D. plants, on the other hand, the data pointed out that their auxin level may be too low for flowering under S.D. conditions and that by making up this deficit artificially, flowering may take place.

**Conclusion.** For a conclusion we refer to LIVERMAN (46, 1955), as just cited, but we may add that the flowers need auxins to develop. Also, we may refer to LEOPOLD (39, 1951), FISHER and LOOMIS (22, 1954) who found that growth hormone and flowering hormone are antagonistic systems.

## 2. THE ROLE OF AUXINS IN THE MECHANISM OF ADVENTITIOUS ROOT-FORMATION

2.1. The benefits of growth substance application in propagation by cuttings have been known since 1929. The complete history of this research may be found in the books of BOYSEN JENSEN (9, 1936), WENT and THIMANN (88, 1937), VAN DER LEK and KRIJTHE (38, 1941), AVERY and JOHNSON (1, 1947) and THIMANN and BEHNKE (76, 1947).

The application of growth promoting substances in solution to cuttings basally and not in the form of paste as used previously proved more practical and gave good results. This had the effect that almost at once throughout the world this method was introduced into the practice of horticulture. A good survey of this research is given in both MITCHELL and RICE's (51, 1942) and THIMANN and BEHNKE's (76) books.

According to WENT (87, 1939): "there are three different opinions concerning the effectiveness of auxin in root-formation.

*a.* Some workers questioned the necessity of the presence of auxins for root formation, because in their experiments root-formation occurred (also) without indoleacetic acid application.

*b.* Others maintain that the auxins themselves are the specific agents for causing root formation.

*c.* Finally, other workers hold the opinion that the auxins are but one of many factors necessary for root-formation".

*Sub a)* The relation of the chemical composition of cuttings, especially the C/N ratio, on rooting was studied by STARRING (70, 1923), RIED (64, 1924) and SCHRADER (69, 1924). They all showed that carbohydrates are important, and that the nitrates were not directly used in the formation of new roots. MARGERY (47, 1929) also found that rooting seemed to be related to the content of reserve starch in rose cuttings. WENT (84, 1935) showed the necessity of sugars for root formation. ZIMMERMAN and HITCHCOCK (93, 1937) proved that tomato plants grown for a long period in darkness lose their ability to respond to growth substances, which was associated with the decrease of carbohydrates and increase of nitrates in the tissues.

*Sub b)* On the other hand PEARSE (69, 1938) with willow cuttings, suggested that indolebutyric acid was the agent concerned in promoting root formation, and that it was used up or chemically changed during the process. GRACE (27,

1939) showed that indole-acetic acid increased the number of roots per rooted cutting, but decreased the mean length of the root. GRIFFITH (30, 1940) succeeded in obtaining 80 to 100 % rooting of the cuttings with dormant buds of Douglas fir and Sitka spruce respectively, treated with either indolebutyric acid or indole-acetic acid. THIMANN and POUTASSE (75, 1941) demonstrated that in the rooting of leafy cuttings three distinct physiological processes are involved: initiation of root primordia, development of roots from these initials, and maintenance of the cutting as an excised organ during rooting. They added that the first process could be brought about by synthetic auxins in many plants, where it did not take place spontaneously, and the second process by food supply.

MITCHELL and RICE (51, 1942) concluded that the most commonly observed effects of growth-regulating substances when properly used in rooting cuttings, were an increase in the number of roots per cutting, and a decrease in the time required for the cutting to produce them. SCHOLZ and SMIDRKAL (68, 1939) demonstrated the effect of heteroauxin on rooting of cuttings of herbaceous plants, i.e. red clover, Moravion lucerne and *Onobrychis sativa*. The treated cuttings formed numerous roots, while only 40 per cent of the control cuttings developed scanty roots and 50 per cent formed a little callus and died.

STOUTEMYER (72, 1954) stated: "One of the striking effects of plant regulators, is the hastening of the formation of root primordia, and the outgrowth of roots on cuttings". In an earlier paper, STOUTEMYER et al. (73, 1940) collected evidence that the failure of the cutting to root normally could be attributed to an auxin deficiency, since abundant roots could be induced with synthetic growth substances.

*Sub c)* As evidence to the hypothesis that auxins are but one of many factors necessary for root formation, one may refer to the above mentioned findings of ZIMMERMAN and HITCHCOCK (93, 1937) that tomato plants grown for a long period in darkness lost their ability to respond to growth substance treatment. The theory of BOUILLENNE and WENT (8, 1933) and BOUILLENNE (7, 1950) is that the factors essential for the regeneration are:

- 1) presence of rhizocaline in the tissues;
- 2) presence of hydrocarbons;
- 3) oxydizing enzymes in the cell itself.

This theory must be considered in more detail. The rhizocaline is a substance formed in fully grown leaves in the light, and it may be stored in the branches or cotyledons. WENT (83, 1934) stated that there is an approximately linear relationship between rhizocaline concentration and number of roots formed. WENT (85, 1938) concluded that auxins are necessary for many growth processes, yet other hormone-like factors (calines) are also required. Rhizocaline for instance, should be present, together with auxin, to cause root formation. WENT (83, 1939) has divided the action of auxin in root formation, into two distinct phases:

- 1) redistribution of rhizocaline within the stem, which could be done by other substances not active in root formation and
- 2) the activation of the accumulated rhizocaline, for which process the presence of auxins was prerequisite.

These postulations are in harmony with those of COOPER (16, 1936) and GREGORY et al. (29, 1945). STOUGHTON and PLANT (71, 1938) suggested that whatever other substances might be concerned in bud and root formation, not only the subsequent growth but also the initial differentiation of meristematic

tissue was determined, at least in part, by the local concentration of growth substance.

**Conclusion.** From the foregoing we can conclude that auxins evidently play a part in root formation, but that they are not the only factor.

2.2. Not only was the effect of synthetic growth substances on the rooting of cuttings studied, but also other factors that might affect the auxin level within the cutting itself and thus affect its rooting capacity. In this section some of these factors will be discussed, namely: leaves and buds, ageing, photoperiodism, growth and position.

LOEB (47, 1917) pointed out the effect of leaves on root formation. He assumed that each leaf had a tendency to send shoot-forming substances toward the apex and root-forming substances toward the base of the stem.

PLETT (63, 1921) observed a stimulating influence of the leaf on root-formation of different herbaceous cuttings. He ascribed this to the nutritive function of the leaf, while transpiration and respiration might also play a part. The bud had a similar influence even if its growth was entirely inhibited; here an unknown stimulus must be assumed.

VAN DER LEK (36, 1925) showed not only the importance of the presence of the bud for root formation in woody cuttings, but also demonstrated that the manner in which the bud was growing affected the way of rooting of the cutting. Cuttings growing vigorously had basal roots, due to fast travelling substances, but slowly developing buds permit the internodal roots to develop.

ZIMMERMANN and HITCHCOCK (91, 92, 1928, 1929) showed a possible correlation between the leafy shoot in light and the type of root system developed in cuttings, as they found that leafy cuttings in light produced many roots with a large number of secondaries. There was no correlation between the type of roots and the carbohydrate supply. They also pointed out that in evergreen cuttings the presence of the leaves was a prerequisite for their rooting. They also showed positive correlation between starch content of the cuttings and their ability to root.

CALMA et al. (11, 1930) reported that the root production in *Coleus* was largely determined by the leaf area on the cuttings. Both the amount of roots and the percentage of rooting were positively correlated with the leaf area on the cutting. Unilaterally defoliated cuttings mostly produced roots on the side with leaves. They thought this was due to the tendency of the plant to balance the top and root growth.

ESPER and ROOF (21, 1931) showed the importance of the presence of leaves on soft-wood cuttings. The number and length of roots per cutting were enlarged by the additional leaf surface exposed.

HAGEMANN (32, 1932) proved that regeneration in some species was dependent on the age of the leaf, and that the interruption of the connection between the growing point and the leaf was a determining factor.

WELLENSIEK (80, 1933) concluded that tea leaves were capable to form a root producing substance which was chiefly transported through the phloem.

The relation between the periodicity of the buds in the mother plant and the root development was shown by VAN DER LEK (37, 1934). He found that dormant buds had a preventative effect on root development, but this decreased at the approach of the end of dormancy, even in disbudded cuttings.

COOPER (17, 1938) indicated that leaves of lemon cuttings, supply a substance

necessary for the differentiation of the root primordia and another for the out-growth of these primordia.

WARNER and WENT (79, 1939) found a general positive correlation between the leaf number and rooting, provided enough humidity in the propagating frames.

DOSTÁL (20, 1945) proved that growing buds of *Scrophularia nodosa* produced roots independent of mere nutrition. The roots were only produced below the growing laterals and not under the leaf whose axillary bud was removed. He also reported some differences in root quality produced by the basal and the apical portions of the stem, which he thought corresponded to the different organ-forming material made by the leaves at the opposite stem poles. He also found that the youngest leaves promoted the development of both roots and shoots, while leaves approaching maturity promoted only root formation, the adult and ageing leaves exerting a marked inhibition on the formation of both organs. The latter effect was found to be decreased by buds in their axils growing out. The importance of photosynthesis and water economy for the growth correlations was proved, but heteroauxin did not affect the results.

OVERBEEK et al. (59, 1945) did not agree with the hypothesis of the formation of a special root-forming substance in their *Hibiscus* leaves. They attributed the effect of leaves, to supplying the cuttings with sugars and other nutritional factors.

It can be concluded from the foregoing that both leaves and buds are responsible, at least to some extent, for root-formation. That may be due to increasing the auxin content of the cutting, but also to increasing other nutritive substances. Not only does the presence of leaves and buds exert an influence, but other factors such as the age of the leaves and the periodicity of the bud also show an effect.

GARDNER (24, 1929) with apples and other species, MIROV (50, 1944) with pines, ZIMMERMANN and HITCHCOCK (94, 1946) with apples and SATOO et al. (67, 1953) with *Cryptomeria japonica* showed the effect of the plant age on rooting and it was found in most cases that rooting capacity decreased with the increase in age of the tree.

MOSHKOV et al. (52, 1939) concluded that the best way to obtain rooting in woody cuttings was to grow the plants under the optimal daylength for their general growth, and when rooting was to take place, they advised continuous illumination for most of the species. STOUTEMYER and CLOSE (74, 1946) also found under their experimental conditions that continuous illumination gave satisfactory results with all of the numerous species used, although in some instances the 16 hour daily illumination was preferable. Satisfactory roots could be obtained under relatively low light intensities in their experiments.

PARAVIDIN (61, 1945) found in *Salix caprea*, *Populus laurifolia*, *Morus alba* and *Syringa vulgaris* that the cuttings taken from the middle third of the stem rooted best, and those near the base or at the tip failed to root unless treated with heteroauxin.

