Comparative anatomy of blind and flowering rose shoots

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COMPARATIVE ANATOMY OF BLIND AND FLOWERING ROSE SHOOTS

BY

Lyle L. Davis

A Thesis Submitted to the Graduate Faculty for the Degree

MASTER OF SCIENCE

Major Subject Floriculture

Iowa State University

1933

Signatures have been redacted for privacy
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INTRODUCTION

Botanists have been interested for many years in the sequence of floral development of plants, but, with the rise of horticultural research, botanists and horticulturists alike have become interested not only in the order of floral development but in those factors responsible for vegetative growth and the development of flowers. Chemical determinations indicate that these factors are very complex, but they have been used to explain the flowering and non-flowering condition of plants.

In 1931, Hubbel (6) began a series of chemical investigations on the hybrid-tea rose to determine the conditions underlying the production of flowers on some shoots and failure of others to produce flowers. The results were significant in that they showed a difference in the chemical constitution of blind and flowering rose shoots, and indicated that blindness was influenced by the supply of nutrients and carbohydrates. In an effort to shed further light on the possible causes of blindness, the writer studied the comparable anatomical development of normal and blind shoots. Three aspects of bud development were studied; first, the time of flower bud initiation; second, the sequence in development of floral organs, and third, the rate of floral development at different seasons.
A short review of that literature dealing with flower bud differentiation and development is pertinent to this report because it indicates variations in the time and sequence of floral development within the Rosaceae family and in several other species of ornamental plants. The order of floral development is not always centripetal, i.e., calyx, corolla, stamens, and pistils. There are many modifications of centripetal development. Hofmeister (7) indicated in the Rosaceae and particularly in the genera Rubus, Potentilla, and Rosa, which have numerous stamens, that the outermost whorl of pistils is initiated long before the innermost cycle of stamens appears. In Hypericum calycinum, the primordia of the sepals appear after those of the stamens.

Pfeffer (11), another early German investigator, found that in the Primulaceae the primordia of the petals appear after those of the stamens. Webb (17), who was interested in the order of floral development in Spiraeas, found the order of succession to be: sepals, inner stamens, petals, outer stamens, and pistils.

Drinkard (2), working with the apple, cherry, pear, peach, and plum, and Bradford (1), working with the peach, were interested not only in the order of floral development, but also in the time of year when floral structures developed.
In all the above cases, the order of floral development was calyx, corolla, stamens, and pistils. Flower primordia appear in the apple bud on fruiting spurs of some varieties on about July 14th of the year previous to flowering.

Kobel (8) confirmed the work of Drinkard (2) on the cherry and pointed out that the calyx, at an earlier stage, resembles a collar with the edges protruding slightly beyond the center of the stem.

Magnes (10) believed that horticultural practices may influence bud development in the apple. He found that a certain amount of leaf area is necessary for the initiation of fruit buds, and that when flower bud initiation is once started, the development continues almost equally on defoliated and undefoliated spurs. Magnes suggested that the food is stored near the point of manufacture. Roberts (13) showed a correlation between the leaf area at a node and the number of fruit buds formed in the axils of the leaves when the leaves were removed. The removal of leaves inhibited fruit bud formation in direct proportion to the extent of defoliation.

Finch (4) and Hardy (5) determined that flower bud formation in the Dunlap strawberry occurs in September. The two cycles of stamens arise practically simultaneously. Schilletter (14), working with the Dunlap strawberry, pointed
out that the initiation of flower buds is associated with a retardation of vegetative growth which may be caused by lack of moisture, or low temperature, or a combination of both.

Pfeiffer (12) and Watkins (16) found the order of floral development in the gladiolus to be: outer spathe, stamens, inner spathe, petals, and pistils. There is a tendency toward "blind gladioli" if the shoot reaches the stage of rapid elongation at a time when the days are short and the light is of low intensity. Fairburn (3) also indicated that differentiation of flower primordia in the gladiolus occurs three to four weeks after the corms have been planted. The development of flower primordia in the various varieties is identical except that some varieties produce inflorescences slightly in advance of other varieties.

Snyder (15) reported that the calyx primordia of the Concord grape first forms a continuous ring, and that the sepals are synchronous in origin and development.