GALSTON (23, 1948) studied the relation between the growth of the stem and the root initiation in excised *Asparagus* stem tips. He found that the root initiation occurred at a time when the stem was making little growth in length. When the stem was making rapid growth, the root-formation was always prevented. He suggested that these processes may be competing. He also concluded that a material other than auxin, essential for root initiation, was formed in the light,

stored in the seed and depleted by prolonged dark culture.

GARNER et al. (26, 1954) found that the number of roots produced by leaf bud cuttings of apples, was not influenced either by the position of the shoot or the time of separation, while the percentage of rooting was affected. They also proved that a fully developed but not senescent leaf was essential for rooting.

Conclusion. The effect of leaves, buds, age of the mother plants, physiological age of the tissues, photoperiod and growth on rooting was pronounced. This may be attributed to their effect on the auxin level and on the other nutritive substances within the plant tissues.

### 3. FLOWERING AND ADVENTITIOUS ROOT-FORMATION

The influence of the flowering process on the rooting capacity of plants has not been thoroughly studied before, so there is little literature on the subject, and it consists mainly of some scattered observations.

According to GARNER (25, 1944), as early as 1913 BAYLEY stated that the presence of flowers on a cutting was generally depressing. On the other hand, TUKEY and BRASE (1934) recorded that they had obtained over 90 % rooting of black and purple raspberry leaf-bud cuttings, even though they were taken from portions having flower buds. In cuttings of *Dahlia*, *Geranium*, *Carnation*, *Chrysanthemum*, *Hydrangea* and *Fuchsia*, WOYCICKI (89, 1938) reported that the presence of flower buds on the cuttings was unfavourable for rooting.

GRACE (27, 1939) showed some differences in the effect of female and male flower buds in Norway spruce (*Picea excelsa*); in cuttings with female flower buds 48 % rooted, while in those with male flower buds 86 % rooted.

The inhibiting effect of flower buds on rooting in *Camellia* and *Chrysanthemum* was also shown by WARNER and WENT (79, 1939). The treatment with indole acetic acid did not help in this case, except after removing the buds.

TUREZKAYA (78, 1941) found in the short day plants *Perilla nankinesis* and *Soja hispida* that cuttings from plants just before flower initiation and at the beginning of flower bud formation formed many roots, while the rooting-capacity was low when flower buds were present and disappeared completely when flowering took place. The long-day treated plants gave cuttings with many thin roots. After a period of 4 hours immersion of the bases of the cuttings in a solution of heteroauxin, the greatest effect was found in the first group with open flowers, but in the last group there was no difference between treated and untreated cuttings. In her opinion, the plant hormones became concentrated in the flowers at the beginning of anthesis and later in the fruits, an insufficient amount being left for root-formation. The addition of heteroauxin acted as a substitute for the natural hormones and so resulted in root-formation.

O'ROURKE (54, 1942) did research on the influence of the flower bud on the rooting of hardwood cuttings of blueberry. He not only showed the inhibiting effect of the flower bud, but also demonstrated that it was the conditions leading to flowering which depressed rooting, and not the presence of the flower bud itself. O'ROURKE (55, 1944) found that the wood of vegetative blueberry plants rooted significantly better than that of the flowering plant in all positions except the basal one.

RESENDE (65, 1949), when studying the flowering in *Bryophyllum daigremontianum* found an incompatibility between root-formation and flowering. He suggested that the flowering process bound a great quantity of free auxin, which is

set free when the plant regresses to the vegetative state, leading to root-formation.

In 1953 an interesting study was reported by ROBERTS (66). From the extract of some flowering plants he separated three crystalline substances, which he found to inhibit callus formation on wound surfaces induced by naturally occurring or applied auxin. Additional effects of the application of these crystals, were the reduction in the stimulation of adventitious roots and a normal development of shoots on topped plants, instead of the reduced growth of axillary shoots typical of plants treated with indole acetic acid applied in lanolin.

The effect of flowering on rooting was studied not only on stem cuttings, but also on root cuttings. DORE (19, 1953) found that the regeneration capacity of root-cuttings of horse radish was low during the months of flowering.

Conclusion: Only with the exception of raspberry (TUKEY et al.) flowering appears to inhibit adventitious root-formation.

#### 4. GENERAL CONCLUSION

From all this above mentioned literature one may conclude in accordance with LEOPOLD (39, 1951), DE ZEEUW (90, 1954) and FISHER and LOOMIS (22, 1954), that growth and flowering are antagonistic systems. If growth is promoted by a certain level of growth substances, the initiation of flowers is promoted by or at least associated with either lower concentrations (S.D. plants) or higher concentrations (L.D. plants). The development of flowering organs needs a certain level of auxins, so that it may occur that too low a concentration of auxin remains for maximal adventitious root-formation.

Thus, one may expect three levels of auxin content in the plant: a specific level associated with flower initiation, a higher one during the elongation of floral parts, and a still higher one for maximal adventitious root-formation.

As the auxins favour root-formation, it is expected that the above mentioned fact is reflected upon the capacity of root-formation.

### III. EXPERIMENTS WITH TOMATO

As tomato is a day neutral plant, hence can be grown under both natural S.D. and L.D. conditions without any influence on its flower initiation, it was thought to be a suitable plant to study the effect of S.D. and L.D. conditions on rooting of the cuttings, without interference of the process of flower induction. The work was carried out in two directions. The first was to study the effect of daylength when applied during the rooting period to cuttings taken from L.D. plants. The second was to study that effect on mother plants before cuttings were taken.

#### I. THE EFFECT OF DAYLENGTH ON ROOTING

##### 1.1. When applied to the cuttings

*Experiment I.* - Seeds of the cultivar Ailsa Craig were sown on 9/12/53, potted on 21/12/53 in a mixture of 2 parts leaf mould and peat and 1 part sand and put under L.D. conditions provided by a high pressure mercury lamp for 16 hours supplementing the daylight. The cuttings were taken from the plants at intervals of one week for seven successive weeks. The plants had different numbers of leaves, so that the way of preparing the cuttings differed from time

to time. The cuttings were first made on 27/1/54 from plants having 4 fully expanded leaves. The plants were first cut about 1 cm above the soil surface to avoid the basal part of the plant in which some root initials were found. They were then divided into three parts by cutting the plant 1 cm above the cotyledons and 1 cm above the second leaf. In another series where the cotyledons had fallen and the plants were bigger, they were divided into 3 to 4 cuttings each usually having 2 leaves.

The cuttings were planted in wooden boxes under double glass in the greenhouse. The mixture used as a rooting medium consisted of 2 parts sand and 1 part peat and it was renewed for every experiment. Special attention was paid to the moisture content of the medium; it was always enough for rooting but never excessive. One group of cuttings was rooted under L.D. conditions of 16 hours, while the other was rooted under S.D. conditions of 8 hours. In all cases, the daylight was used as the source of light supplemented by ordinary incandescent bulbs. Ten plants were used in a series. The total number of roots and their total length were recorded for each cutting after 9 days from the cutting date.

**Results and discussion.** – Considering the number of roots per cutting, it can be seen from table 1, columns 2 and 3, that there is no difference between cuttings taken from L.D. plants when rooted under either L.D. or S.D. conditions. Hence the above findings show clearly that the difference of photoperiod during the rooting of the cuttings does not affect the number of roots. The developing buds had a stimulating effect on rooting as the terminal cuttings possessing such buds, had long rooting areas with many roots.

TABLE 1. Experiments I and II. The effect of daylength on rooting of tomato cuttings expressed as mean number of roots/cutting.

	1	2	3	4
Treatment		Cuttings from L.D. plants rooted under S.D. conditions	Cuttings from L.D. plants rooted under L.D. conditions	Cuttings from S.D. plants rooted under L.D. conditions
Series				
1		20.9 ± 3.4	23.0 ± 4.1	–
2		20.7 ± 3.3	25.0 ± 4.6	–
3		12.6 ± 1.5	10.3 ± 1.2	–
4		19.8 ± 2.3	17.2 ± 1.7	19.6 ± 2.6
5		14.9 ± 1.4	17.7 ± 1.3	19.0 ± 1.2
6		14.0 ± 1.7	13.0 ± 1.8	18.0 ± 2.1
7		24.9 ± 1.9	23.0 ± 1.4	–

### 1.2. When applied to the mother plants.

*Experiment II.* – Thirty plants from the material of experiment I were transmitted on 30/1/54 to S.D. conditions of 8 hours. After 15, 22 and 29 days of S.D. treatment successively, a series of 10 plants was made into cuttings on the same day on which the cuttings of the former experiment were made. The cuttings were prepared in the same way and were rooted under L.D. conditions. It was noticed that plants grown under S.D. conditions were somewhat taller with longer internodes, while the flower primordia, although present, were not as big as those of L.D. plants. Moreover, plants grown under S.D. conditions had bigger leaves, but were yellowish in colour.

**Results and discussion.** – In comparing the data presented in the 3rd and 4th columns of table 1, it can be seen that almost no differences exist between



cuttings taken from L.D. treated plants and those from S.D. treated plants, in the quantity of roots produced by the cuttings. It was also noticed that the quality of the roots of S.D. plants was somewhat inferior to that produced by cuttings taken from a L.D. treated plant. It can also be seen in comparing the figures of the 4th column with each other, that there is almost no difference in the mean number of roots per cutting of plants having had 15, 22 and 29 days of S.D. treatment.

It may be concluded that S.D. treatments when applied to the mother plant before cuttings were taken, had no effect on the rooting capacity of its cuttings.

## 2. THE EFFECT OF FLOWER DEVELOPMENT ON ROOTING

In tomato it is impossible to prevent flower initiation. So it was decided to study the effect of flower development on rooting.

*Experiment III.* – Seeds were sown on six successive dates with intervals of 1 week beginning on 25/1/54 and ending on 1/3/54. The plants were potted after 15 days and received the same treatments as in experiment I. On 23/3/54 10 plants from each of the first five series (*Experiment IIIA*) were made into cuttings. From the first 2 series 3 cuttings from each plant were obtained, while in the second 2 groups only 2 cuttings per plant could be prepared, while the last group yielded only one cutting per plant. The number of leaves per plant differed from 2 to 3 in the smallest to 6 in the oldest series. The flowering stages of the plants ranged from young flower primordia, to mature flowers (see table 2). The two oldest groups had the stages of complete flower development, and the beginning of the development of the vegetative bud to form a new branch. Series 3 and 4 represented the earlier stages of flower development, while the rest showed the earlier stages of flower initiation. The cuttings of experiment *IIIB* were prepared on 29/3 from 6 series, the preceding five series and a new one, i.e. the youngest series. The cuttings were grown under L.D. conditions. Counting of the roots took place 8 days after planting.

*Results and discussion.* – From the data in table 2 and figure 1 it can be seen that the flower development in tomato has no effect on the rooting capacity of cuttings. The low value in the first series of experiment *IIIA* is due to the nature of the plants as they were relatively poor rooting plants. This can be confirmed by the fact that the second series in experiment *IIIB*, which originates from the same plants as in experiment *IIIA*, also showed a low value.

TABLE 2. Experiment *III*. The effect of flower development on rooting in tomato, expressed as mean number of roots per cutting.

Series	Condition of flowering bud	Experiment <i>IIIA</i>	Experiment <i>IIIB</i>
1	Young flower primordia	22.0 ± 1.6	30.0 ± 2.1
2	Outer sepals initiated	32.0 ± 2.1	23.0 ± 2.0
3	Inner sepals initiated	40.0 ± 5.2	30.0 ± 2.6
4	Flowers completely initiated and starting to grow	36.0 ± 4.1	28.0 ± 3.0
5	Flowers complete, sepals big, vegetative bud beginning to grow	33.0 ± 3.0	31.0 ± 2.6
6	Flowers complete, lateral buds beginning to develop	–	27.0 ± 3.0

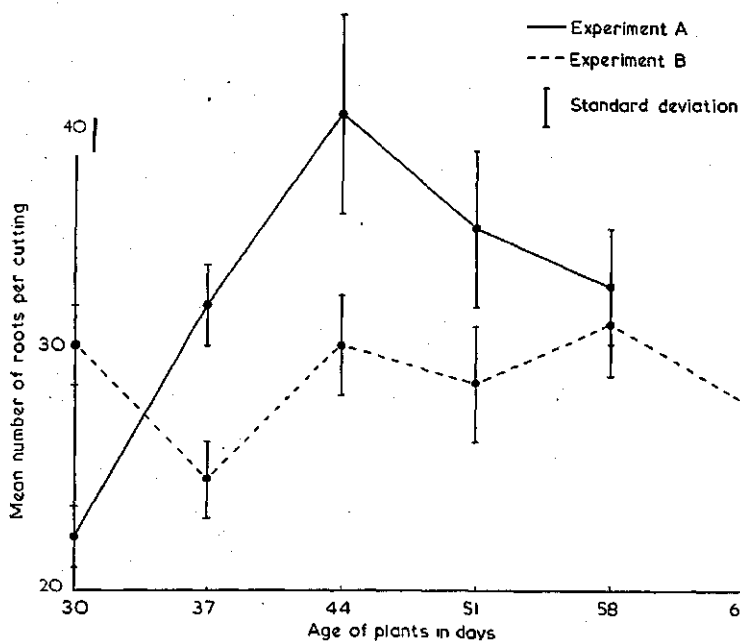


FIG. 1. Experiment III: The effect of flower development on the rooting capacity of tomato cuttings.

#### IV. EXPERIMENTS WITH PERILLA

##### 1. EXPERIMENTAL METHODS

*Perilla crispa* was used as an example of the S.D. plants. It roots readily and its photoperiodic reactions have been studied in detail by former investigators e.g. WELLENSIEK (81, 1952) and DE ZEEUW (90, 1954). At first it was intended to use homogeneous material for the experiment by using branching plants and keeping one branch under inductive and the other under noninductive conditions. Although this was practically possible, the results were not satisfactory, so that it was more advantageous to use ordinary seedlings after determining the proper sample to use. This was done by carrying out a blank experiment.

*Experiment IV.* - A blank experiment with *Perilla*. - One hundred vegetative plants were divided into about 290 cuttings which were planted in groups each having the cuttings of one plant. After 8 days the numbers of roots on these cuttings were counted.

Samples of different numbers of plants, namely 5, 10, 15, 20, 25, 30, 40, 50, 60, 75 and 100 plants were chosen at random. The mean number of roots of the sample, its variability, the standard deviation and the coefficient of variability were calculated for each sample, see table 3.

As it can be seen from the table, a practical size of the sample lies between 20 and 25 plants, as at that location the coefficient of variability is low. It was

TABLE 3. Experiment IV. A blank experiment with *Perilla*.

Number of plants per sample	Mean number of roots per cutting in the sample	Standard deviation	Coefficient of variability
5	7.06	1.788	25.32
10	9.4	1.020	10.85
15	9.2	0.7749	8.42
20	10.1	0.8241	8.16
25	11.56	0.5766	4.99
30	9.37	0.6180	6.59
40	9.71	0.5118	5.27
50	9.94	0.4438	4.46
60	10.02	0.4692	4.68
75	10.09	0.4064	4.03
100	9.93	0.3464	3.48

then decided that the proper sample to be used is from 20–25 plants for each treatment, in the case of having 2 to 3 cuttings from each plant.

*Experiment V.* – Vermiculite as a rooting medium. – It was suggested by MULLARD (53, 1954) that acid vermiculite was a good medium for both soft and hard wood cuttings. The cuttings he used did not show any sign of flagging nor did they lose their leaves. He also concluded that the cause of leaf fall in the cuttings, was the rotting of the cutting base which inhibited the uptake of water.

As leaf abscission was frequent among the *Perilla* cuttings, it was decided to try MULLARD's medium. Asbestos boxes were filled with water saturated vermiculite and covered with a layer of sand. The effect of covering the boxes was studied by covering some with glass, while others remained uncovered. The experiment started on 24/1/55 and the cuttings were kept under L.D. conditions in the greenhouse till 6/2/55 when they were observed. About 220 cuttings were used in this experiment.

Results and discussion. – From table 4 the following can be noticed.

- 1) The rooting percentage of the cuttings was low, since *Perilla* in most cases roots for nearly 100 %.
- 2) Drooping leaves were found in both covered and uncovered boxes, but wilting ones were only found in covered boxes.

TABLE 4. Vermiculite as a rooting medium for *Perilla* cuttings.

Series	Treatments	Total number of cuttings	Number of rooted cuttings	Number of un-rooted cuttings	Number of dead cuttings	Cuttings with wilting and drooping leaves	Cuttings with dying bases	Total number of roots	Mean number of roots		Percentage of rooting
									per root-ed cutting	per cutting	
1	covered	54	24	23	7	9	6	99	4.0	1.8	44.4
2	uncovered	55	20	32	3	6	0	80	4.0	1.4	36.4
3	covered	54	40	14	0	7	0	260	6.5	4.8	74.0
4	uncovered	56	27	29	0	3	0	184	6.8	3.3	48.2

- 3) The covering of the boxes did not affect the number of roots per rooted cutting, while it did affect the percentage of rooting.
- 4) More cuttings died in covered than in uncovered boxes. Also it was observed that: 1) Many cuttings with a dead base kept their leaves. 2) Many of the unrooted cuttings remained in a good condition.

It can be concluded that the leaf abscission in *Perilla* cuttings is properly a question of high humidity of the atmosphere around the tops, as it occurred only in covered boxes, where the humidity was high. The medium then had nothing to do with this abscission. As it was not possible to control the leaf abscission in vermiculite, it was decided to study the effect of the existence of either the leaves or the buds, during the rooting of the cuttings on the rooting capacity of these cuttings in the ordinary medium.

### General remarks

For the following series of experiments, the plants were grown from seeds sown at different dates, and potted in flower pots after a period of 10 to 15 days in a medium of 1 part sand and 1 part leafmould. They were grown under L.D. conditions of 16 hours. Unless otherwise stated, the experiments started when the plants were about 75 days old. The cuttings were made about 2 cm long,  $1\frac{1}{2}$  cm from the internode below the node being used and about  $\frac{1}{2}$  cm from that above it. They were inserted in the soil to a depth of  $1\frac{1}{2}$  cm, so that the leaves were almost lying on the soil. The cuttings were mostly stripped of their buds before being inserted into the soil, in order to exclude the effect of the bud development during the rooting. It was thought that the development of the buds during the rooting of the cuttings, might affect the results due to change in auxin content of the tissues.

COOKE (15, 1953) found that: "in plants suddenly changed from L.D. to S.D. the auxin content increases in the first few days, but those suddenly brought from S.D. into L.D. had a decrease in auxin content for the next few days". He also assumed that these changes in auxin content were associated with a sudden change in photoperiod and not with any photoinduction process. It was then decided, in order to avoid these difficulties, to grow the cuttings under the same conditions as the mother plants, i.e. cuttings from L.D. plants to be grown under L.D. conditions and vice versa. As it had been found previously that S.D. and L.D. conditions had no effect during the rooting period on tomato cuttings, it was thought that this would hold true also for *Perilla*. This will be proved later.

One bench in a greenhouse was prepared for S.D. treatment (8 hours light and 16 hours darkness), and another one received L.D. treatment by supplementing the daylight to 16 hours illumination with ordinary incandescent bulbs of 60 watt, if needed.

The cuttings were rooted in a mixture of 2 parts sand and 1 part peat. They were arranged in rows that were 20 cm apart, the distance between two cuttings in a row being 5 cm. The cuttings taken from one plant were grown in the same order as they had grown on the plant.

The number of roots of each series was counted after 8 days from the cutting date, in order to have the roots in a condition that enabled easy counting and measuring. The root initials that were visible on the surface were also counted.

2. THE EFFECT ON THE ROOTING CAPACITY OF THE PRESENCE OF EITHER THE LEAVES OR THE BUDS DURING ROOTING

*Experiment VI.* – Cuttings were made from L.D. plants and from plants having received S.D. treatment for 21 days. The plants were about 2 months old when the S.D. treatment started.

The first three nodes at the base of the plant were used. In both L.D. and S.D. plants buds and/or leaves were removed as follows:

1. control: leaves and buds at cutting
2. buds at cutting, leaves 2 days later
3. buds at cutting, leaves 4 days later
4. buds at cutting, leaves 6 days later
5. buds at cutting, leaves 8 days later
6. leaves at cutting, buds 2 days later
7. leaves at cutting, buds 4 days later
8. leaves at cutting, buds 6 days later
9. leaves at cutting, buds 8 days later

**Results and discussion.** – It can be seen from figure 2 that the rooting capacity falls to the control level, when either the leaves or the buds were removed 2 days after planting in both S.D. and L.D. groups. Removal after 4 and

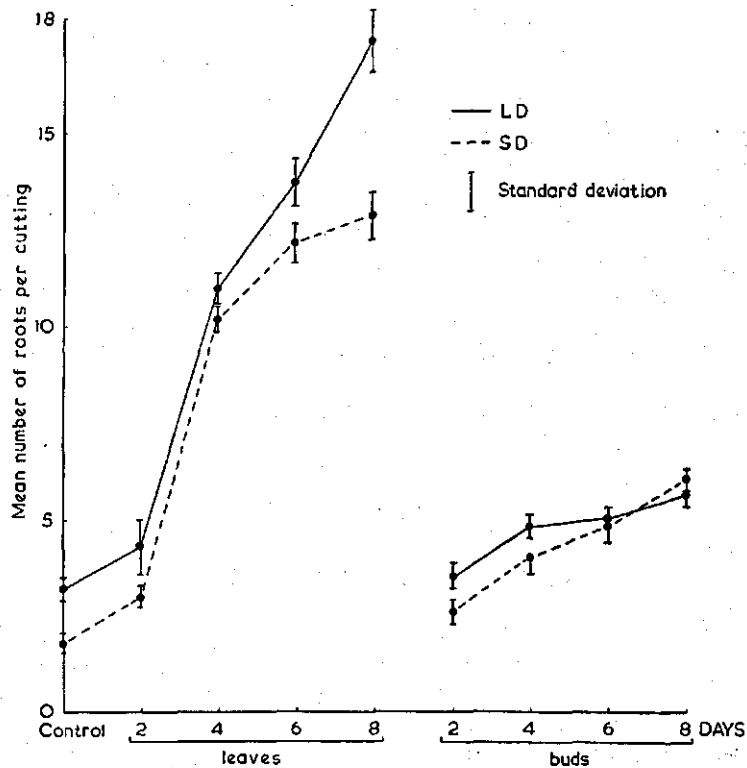


FIG. 2. Experiment VI: The effect on the rooting capacity in *Perilla* of the presence of either leaves or buds during the rooting periods. (The number of days represents the length of the period after which the organ was removed).