Hubbel (6) stated that increased monthly illumination in the spring increased flower production over blind shoot production, and decreased monthly illumination in the fall and winter had an equally depressing effect on both flower and blind shoot production in the hybrid-tea rose.
Flowering shoots and blind shoots for this investigation were obtained from one hundred Mme. Butterfly greenhouse grown rose plants. The plants had been in the bench one year and had been handled according to the usual commercial cultural methods during the previous season. While the experiment was in progress, the plants were given the usual commercial care. Each plant was numbered, and, during the course of the experiment, three hundred and fifty buds were given individual numbers. A record was kept of the time elapsing between heading back (pruning the shoot back to an axillary bud) and commencement of shoot growth (breaking of the bud scale). Weekly growth records of all shoots were taken, and, at seven day intervals, the apical points of some of the shoots were collected for histological study. Observations were made to determine whether the shoot arose from a lateral bud located on a blind stem or on a normal stem, and whether the stem had been headed back to a node having a leaf with three leaflets or five leaflets.

Material for histological study was killed in the following solution: ninety five per cent ethyl alcohol fifty cc., glacial acetic acid seven cc., formalin (forty per cent) three cc., distilled water forty cc. Chrome-acetic was tried, but it was found that a gummy residue remained in the material.
In order to obtain better killing and infiltration with paraffin, one side or the tip of the bud was shaved off until the inner part of the flower was partially exposed. After a minimum of twenty four hours in the killing fluid, the material was dehydrated in alcohol, cleared in xylol, and infiltrated with paraffin. Serial sections were cut twelve microns thick and stained in "Fast green" dissolved in ninety five per cent ethyl alcohol. Outline drawings were made with the aid of a microprojector.
Growth habits of rose shoots

In January the normal flowering shoot of the hybrid-tea rose has approximately seven nodes and an average total length of eight inches. In April the normal shoot has the same number of nodes, but its average length is fourteen inches. In January the blind shoot seldom exceeds five nodes and attains a length of four inches, while in April, the blind shoot has the same number of nodes, but is only three and one-half inches long.

The blind shoot of the variety Mme. Butterfly is terminated by a hard, bud-like structure. Just below this structure there are one to three axillary buds, one or all of which may grow into shoots. The shoots from any or all of these buds may produce normal flowers or may continue as blind shoots. As a rule, the blind shoot is slender and bends easily, while the normal shoot has a larger diameter and breaks easily.

At the point of attachment of the shoot to the mature stem, there are several undeveloped buds. These buds are usually very small, but under certain conditions, such as severe pruning, heading back the individual shoot below the first node, adding excessive amounts of nitrogen, or
exposure to natural gas, the dormant buds enlarge, break the scales and produce blind or flowering shoots. As the diameter of the mature stem increases, the ability of these buds to grow decreases.

**Pruning experiments**

Ordinary commercial greenhouse practice consists in cutting back the average flowering shoot at maturity to two nodes above the point of its origin. Superficial examination of the buds after "heading-back" the shoot indicated that some buds started growth within a few days after pruning, while other buds did not begin active growth for many days. More careful studies show that the average lateral bud breaks its bud scales and undergoes visible elongation in ten days regardless of the time of year. In April an occasional bud breaks its bud scales in six days. In January the shortest time observed before visible growth commenced was nine days. Slow breaking buds develop into either flowering or blind shoots.

The leaf at the first node of the shoot often has three leaflets, while the leaf at the second node on the same shoot usually has five leaflets. Observations made by measuring the total length of the shoots arising from fifty axillary buds indicate that there is no particular advantage
Initiation and development of the flower bud

The first microscopical evidence of flower formation is a broadening and flattening of the rounded growing point (Figs. 1 & 2). The calyx arises at first as a continuous ring and has no indication of the individual sepals. Presently five sepals appear as projections on the meristematic ring (Figs. 3 & 3a).

The petals arise as rounded projections on the inner edge of the calyx tube (Figs. 4 & 5). The first cycle is composed of five petals which are alternate with the sepals. Each cycle of petals is synchronous in origin and development. The number of cycles of petals varies from three to eight. However, the inner cycles are often incomplete in number and the petals do not attain full size. Each cycle appears to originate from the lower inner edge of the preceding cycle. During this stage of development, the axis continues to broaden and elongate. (Compare Figs. 4, 5 & 6).

The stamens of the first cycle arise as minute projections around the edge of the axis (Fig. 6). From this stage of development, successive cycles of stamens develop rapidly in centripetal order.

Pistil primordia arise as outgrowths on the axis.
The first pistil primordia arise on the periphery of the axis (Fig. 7). The formation of successive cycles of pistils is in centripetal order and appear simultaneously with the last cycles of stamens.