6 days increases the rooting capacity. It can also be noticed that the S.D. groups always yielded less roots than the L.D. groups. This difference was more pronounced in the groups having leaves than in those having buds.

It was also noticed in the control and can be ascribed to the fact that the stems can also stimulate the buds to flower, as will be proved later (page 27).

On comparing the rooting capacity of the S.D. and L.D. groups which kept either the leaves or the buds for 8 days (table 5), it was found that the ratio was somewhat higher in the S.D. group than in the L.D. one. This may be due to the fact that the buds of the S.D. group are induced to flower. Moreover the S.D. group having leaves (column 5) yielded less roots as a result of the induction. The differences between S.D. and L.D. groups were more obvious in the cuttings having leaves when the leaves were kept longer. The reverse was true on the cuttings with buds only.

TABEL 5. Experiment VI. The ratio between the mean number of roots per cutting, produced by cuttings with leaves or with buds.

1	2	3	4	5	6	7
Replicas	L.D. groups			S.D. groups		
	Mean number of roots/cutting with leaves	Mean number of roots/cutting with buds	Column 3 as % of column 2	Mean number of roots/cutting with leaves	Mean number of roots/cutting with buds	Column 6 as % of column 5
A	17.4	5.6	32.2%	12.9	6.0	46.5%
B	12.6	7.5	59.5%	11.0	7.9	71.8%

Results regarding the three individual cuttings per plant point to the same direction as in experiment VII, where they will be discussed in detail.

The results of the two replicas were in linear agreement.

### 3. THE EFFECT OF DIFFERENT COMBINATIONS OF LEAVES AND BUDS ON ROOTING

As the effect of either leaves or buds was studied in the previous experiments, it was necessary to study the combined effect of these organs, meanwhile going into more detail concerning the effect of leaves and buds on rooting, and trying to determine the number of roots each organ is able to produce.

*Experiment VII.* – In each of the two replicas of this experiment 250 plants were used. The seeds were sown on 8/3 and 13/3 and potted after 10-15 days, kept continuously under L.D. conditions, cut on 25/5 and 29/5 and observed on 2/6 and 6/6 respectively.

In this experiment only L.D. plants were used, as it had been found in a previous experiment that they react similarly to S.D. plants, and moreover to avoid the influence of differences in the stage of development of the flower buds in S.D. plants. The cuttings were prepared from the lower three nodes of the plant. Ten groups of cuttings were made:

1. with two leaves and two buds
2. with one leaf and two buds
3. with one leaf and one bud in its axil
4. with one leaf and one bud on the opposite side of the leaf
5. with two leaves only

6. with one leaf only
7. with two buds only
8. with one bud only
9. without leaves or buds
10. with only a small portion of the leaves, namely a portion of about 1 cm long of the middle vein with a small portion of the leaf surface ( $\pm 3 \text{ cm}^2$  on each side).

Results and discussion. — The curves presented in figure 3 give a clear picture of the effect of both leaves and buds on rooting.

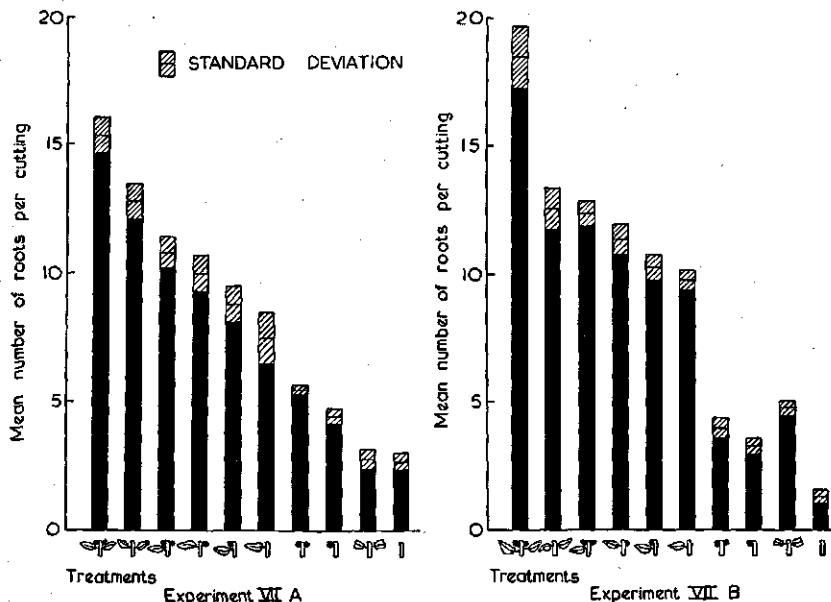


FIG. 3. Experiment VII: The effect of different combinations of leaves and buds on rooting in *Perilla*.

It is seen that the best rooting was obtained in cuttings with two leaves and two buds. Other combinations of one leaf and one or two buds, gave less roots than cuttings with the two leaves only. It was noticed that the cuttings with one leaf and a bud in its axil yielded nearly as many roots as cuttings with one leaf only. There was not much difference between the rooting capacity of cuttings having one or two buds. The effect of the small portion of the leaf was pronounced only in experiment B, where it remained on the cuttings for a long time, but when it wilted and died as in experiment A it gave no effect.

The effect of different locations of the cuttings on the stem has been presented in figure 4. From this graph we conclude that in the groups of cuttings having leaves, except that with only one leaf, the curves slope down from the upper node to the lower one, but in the group with one leaf only the upper two cuttings yielded nearly the same mean number of roots, while the lower yielded less. In the other four groups the curves slope up from the upper portion to the lower one.

From these results and those of the former experiment in both S.D. and L.D.

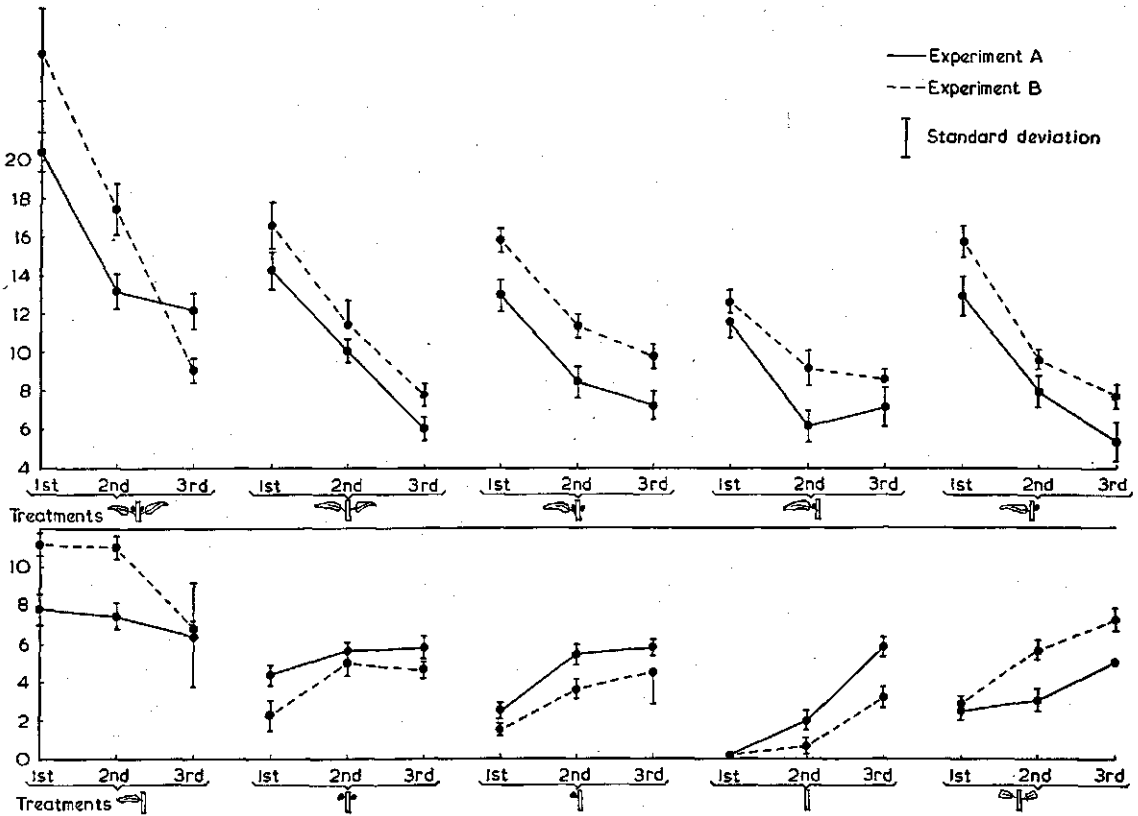


FIG. 4. Experiment VII: The rooting capacity of different portions of the stem as effected by different combinations of leaves and buds in *Perilla*. (1st, 2nd and 3rd represent the position of cuttings from top to base).











groups, one can conclude that there are three factors playing a part in the rooting of *Perilla* cuttings. The first one is coming from the leaves, the second from the buds and the third is the physiological age of the stem tissues. The relatively young leaves are capable of inducing more roots and this capacity decreases with the ageing of the leaves. The young buds, on the contrary, induce few roots and this capacity goes up with the development of the buds. That may be due to the fact that developing buds have some leaves. The effect of the physiological age of the tissue goes parallel with that of the buds, but the presence of the buds causes some increase. When both leaves and buds are present, the effect of the leaves masks that of both the bud and the stem, while one leaf is sufficient to exert this masking effect.

With regard to the rooting habits of those different groups, table 6 summarises the observations.

From this table it can be noticed that if root-formation is regulated by a specific substance, this substance comes mostly from the leaves and to some extent from the buds. The cuttings deprived of leaves and buds yielded very few







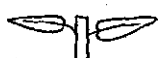





TABLE 6. Experiment VII. The rooting habits of different groups of cuttings as influenced by leaves and buds.

Treatments	Location of roots on the cuttings
1 	All over.
2 	Mostly on the leaf side even in cuttings with big buds. Buds gave long roots, while leaves gave shorter but more.
3 	Only on the side of leaf and bud.
4 	The leaf side yielded short roots, but more than the long ones on the bud side.
5 	All over.
6 	The side without leaf and bud had no roots.
7 	All over, but mostly on the sides of the buds.
8 	On the bud side only.
9 	Not on a distinct portion.
10 	All over.

roots, while with either the leaves or buds some root-formation occurred. The effect of the leaves is more pronounced than the effect of the buds. The existence of a bud on the opposite side of the leaf, caused some disturbance to the distribution of the root-forming substance, as it had spread and resulted in rooting all over the cut surface.

With regard to the relative effect of different organs on root production, table 7 shows that treatment 9, i.e. small portion of the stems, resulted in experiments A and B respectively 16 and 7 % roots. The presence of the two buds (treatment 7) had raised that percentage to a value of 17 and 15 % respectively, while the presence of the two leaves only (treatment 5) resulted in a net gain of 62 and 61 % in experiments A and B respectively. The presence of one bud (treatment 8) resulted in an increase of 11 % in both the experiments. One bud combined with one leaf exerted different effects on the rooting capacity of the cutting. If it was located in the axil of the leaf (treatment 3), it resulted in a net increase of only 3-7 %, while on the opposite side of the leaf (treatment 4) the cutting gained 9 to 15 % net increase in its total number of roots. That might be caused by a disturbance of the unilateral distribution of the root forming substance, by the bud found on the opposite side of the leaves, as previously indicated (see table 6).

TABLE 7. Experiment VII. The percentage of roots given by leaves and buds in different combinations.

Treatments	Percentage of roots	
	Experiment A	Experiment B
1 	100.0	100.0
2 	65.0	67.0
3 	53.0	56.0
4 	61.0	62.0
5 	78.0	68.0
6 	46.0	53.0
7 	33.0	22.0
8 	27.0	18.0
9 	16.0	7.0
10 	17.0	25.0

#### 4. THE EFFECT OF THE PLANT AGE ON ROOTING

In this section the effect of the age of the mother plant on rooting will be discussed. This study will also be completed to investigate the effect of the physiological age on rooting.

*Experiment VIII.* - Plants were sown at regular intervals of 3 days from 31/3/55 till 21/4/55 which resulted in 8 groups of plants. The plants were potted 10-15 days after sowing and kept under L.D. conditions till the seventh group was 70 days old. From each of the first seven groups, 25 plants were made into cuttings. In order to have the cuttings made from tissues of different age, the second and third nodes (from the base) were used. For studying the effect of the physiological age on rooting, all nodes were made into cuttings in the plants of the oldest group. Those plants had mostly 4 to 5 pairs of mature leaves, so they were divided into 4 to 5 cuttings each.

In the second (replicated) experiment, conducted 3 days after the first one, the last seven groups of the above mentioned 8 groups of plants were used, i.e. 2, 3... and 8, and the group of which all nodes were used was group 2. In both experiments the difference in age between the plants was about 18 days which was considered to be large enough.

Results and discussion. - It is obvious in figure 5 that the rooting capac-

ity of the plants does not bear a linear relationship to their age. The fluctuation of the rooting capacity must be due to other factors than those of the age.

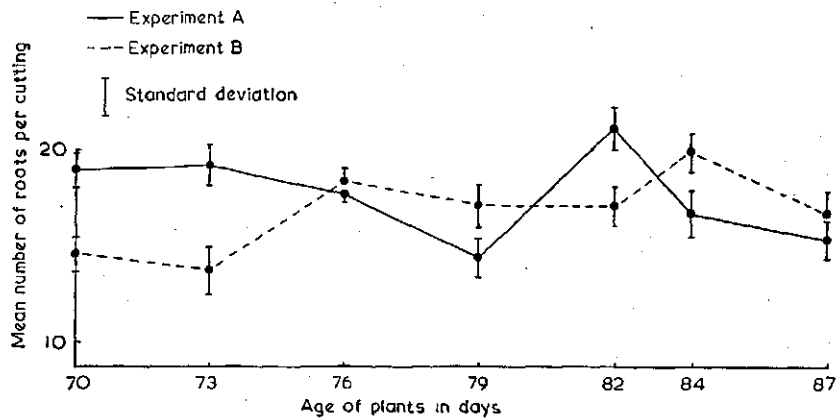


FIG. 5. Experiment VIII: The effect of the plant age on rooting in *Perilla*.

When considering the physiological age of the tissue, one can easily see that it has a pronounced effect in both experiments as shown in figure 6.

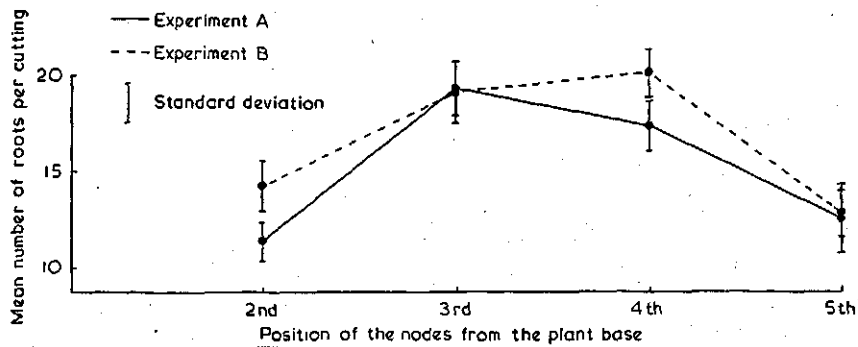


FIG. 6. Experiment VIII: The effect of the physiological age on rooting in *Perilla*.

It is obvious that the cuttings taken from the intermediate zone of the stem, i.e. 3rd and 4th nodes from the base, rooted better than either the 2nd or 5th nodes. This might coincide with the earlier finding (61, see page 8) that the middle portion of a branch or stem, roots better than the terminal and basal portions. We may remark that in the previous experiment the plants have had more than three pairs of leaves, while only the lowest three nodes were used as cuttings. Hence the former result that the third node gave the best rooting, is not in contrast with the results of the present experiment.

From the above data one may conclude that the differences in age of the plants have no reaction on the rooting capacity of the cuttings. This may be caused by the relatively small differences in this experiment (only 18 days). However, the results in this case were satisfactory for the purpose of this study.

One is now sure that using plants between 70 and 90 days old, does not influence the results from the point of view of age.

The physiological age may be considered of much importance, as it had a pronounced effect on the rooting capacity. Much attention must be paid to this factor. As it was previously found that the leaves have much effect on the rooting capacity (page 20), the effect of the physiological age may be explained in terms of age of the leaves. One may think it due to the age of the leaf itself and so may say that both relatively young and relatively old leaves result in fewer roots.

5. THE EFFECT OF FLOWERING ON ROOTING

After studying the previous factors affecting the rooting capacity, we proceeded to study the effect of flowering. It was clear from experiment IV (page 13) that there was a relationship between the factors leading to root-formation and those leading to flowering. Since in the above mentioned experiment only the stage of flower initiation was studied, the present experiment was undertaken to study the effect of further stages of flower development on root-formation.

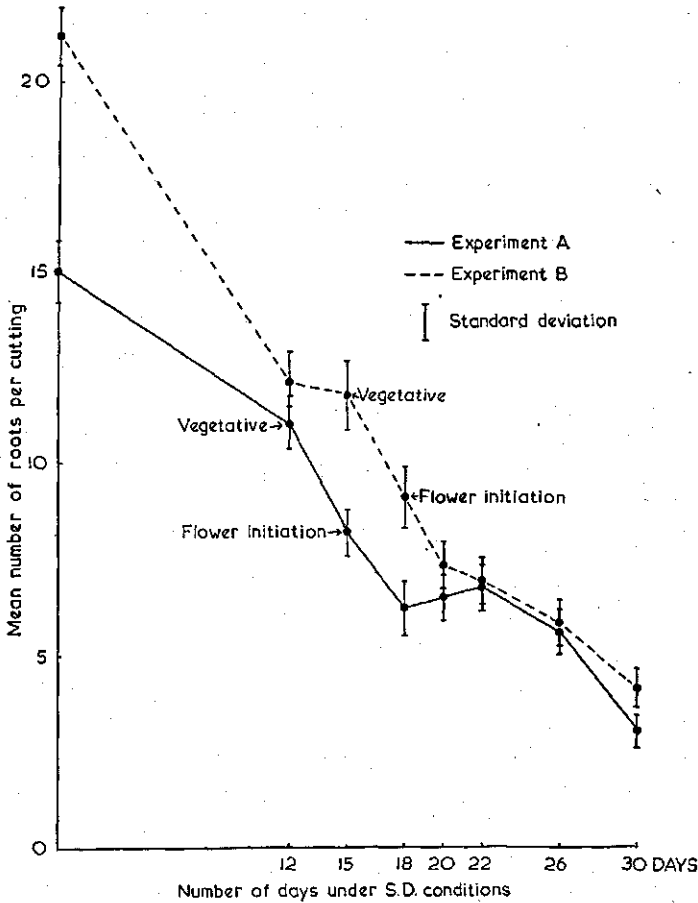


FIG. 7. Experiment IX: The effect of flowering on rooting in *Perilla*.

*Experiment IX.* – On 18/4 and 21/4 seeds were sown to produce  $2 \times 200$  plants. The plants after having been potted, received L.D. treatment till 2/7 and 5/7 respectively, when the S.D. treatment began. This started with seven groups in succession in order to obtain groups that had received S.D. treatments for 12, 15, 18, 20, 22, 26 and 30 days, respectively. The eighth group served as a control and received only L.D. Having had those different photoperiodic treatments, the terminal buds of the plants ranged from vegetative in the group having received only 12 short days, to the stage of open flowers in those having had 30 short days. The cuttings were prepared on 1/8 and 4/8 and observed on 9/8 and 12/8 respectively. When making the cuttings, only the upper nodes were used, since in these nodes the flower bud initiation occurs most readily. As in experiment IV (page 13) cuttings from L.D. plants were grown in L.D., while cuttings from S.D. plants were grown in S.D.

*Results and discussion.* – The effect of flower initiation and development on rooting can easily be seen from figure 7.

The completely vegetative plants, kept continuously under L.D. conditions, gave by far the highest yield of roots per cutting; then the curves slope down, when the plants are induced to flower and continue to go down until the flowers are completely open. The curves do not give any sign of recovery even when the plants have open flowers with ovules producing auxins. This may suggest that all auxins produced by the flowers are used up in the bolting of the plant or the further development of the young flowers. Anyhow, it is clear that the flowering of the plant does not enrich it with a substance leading to root-formation. The effect of S.D. treatment does not stop at flower initiation, but it continues during the flower development also. Hence the conclusion may be drawn that initiation of the flower, its further development and the bolting of the plants exert an inhibiting effect on the root-formation.