Simultaneously with the differentiation of the archesporium, there is a very rapid elongation of the cells of the receptacle, especially in the inner portion. This results in the formation of a lip on the inside edge of the torus, thus, partially enclosing the pistils (Fig. 9). The sepals, petals, and stamens seem to be moved to the outer edge of the lip on the torus, although in reality they have been merely raised from their original position by the growth of the receptacle.

Differences in floral development in winter and spring

Studies of the rate of floral development in winter as compared with spring revealed that the changes involved proceeded more rapidly in the latter season. The initiation of calyx primordium takes place in the average shoot by the end of the seventh day in the winter period (Fig. 16). At the end of the fourteenth day, the first cycle of petals appears, and at the end of the twenty-first day another cycle of petals appear. From the twenty-first day until the twenty-eighth day the inner cycles of petals appear; the stamens and
pistils develop rapidly, and the torus is about one-half its full size. After thirty five days, the flower bud is completely developed and ready to unfold.

Flower primordia do not appear as soon in the spring as in the winter, but after the calyx appears the development is much more rapid. In the spring at the end of the seventh day, the average shoot does not have a well defined calyx. A calyx of the same stage of development as that reached on the seventh day in the winter is not developed until the eighth day. By the fourteenth day, the calyx, corolla, stamens, and pistil primordia have appeared. The pistils and stamens complete their development, and the torus finishes its growth by the thirty-fifth day. Except for an enlarging of the tissues, no further visible changes take place before the flower is ready to unfold.

Growth of the normal shoot

Growth and elongation records of the normal shoot were taken from January 18 to May 23, 1933. For purposes of comparison, this record was divided into two periods of forty two days. The first period, designated as the winter period, extended from January 18 to March 3, and the second period, designated as the spring period extended from April 11 to May 23, 1933.
Serial sections of the vegetative bud show one growing point (Fig. 1). Longitudinal sections of the shoot after flower primordia have developed reveal as many nodes as can be counted in the average mature shoot.

The average growth record, as plotted (Fig. 17), shows that in the winter a normal shoot grows only three-fourths of an inch in the first week after it breaks its bud scales. At twenty-one days the shoot is six inches long, and at thirty-five days the shoot has attained its full length of eight and one-fourth inches.

In the spring, the normal shoot grows seven-eighths of an inch the first week after breaking its bud scales. Growth is very rapid from the seventh to the fourteenth day, which is followed by a gradual tapering off of growth until at thirty-five days it reaches its full length of fourteen and one-half inches.

Initiation and development of the blind shoot

The so called "blind shoot" originates in the same way as a flowering shoot. The rounded vegetative growing point undergoes the same early course of development as in the formation of a flower. The calyx and corolla develop in the usual manner. At this stage, a diagnostic feature of blindness may be observed. The epidermal and hypodermal
cells of the calyx show a premature thickening of the cell walls (Figs. 10 & 13) and a brown secretion in deposited in more and more cells and especially in the vascular elements, until eventually it extends below the tip of the flowering axis. Following the deposition of this substance, there is the formation of a periderm-like layer below the bud, which effectually stops all further development of tissues beyond this layer. The deposition of the brown substance, and the development of the periderm may extend to the first node below the flower primordium, or it may extend down through all nodes of the unexpanded shoot. The length of the shoot is determined by the time at which the normal development of the growing tip becomes abnormal. If the arresting of the normal development of the flower occurs shortly after the calyx primordium appears the shoot does not elongate. Symptoms of blindness may be initiated at any stage preceding the development of the pistils.

Further studies may throw light on the chemical constitution of the materials that are deposited in the cells of the blind shoot. The secretion seemed to be of a gummy nature, but its chemical constitution was not determined. The nature of the periderm-like layer was also not determined.
Growth and elongation of the blind shoot

Growth and elongation records on the blind shoot correspond to those of the normal shoot. Figure 18 shows that the average growth in the winter of three-fourths of an inch at the end of the seventh day for the blind shoot was the same as for the normal shoot. At twenty-one days, the blind shoot is three and three-fourths inches long, and, from the twenty-first day to the thirty-fifth day, it slowly elongates to four and one-fourth inches. The growth curve in the spring follows the same trend as in the fall, but it is not as long. At seven days, it is only one-half inch long and at thirty-five days it is three and three-fourths inches long. Elongation of the blind shoot does not take place after the thirty-fifth day.
DISCUSSION

The problem of blind wood formation in roses can be resolved into two phases, i.e. the physiological conditions which produce blind wood, and the anatomical changes incident to the development of blindness. Roberts (13) showed that defoliating the spurs of the apple retards or prevents the growth of the flower buds. This would indicate that the leaf area near the point of origin of flowers influences the initiation of flowers. In the rose there is no difference in the rate of growth of a shoot arising from a three leaflet or a five leaflet node. It appears probable that, unlike the apple, the rose shoot, which completes its growth in five to seven weeks, is dependent for a carbohydrate supply on the stem from which it arose, or on the plant as a whole rather than on a group of leaflets at the base of the shoot.