#### 6. THE EFFECT OF FLOWER PRECURSOR AND STIMULUS ON ROOTING

CARR (12, 1953) showed that detached leaves of the S.D. plants Biloxi soybean and *Xanthium pennsylvanicum* cannot be photoperiodically induced unless they are in organic connection with a shoot apex. With disbudded S.D. plants *Xanthium* and *Chenopodium amaranticolor* he concluded that:

- 1) during photoperiodic induction the leaves supply some precursor of the "flower hormone" to the shoot apex;
- 2) in the absence of a shoot apex this precursor is dissipated;
- 3) summation of the effects of successive inductive photoperiodic cycles takes place in the shoot apex, and there is no storage of "florigen" in either leaves or stems.

As the precursor is activated by the presence of the buds, the more buds there are, the more stimulus can be produced. Therefore the effect of the presence of the buds during S.D. treatment on rooting was studied.

*Experiment X.* – The following treatments were applied:

- 1) Continuous L.D. or S.D. treatment of plants during 21 days.
- 2) Continuously disbudded except the terminal buds, or not disbudded.
- 3) Terminal buds removed at the beginning of the S.D. treatment on the day of cutting, or buds preserved.

There were 8 combinations, namely:

1. disbudded, L.D.
2. disbudded, S.D.
3. all buds except terminals removed, L.D.
4. all buds except terminals removed, S.D.
5. buds removed on cutting-day, L.D.
6. buds removed on cutting-day, S.D.
7. buds preserved, L.D.
8. buds preserved, S.D.

The S.D. treatment started when the plants were about 60–66 days old. The plants to be kept disbudded continuously were regularly inspected for any sign of regeneration, and any new bud was removed as soon as it could be observed. It was difficult to keep the plants without buds as the axil of each leaf has 3 buds and only 2 of them could be seen by the naked eye at the beginning. Some callus-like tissues formed in the axils of the leaves, on the wounds caused by the removal of the buds. Those were also removed.

The plants were sown in the second half of January 1955, and they had 3 pairs of mature leaves at the beginning of the experiment, but the 4th pair was expanding in the groups having their buds (i.e. groups 3 to 8). The S.D. treatment started on 22/3 and 24/3, cuttings were made on 11 and 14 April and the roots were observed on 19 and 22 April in both experiments.

Results and discussion. – It can be clearly seen from figure 8 that the presence of the buds on the plants during S.D. treatments, whether only the terminals (treatment 4) or all the buds (treatment 6) gave no difference in rooting capacity as compared to the S.D. cuttings without a bud (treatment 2), when considering the three cuttings per plant as one unit.

The effect was the same in L.D. treated plants. The presence of buds during

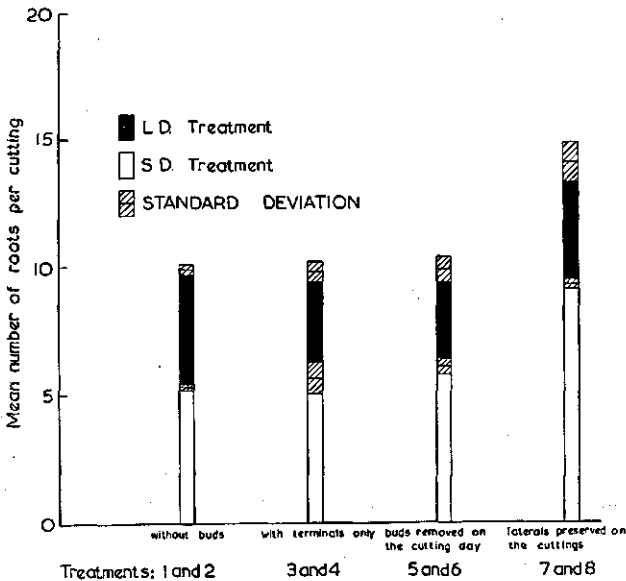


FIG. 8. Experiment X: The effect of flower precursor and stimulus on rooting in *Perilla*.

the rooting period of the cuttings (treatment 7 and 8) increased the mean number of roots per cutting in both L.D. and S.D. groups. The ratio between S.D. to L.D. groups may be said to increase with the presence of the bud. In experiment A it was 48,1 %, 57,1 %, 61,6 % and 66 % for the four groups respectively, that is to say that the presence of buds during the S.D. treatment stimulated the rooting of the S.D. groups. If we look more closely into these ratios, we can see that the presence of the terminal buds raised the ratio by about 9 %, the lateral ones by about 4,5 %, and the laterals during rooting by a further 4,5 %. This means that the stimulation is greater when buds are present for a longer period. In other words, the effect produced by the leaves without any connection with the buds under S.D. conditions was different from that exerted by the leaves and buds together. Moreover, the terminal bud in connection with the leaves exerted a big effect, but not as great as that caused by the whole group of buds on the plant. The effect of the presence of buds was also continued during the rooting of the cuttings. These findings can only be explained by the assumption that the presence of buds on the plant causes an accumulation of the auxins from other regions of the plant in the apical region of the stem. The amount of auxin accumulated in the apical region, seems to be related to the number of buds present on the plant. If there was any liberation or production of new auxins, as one may think, then an increase in the rooting capacity of the treatments with the buds would be expected. That was not the case in this experiment,

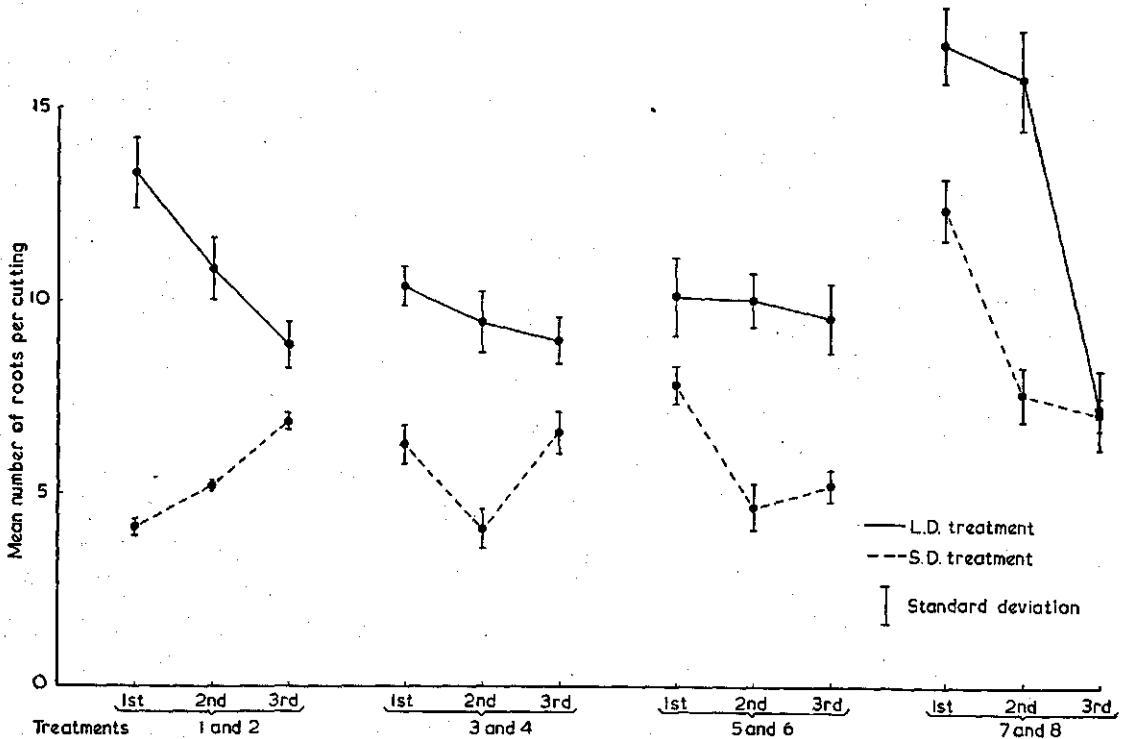


FIG. 9. Experiment X: The effect of flower precursor and stimulus on the rooting capacity of different cutting locations in *Perilla*. (1st, 2nd and 3rd represent the position of cuttings from top to base).

as it can be seen in figure 8 that there was no difference between treatments 2 and 4, or 2 and 6.

Other differences can be easily recorded, on observing the nature of rooting of different nodes from the plants of these treatments which are represented in figure 9.

The difference between L.D. and S.D. plants of the first and second treatments, i.e. disbudded, L.D. and S.D., appears different from those in other treatments. In L.D. plants the uppermost cutting yielded the highest number of roots and the basal cutting yielded the lowest number, while this is the reverse with the S.D. treated plants. In other groups the L.D. treated cuttings showed more or less the same trend as that of the first treatment, while the shape of the curves of the S.D. treated cuttings differed from that of the second treatment. The sudden rise in rooting capacity of the terminal cuttings of treatment 4 is remarkable. This rise still holds true and goes up in the other treatments namely 6 and 8. It can be also noticed that as the difference between the two apical cuttings of a L.D. and its respective S.D. treatment (i.e. 5 and 6, or 7 and 8) decreases, that between the other two portions grows respectively wider. This clearly shows that the differences noted between these treatments are due only to the distribution of auxin among different portions of the stem. The presence of buds on the plant during S.D. treatment seems to have caused the accumulation of auxins in the terminal regions of the stem and thus yields more roots, while other regions of the plant showed a drop in their rooting capacity owing to the lack of auxin.

The S.D. treatment caused the decrease of the auxin level of the plants. The younger tissues seem to be more affected by this treatment, while the older tissues stood it better, thus resulting in different auxin economy within the treated plants. The plants with buds were induced to flower by this treatment, and as the development of the flowers needs a certain level of auxin, that was achieved by withdrawing the auxin from other portions of the stem to the apical portion.

The foregoing may be explained by assuming that there was no difference in rooting due to the suggested precursor and the flowering stimulus except in the altering of the auxin economy within the plant.

#### 7. LEAF LOCATION AND FLOWERING

To study the influence of different leaves on the flower initiation, a preliminary experiment was conducted, in which the plants were deprived of their leaves and lateral buds except one pair of leaves in different locations, while the terminal buds were always kept. Plants used had the same age and leaf number as those used in the previous experiment. The plants were kept under S.D. conditions and were examined continuously to remove any unwanted buds and leaves. All plants flowered on the same date, but there was some difference in the flower development and the length of the inflorescence. As the leaves, although having different surfaces and different ages, had the same effect on flowering, it was thought that there might be factor other than leaves leading to flowering, and the following experiment was conducted to verify this.

*Experiment XI.* – Plants of 66 days old were used, having 5 pairs of leaves. Six groups, each of 10 plants, were used, one as a control having no leaves at



all, and the others having leaves only at the 1st, the 2nd, the 3rd, the 4th and 5th nodes, respectively. The total leaf area used was about 6 cm<sup>2</sup>, i.e. 3 cm<sup>2</sup> of each leaf. All the buds except the terminal ones were completely removed during the whole of the experimental period. The plants were kept under S.D. conditions, with the exception of 3 from each treatment kept under L.D. conditions, and they were defoliated until those under S.D. conditions began to bolt.

**Results and discussion.** – After about 18 short days all groups, including the one without leaves, had initiated flower buds. On the 21st day the buds could be easily observed by the naked eye. During the development of the inflorescence there were some differences between the groups in length of the inflorescence and in size of the flowers, but the number of flowers per inflorescence was about the same in all groups, see photo 1 at the end. The uppermost leaves produced the longest inflorescence and the largest flowers. All L.D. plants remained vegetative.

The differences observed in the development of the flowers was expected, as differences between the leaves in the rate of photosynthesis and auxin content are evident. The flowering of the completely defoliated plants could be explained by the fact that the stems of the plants, having the same pigments as the leaves, were capable to induce the buds.

From these results it follows that in the preliminary experiment the stem of the plant was the factor influencing flowering, and the effect of the leaves was only an influence on the development of the inflorescences.

#### 8. THE EFFECT OF S.D. AND L.D. CONDITIONS ON THE ROOTING OF VEGETATIVE CUTTINGS

As in former experiments, the cuttings were rooted under the same conditions under which the mother plants had been growing. It was thought to be of importance to determine the effect of S.D. and L.D. during the rooting period on the rooting capacity of the cuttings and this was done in the following experiments.

##### Under greenhouse conditions

*Experiment XII.* – The cuttings were deprived of their lateral buds, in order to undergo the same treatments as those used in previous experiments. In this as in the following experiments the cuttings were prepared in a way that would result in the smallest possible differences. This was done by arranging the plants in pairs which included two similar plants. From each plant two cuttings were prepared, and one cutting from one plant combined with its alternative from the other plant were used for L.D. treatment, while the analogous pair was used for S.D. treatment. The cuttings were planted in soil.

**Results and discussion.** – From the results in table 8 one can conclude that the S.D. and L.D. conditions have no effect on the rooting capacity, if these treatments are applied only during the period of rooting of the cuttings.

TABLE 8. Experiment XII. The effect of S.D. and L.D. conditions during the rooting of cuttings.

Replicas	Mean number of roots per cutting	
	S.D.	L.D.
A	16.3 ± 0.7	17.9 ± 1.1
B	19.0 ± 1.3	17.0 ± 1.1

### Under controlled conditions

The second group of experiments took place under controlled conditions of temperature, humidity and light. The light was supplied by fluorescent (T.L.) tubes. All cuttings had buds as they did not stand disbudding. They were rooted in opaque bottles with a volume of 50 cm<sup>3</sup>, filled with tap water and refilled daily. The bottles were inserted in sand, through which ran electric wires for bottom heat. They were kept at a temperature of about 23–25°C and the relative humidity of the air was approximately 60–70%. Special care was taken to keep humidity and temperature in both the L.D. and S.D. compartments the same.

*Experiment XIII.* – In these experiments the cuttings were rooted under S.D. conditions of 16 hours continuous darkness and L.D. conditions of 16 hours continuous light. Accidentally, because we did not have a light-meter at that time, the light intensities were not the same. The S.D. treatment had a light intensity of 980  $\mu\text{W}/\text{cm}^2 \text{ } \varnothing$ , while the L.D. one received a light intensity of 1736  $\mu\text{W}/\text{cm}^2 \text{ } \varnothing$  for 8 hours and 784  $\mu\text{W}/\text{cm}^2 \text{ } \varnothing$  for the other eight hours.

The mean number of roots in S.D. and L.D. respectively was  $18.7 \pm 1.5$  and  $21.0 \pm 2.0$  in experiment *XIIIA*, and  $26.4 \pm 2.8$  and  $29.7 \pm 2.8$  in experiment *XIIIB*.

Consequently there is no difference between the two groups and this confirms the previous finding (page 28). It is clear in both experiments that neither the flowering stimulus nor its precursor existed or at least had not exerted their effect. Hence, excised cuttings are not affected by the S.D. treatments, at least during the first 8 days.

*Experiment XIV.* – In order to study the present problem in more detail, the following experiment was conducted. The periods of light or darkness were shortened in order to remove any possible induction effect. The S.D. treatment was applied as 2 hours darkness and 1 hour light, while the L.D. treatment consisted of 2 hours light and 1 hour darkness, with 4 cycles of the high light intensity, followed by 4 of the low light intensity as mentioned in the above experiment. Under such conditions the plants did not show any sign of induction even after 40 days of treatment. The mean number of roots in S.D. and in L.D. was  $25.0 \pm 3.6$  and  $13.9 \pm 1.7$  respectively in experiment *XIVA*, and  $22.7 \pm 3.3$  and  $12.2 \pm 1.5$  respectively in experiment *XIVB*. This result is rather striking. The S.D. group has yielded nearly twice as many roots as the L.D. group. That result was unexpected as the literature indicates that L.D. conditions are more favourable for rooting (74).

In order to investigate this new result, it was thought best first to try and find other combinations which would have the same effect.

*Experiment XV.* – The combination of 4 hours darkness and 2 hours light and its reverse were tried. The mean number of roots per cutting in the S.D. and L.D. treatments was  $40.5 \pm 3.2$  and  $45.9 \pm 4.1$  respectively. This result does not reveal any difference.

*Experiment XVI.* – The effect of the difference in the light intensity that occurred between the two compartments had to be studied. That was done by giving both compartments a circulation of light of 1 hour dark and 1 hour light. In the L.D. compartment six cycles of the high intensity and the other 6 of the low intensity were given. The S.D. compartment and the L.D. one yielded a mean number of roots per cutting of  $35.5 \pm 3.4$  and  $33.6 \pm 2.8$  respectively.

Thus, the difference in light intensity was too small to exert any effect on the rooting capacity of the cutting.

*Experiment XVII.* – By eliminating light intensity as a cause for the deviating results of experiment *XIV*, the question arose what the cause must be. It was thought to combine the inductive treatment with the noninductive one, i.e. a treatment 16 hours darkness and 8 hours light, and that of 2 hours darkness and 1 hour light and investigate whether it would give any difference or not. By such an experiment one can easily observe whether the induction had any part to play. The results of the inductive treatment and the noninductive one were  $28.1 \pm 2.9$  and  $33.9 \pm 2.8$ , respectively, and thus were hardly significant. This confirms that induction has no effect on the cuttings, at least during the first 8 days.

There was another factor that could have an effect in this case. This factor must lie in the light period. If one examines closely the results of experiment *XIV*, one can see that there was no increase in the mean number of roots of the S.D. cuttings compared with the ordinary case, but there was a decrease in rooting in the L.D. cuttings. The explanation may be that the cuttings were grown in open bottles, through the neck of which the light can easily penetrate. As the light period of the L.D. cuttings was twice that of the S.D. ones, the bases of the cuttings were illuminated twice as long as the S.D. ones. This direct light inhibited the initiation and growth of the roots of the L.D. group, and so yielded a low level of rooting. This inhibition only occurs when a maximum of one hour of darkness is followed by more than one hour of light. To confirm this, the following experiment was conducted.

*Experiment XVIII.* – The cuttings received the same treatments as experiment *XIV*, but the bottles were covered with black paper, in order to exclude the penetration of the light through the water. The results confirmed that light has a direct effect, as the S.D. and L.D. compartments yielded  $36.9 \pm 2.1$  and  $34.7 \pm 1.6$  roots per cutting, respectively.

From this one may conclude that the S.D. or L.D. treatments to cuttings have no effect on rooting. The recorded effect is only the direct effect of illumination on the bases of the cuttings.

## V. EXPERIMENTS WITH RED CLOVER

As red clover is an open pollinated plant, which may show genetically controlled differences in photoperiodic response, clonal material was used. Vegetative propagation was accomplished by means of crown cuttings taken from plants grown in S.D. and rooted under the same conditions, because red clover is a typical L.D. plant which remains vegetative under S.D. conditions. The method used in propagating the plants was the same as used by BARRALES and LUDWIG (2, 1952). Ten days after planting the cuttings were potted. They were kept under S.D. conditions until they were about 85 days old from the cutting date. The plants at that age were suitable for preparing new cuttings. Moreover, LUDWIG et al. (48, 1953) had shown that plants older than two months react readily to photoperiod. Several plants were chosen to produce clonal material, but most of them were omitted for their shy rooting, for having been induced to flower, or for slow rate of growth. The most suitable clone was one which rooted readily and for more than 90 %. The plants grew so rapidly that the first group of cuttings could serve as mother plants for further propagations. This clone was used in the present investigations.

In a preliminary experiment, it was established that after 9 long days of 16 hours flower initiation starts, while after 12 L.D. bolting begins. Since this bolting may alter the structure of the cuttings which may interfere with the results, the observations were stopped after 12 days.

*Experiment XIX.* – The treatments in the main experiment were: continuous S.D. (as a control), and exposure to L.D. for 6, 9 or 12 days before cutting. The L.D. groups were replicated on two successive days. On preparing the cuttings from the plants only the main stem was used, and one cutting with a length of about 2 to 2½ cm was made out of each plant. All the leaves except the apical one which was just developing were removed. The cut was made mostly in the internodes. The cuttings received the same treatments as their mother plants, i.e. either S.D. and L.D. The roots were counted 8 days after cutting.

Results and discussion. – From table 9 and figure 10 it follows that the plants which received 5 or 6 long days and were still in the vegetative stage had rooted better than the controls kept continuously under S.D. conditions. This could be explained by supposing that plants under L.D. conditions produce more auxin than those under S.D. conditions. As soon as the plants initiate their flowers, the amount of available auxin decreases and the rooting capacity drops, which continues during the first stages of the flower development.

TABLE 9. Experiment XIX. The effect of flower formation on the rooting of red clover cuttings expressed as the mean number of roots per cutting.

Treatments replicas	Control	5 or 6 long days vegetative	9 long days flower initiation	12 long days flower development
A	13.5 ± 1.1	18.8 ± 1.1	11.3 ± 1.2	10.5 ± 0.9
B		16.4 ± 1.4	12.6 ± 1.1	11.4 ± 1.1

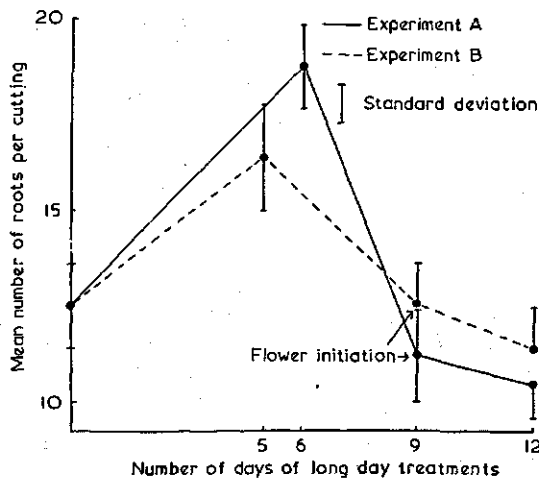


FIG. 10. Experiment XIX: The effect of flowering on rooting in red clover.