Seasonal variations in environmental conditions may suggest clues to the possible causes of blindness. The time required before flower bud differentiation is initiated in "water sprouts" varies with the vigor of the shoots. Ordinarily, the initiation of calyx primordia takes place in seven days in the winter and in eight days in the spring. In April there are no more nodes per shoot than in January, but flowering shoots thirty-five days old are about fourteen inches long in spring, while in the winter they are eight
inches long. There are two contributing factors that would account for the increased length of the flowering shoots in the spring. Since the initiation of flower primordia is slower in the spring, it might indicate that a greater number of meristematic cells are laid down before the flower primordia arise. A greater increase in the size of the same number of cells would also account for the difference in the length of the shoot.

Anatomical study of normal developmental history of flower buds afford a basis for the study of blind buds. Snyder (15) and Kobel (8) working on the grape and cherry respectively found that the calyx arises as a continuous ring from which the sepals appear as projections on the meristematic ring. The calyx of the rose appears in like manner. The present work also shows that the outer cycles of pistils develop simultaneously with the inner cycles of stamens. This is supported by Hofmeister (7) in his studies on other Rosaceae.

Slow breaking buds are of no diagnostic value in determining whether they will be blind or flowering shoots. Likewise, the chemical determinations of flowering and blind rose shoots by Hubbel (6) do not indicate a practical method of determining which buds will develop into flowering shoots.

As shown in Figure 18, blind shoots seven days old average only one-half inch long in the spring, as compared to three-fourths of an inch at a comparable age in the winter.
In view of the fact that in the spring there is a drop in the percentage of blind buds and a decrease in the length of blind shoots, associated with an increase in the percentage of flowering wood and an increase in length of normal shoots, it seems that the rapidly growing flowering shoots inhibit the production of blind shoots.

Symptoms of blindness are manifested by stratified layers of cells in the calyx and corolla. Such symptoms may appear at any stage prior to the development of the pistils. Anatomical investigations do not show why blindness occurs prior to the formation of pistils. These findings of blind or "blasted" flower buds are supported by Pfeiffer (12).

The nature of the gummy substance deposited in the calyx and the corolla of blind shoots; the seasonal variations in the rate of growth of blind and flowering shoots; the size and number of the meristematic cells laid down before flower bud initiation; and the origin of the buds at the base of flowering and blind shoots need further investigation. Further research must be directed toward determining the water and light requirements of the hybrid-tea rose at various seasons. It is possible that the ordinary rose grower allows his bench to dry out as the danger of mildew infection reaches its maximum during the months of December, January, and February. There may be an association between the production of blind wood during these short day months and the available water supply.
An anatomical investigation of blind and flowering hybrid-tea rose shoots of the variety Mme. Butterfly was made to determine the time of flower bud initiation, the sequence of floral development, and the relative rate of floral development at different seasons. Flower buds were selected for study from January 1, to May 23, 1933. The investigations revealed:

1. There is no difference in the time required for the axillary bud to break when headed back to a three leaflet or a five leaflet node.

2. The average lateral bud breaks its bud scales and undergoes visible elongation in ten days after heading back, regardless of the time of year.

3. Initiation of calyx primordium takes place in the average shoot in seven days in the winter and in eight days in the spring. At this stage the shoot is three-fourths of an inch long in the winter and seven-eighths of an inch long in the spring.

4. The calyx arises as a continuous ring from which five sepals appear as projections on the meristematic ring.

5. The five petals of the first cycle arise as rounded projections on the inner edge of the calyx tube and
are alternate with the sepals.

6. The members of each succeeding cycle are synchronous in origin and development. The number of cycles of petals varies from three to eight, with the inner cycles often incomplete in number.

7. The stamens of the first cycle arise from the edge of the axis, and each successive cycle develops in centripetal order.

8. Pistil primordia arise as outgrowths on the axis in a more or less centripetal order of cycles. The later cycles of stamens appear simultaneously with the first cycles of pistils.

9. Growth of the receptacle, especially in the inner portion, results in the formation of a lip from which the stamens appear to arise.