## VI. DISCUSSION AND CONCLUSION

In the investigations, described in the foregoing pages, no effect of flower development on rooting was found in the day neutral tomato. This could be explained by assuming that an effect of flowering on rooting is completely overshadowed by the terminal vegetative bud resulting from the sympodial growth of the plant. The vegetative bud also exerted an effect on the habit of rooting, as the terminal portion of the stem, when used as a cutting, was found to result in many roots, distributed over a long rooting area.

A problem which remains for future study therefore, is the question whether, as a general rule, in plants with a sympodial growth rooting is not influenced by flowering, while in plants with a terminal flower it is.

Since tomato plants do not react to photoperiodical differences, it is according to expectation that S.D. or L.D. treatment did not result in quantitative differences of rooting capacity.

In the S.D. *Perilla crispa* the effect of flowering on rooting is quite clear. The flower initiation diminished the rooting, but the flower development exerted even a greater diminishing effect. The more developed the flowers are, the fewer roots the cuttings yield and this indicates that the suggestion of TUREZKAYA (78), as discussed on page 9, holds true for this case. She suggested that the plant hormones became concentrated in the flowers at the beginning of blossoming and later in the fruits, an insufficient amount being left for root-formation. Also, our former conclusion from the literature (page 10) is in accordance with these results. In terms of auxin content a certain level seems to be associated with flower initiation, while another level is associated with flower development. When the plants are brought under S.D. conditions, a lowering of the auxin content takes place, resulting in less rooting, although flower initiation has not yet started. The rooting becomes even less, when flower initiation has taken place and still further until the stage of open flowers has been reached. Hence, the development of flowers seems to require so much auxin that very little is left in other parts of the plants for root-formation.

As discussed on page 24 CARR found evidence of the existence of a flower precursor and a flower stimulus in S.D. plants. In our experiments there was no difference in effect on the rooting capacity of the whole plant between the flower precursor and stimulus, as the plants yielded nearly the same mean number of roots per cutting. The only effect was that the presence of the buds on the plant during the S.D. treatment, caused the accumulation of the growth substances in the apical portions of the stem for use in flower development. This accumulation caused a sudden increase in the number of roots produced by the apical cutting of the plant, while the other cuttings showed a proportional decrease. This shows that the presence of the buds during the S.D. treatment had altered the distribution of the auxins within the plant tissues and there was no liberation or production of new auxins. This difference in effect may be an argument in favour of the suggestion that the action of the flowering process on adventitious root-formation is not a direct one, but operates via auxin.

In the L.D. red clover the auxin content of the plants seems to increase under L.D. conditions. When a certain level is reached, flower initiation takes place and this results in a decrease of the auxin content with diminished root-formation as a result.

Both in the S.D. *Perilla* and in the L.D. red clover flowering has the same inhibiting effect on the rooting capacity of their cuttings, in spite of the differences between the factors leading to flowering in both groups. Rooting and flowering are antagonistic systems in both S.D. and L.D. plants, due to the distribution of auxin during the flower initiation and flower development. This does not hold true for day-neutral plants with a vegetative terminal bud, but it may hold true for day-neutral plants with a terminal flower bud.

## VII. SUMMARY

- I. Experiments were conducted to study the relation between flowering and adventitious root-formation.
- II. The literature on the subject has been discussed at length.
- III. Experiments with tomato (day-neutral plant).
  1. There was no quantitative effect on the rooting capacity after S.D. or L.D. treatments, when applied to either the mother plants before being cut or to the cuttings themselves.
  2. The development of the flowers had no effect on the rooting capacity of the cuttings.
- IV. Experiments with *Perilla crispa* (S.D. plant).
  1. The correct number of plants to use per sample was found by the use of a blank experiment to be 20-25.
  2. If adventitious root-formation is regulated by a substance coming from the leaves or the buds, this substance needed more than 2 days to begin movement out of the organ.
  3. The leaves alone were responsible for the production of  $\pm 61\%$  of the roots, while the buds alone were responsible for  $\pm 16\%$ . The stems alone could induce some root-formation. The combination of these different organs causes some increase in the number of roots produced compared with the sum of the individual effects.
  4. The age of the plant as a whole exerted no effect on the rooting capacity, while the physiological age, (the position of the cutting), had a pronounced effect.
  5. Not only did the flower initiation exert an inhibiting effect on rooting, but also the development of the flowers showed a great inhibiting effect.
  6. The presence of the buds during the S.D. treatment of the plants, (thus causing, in CARR's opinion, the inversion of the flower precursor to a flower stimulus), may have caused an alteration in the distribution of the auxin within the plants, as it became concentrated in the apical region and resulted in some stimulating effect on the rooting capacity in those regions.
  7. The stems of the plants were found capable of inducing the plants to flower.
  8. The effect of S.D. or L.D. conditions on the rooting capacity of the vegetative cuttings was undetectable when applied during the rooting period. Only a direct inhibiting effect of the light on the bases of the cuttings was observed.

- V. Experiments with red clover (L.D. plant).  
Flower initiation caused an inhibiting effect on the rooting capacity of the cuttings.
- VI. It is concluded that adventitious root-formation and flowering are antagonistic systems in both S.D. and L.D. plants, due to the distribution of auxin during the flower initiation and flower development. This does not hold true for day-neutral plants with a vegetative terminal bud, but it may hold true for day-neutral plants with a terminal flower bud.

### ACKNOWLEDGEMENTS

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Thanks are also due to Dr. Chre. J. GORTER and Dr. Ir. J. DOORENBOS for their continued interest.

### SAMENVATTING

#### HET EFFECT VAN BLOEI OP ADVENTIEFWORTELVORMING

- I. Er werden proeven genomen om het verband tussen bloei en de vorming van adventieve wortels te bestuderen.
- II. De betreffende literatuur werd besproken.
- III. Proeven met tomaat (dag-neutrale plant).
  1. Er kon geen invloed op het wortelvormend vermogen worden vastgesteld van korte of lange dag-behandelingen, toegepast hetzij op de moederplanten hetzij op de stekken.
  2. De ontwikkeling van bloemen had geen invloed op het wortelvormend vermogen van stekken.
- IV. Proeven met *Perilla crispa* (korte dag plant).
  1. In de blanco proef werd vastgesteld, dat elk object uit 20-25 planten moet bestaan.
  2. Als adventief wortelvorming beheerst wordt door een stof, welke afkomstig is uit de bladeren of de knoppen, dan begint het transport van deze stof uit het betreffende orgaan pas na meer dan 2 dagen.
  3. Een ontknopte stek vormde 61 %, een ontbladerde 16 % van het aantal wortels, dat een intacte stek vormt. Ook een stek, die zowel ontbladerd als ontknoot was, leverde nog enkele wortels.
  4. De leeftijd van de plant als geheel oefende geen invloed uit op het wortelvormend vermogen; de physiologische ouderdom (de plaats van de stek) had echter een uitgesproken invloed.
  5. Niet alleen de aanleg, maar ook de ontwikkeling van de bloemen, had een sterk remmende invloed op de beworteling.
  6. Indien de knoppen tijdens de K.D.-behandeling aanwezig waren, was het wortelvormend vermogen van de stengeltop groter dan bij stekken

- van ontknopte moederplanten. Dit wijst op een verandering in de verdeling van de groeistof.
7. Ook de stengel van de plant kan de K.D.-invloed percipiëren, zodat ook een ontbladerde plant in K.D. tot bloei komt.
  8. Tijdens de wortelvorming had de daglengte geen invloed. Wel bleek, dat licht een direct remmend effect op de wortelvorming heeft, wanneer het op de stekbasis valt.
- V. Proeven met rode klaver (lange dag plant).  
De bloemvorming had een remmend effect op het wortelvormend vermogen van stekken.
- VI. Er wordt geconcludeerd dat er zowel bij K.D. als in L.D. planten een antagonisme bestaat tussen de vorming van adventieve wortels en bloei, als gevolg van wijzigingen in de verdeling van de groeistof tijdens bloeiinductie en bloemontwikkeling. Bij dag-neutrale planten met een vegetatief blijvende eindknop is dit niet het geval, doch mogelijk bestaat het antagonisme wel bij dag-neutrale planten met een eidelings bloemknop.

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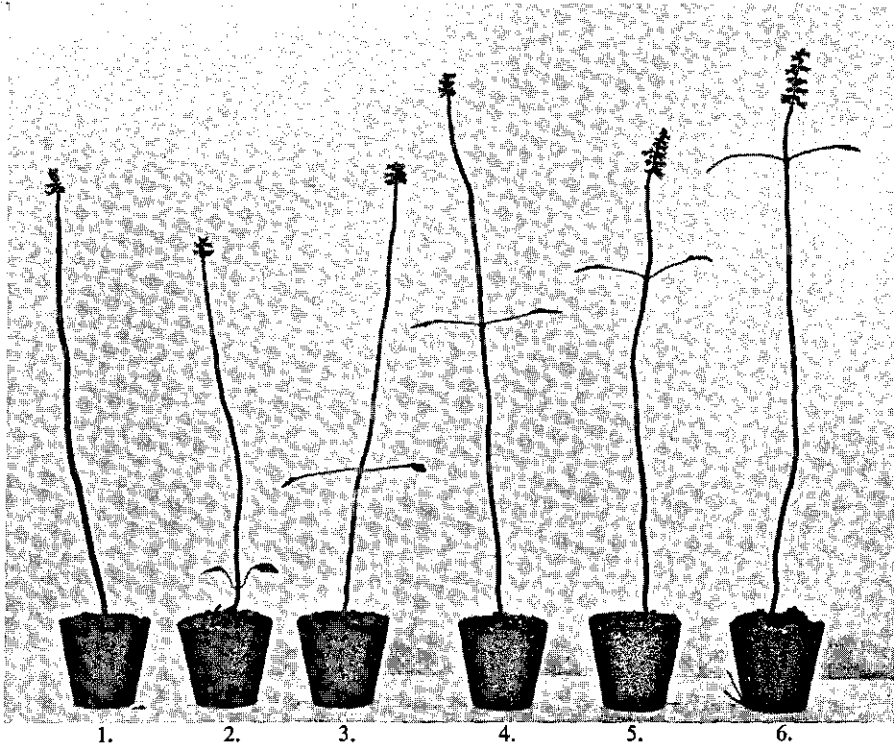


PHOTO 1. Experiment XI. The effect of different leaf locations on flowering of the terminal bud in *Perilla*. The plants from left to right are:

1. control without leaves.
2. the special leaf area of the first pair of leaves.
3. the special leaf area of the second pair of leaves.
4. the special leaf area of the third pair of leaves.
5. the special leaf area of the fourth pair of leaves.
6. the special leaf area of the fifth pair of leaves.

The leaves did not affect the flower initiation, while the flower development was affected as it can be seen above.