10. Slow-breaking buds may become either blind or flowering shoots.

11. All shoots whether blind or flowering grow three-fourths of an inch in winter the first week after the buds break their scales, but in the spring shoots that subsequently become blind shoots elongate only one-half inch the first week.

12. Blind shoots originate in the same manner as flowering shoots, and anatomically blind and flowering shoots are apparently identical during the early
stages of their development.

Preceding the development of the pistils, symptoms of blindness are evident in the form of layers of periderm-like proliferations.


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PLATE I

1. 

1a. 

2. 

3. 

3a.
EXPLANATION OF PLATE I

Outline drawing of flowers in longitudinal and cross section showing the development from the vegetative point to calyx initiation. Magnification X 73.

Fig. 1. A shoot at a very early stage before flower primordia have formed. The rounded growing point (g) is unmistakable and the leaves (l) mark the location of the nodes.

Fig. 1a. A cross section of a shoot at the same stage of development as figure 1.

Fig. 2. A shoot at a later stage of development than Fig. 1. The flattened point (g) indicates that a change from vegetative shoot to flowering shoot is taking place. Flower primordia have not started.

Fig. 3. This shoot shows the initial development of the calyx (c). A lateral shoot bud (b) appears in the axil of one of the leaves.

Fig. 3a. This represents a bud slightly more advanced than figure 3. The sepals (a) appear as separate units although at their earliest stage the calyx appears as a lip surrounding a sunken area.
EXPLANATION OF PLATE II

Outline drawing of flowers in longitudinal and cross section showing the development from the time of petal formation to stamen initiation. Magnification X 73.

Fig. 4. A shoot showing the first petal initiation (p) just inside the lip formed by the calyx (c).

Fig. 4a. Cross section of a shoot at the same stage of development as figure 4.

Fig. 5. A shoot showing the initiation of the second row of petals (p₁). It will be noted these petals arise from the lip formed by the calyx (c) and the first row of petals (p).

Fig. 6. A shoot showing the initiation of a third row of petals (p₂) and the first indication of stamen (s) development.

Fig. 6a. A cross section of a shoot of the same age as Fig. 6.
-30-

PLATE III

7.

7a.

8.
EXPLANATION OF PLATE XIII

Outline drawing of flowers in longitudinal and cross section showing the arrangement of the petals in the flower bud and the initiation and partial development of the pistils.

Fig. 7. A flower showing the development of a second row of stamens (st) and the initiation of pistil primordia (ps). X 35.

Fig. 7a. A flower in cross section showing the arrangement of three rows of petals (p) (p₁) (p₂) inside the sepals (s). X 35.

Fig. 8. Inflorescence showing continued development of the flower. The torus is beginning to enclose the pistils. X 20.
EXPLANATION OF PLATE IV

Outline drawing of mature flower ready to unfold. Magnification X 20.

Fig. 9. A mature flower in which the anthers contain separate pollen grains.

Fig. 9a. A cross section of a mature flower in which the perianth has been removed. The anthers are ready to dehisc.
EXPLANATION OF PLATE V

Outline drawing of the degeneration of flowering shoot to blind shoot. Magnification X 73.

Fig. 10. A flower bud showing the first indication of some disorder. The darkened tips of the calyx (c) are caused by the deposition of a gummy substance in the cells.

Fig. 11. A flower bud showing the deposition of a gummy substance in the calyx, corolla, and extending down the edge of the bud to the first node represented by the bud (b).

Fig. 12. A blind shoot showing the disorganization of the flower and the deposition of gum in all parts of the flower and in the leaves (l) adjacent to the flower.

Fig. 13. A flower bud a little more advanced than Fig. 10. The gummy substance, represented by the darkened portion, is deposited in the outer tissue of the calyx (c) and in one of the leaves (l).
Fig. 16. Degree of flower development
EXPLANATION OF FIGURE 16

Rate of floral development at two different periods of time. The broken line represents the degree of floral development in April and May, while the unbroken line represents the degree of floral development during January and February.

The numbers on the vertical line correspond to the figure numbers on plates I, II, III, and IV, which showed the following stages in development:

1. Rounded vegetative point.
2. Flattened vegetative point.
3. Flower showing calyx primordia.
4. Flower showing calyx and first row of petals.
5. Flower showing calyx, and more than one row of petals.
6. Flower showing stamen initiation.
7. Flower showing pistil primordia.
8. Flower with receptacle one-half developed.
Fig. 17. Comparative growth and elongation of the normal shoot
Fig. 18. Comparative growth and elongation of the blind shoot