HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOLUME 10 | MAY, 1937 | NUMBER 15

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This Issue Completes Volume 10

UNIVERSITY OF CALIFORNIA • BERKELEY, CALIFORNIA

H I L G A R D I A

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOL. 10 MAY, 1937 No. 15

FRUIT-BUD AND FLOWER FORMATION IN THE SULTANINA GRAPE[1]

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INTRODUCTION

THE FRUITING HABIT of the Sultanina[4] grape has required the development of special cultural methods to secure satisfactory crops. These methods, however, are based solely on empirical field observations. An anatomical study of the buds should reveal the differences in fruiting habit of this variety as compared with other varieties and might lead to the development of better cultural practices. The specific objects of this study were to determine (1) the time at which fruit-bud differentiation occurs in the Sultanina, (2) the fruitfulness of the individual buds from the basal to the 20th bud, (3) the rate at which the cluster primordia develop in buds at different positions on the canes, (4) the extent of development of the cluster primordia by the end of the growing season, and (5) the sequence and rate of development of the inflorescences after growth starts in the spring.

REVIEW OF LITERATURE

Former studies of grape-bud anatomy have dealt with the differentiation and early development of the fruit buds and to a less extent with the later stages of flower development. These studies, consisting primarily of field experiments, throw little light on the subject in question. Although Goff[(8)][5] presents considerable data on the initial stages of bud differentiation of different deciduous fruit trees, he simply states that in the grape the embryonic flower is discernible in the autumn prior to blooming. Dorsey[(6)] mentions embryonic grape clusters in the buds before opening and recognizes that each secondary division of the embryonic

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[4] Also called Thompson Seedless in California, and Sultana in Australia.

[5] Superscript numbers in parentheses refer to "Literature Cited" at end of this paper.

cluster occupies a position axillary to a bract. In his textbook Perold,[12] quoting from Müller-Thurgau, points out that the first cluster is initiated about the middle of June, the second cluster about July 1, and that no further initiation occurs in the buds after August 1. Partridge[10] places the time of fruit-bud initiation at midsummer. According to him, the primordium remains a mass of heavily nucleated cells until spring, when the cluster develops after growth starts. Snyder[14] shows that differentiation in the Concord begins early in June and continues in the newly forming buds throughout the growing season. Barnard[1] and Barnard and Thomas,[3] studying Sultana in Australia, discuss the problem rather extensively. Their results, however, are concerned primarily with the distribution of fruit buds on the canes and with the percentage of fruitful buds in a given location.

METHODS USED

The materials studied were collected from the experiment vineyards of the University Farm, Davis, California. Although the soil and vines were fairly uniform, there was some variation in the size and length of individual canes on each vine. This reflected itself as variations in the sizes of the primordial clusters of buds collected on the same date and taken from the same position on different canes.

The collections of buds were made on June 7, 19, and 29; July 11 and 22; August 1 and 22; October 6; and December 5, 1933; and on March 4, 1934. A collection consists of one cane taken from each of fifteen vines. All buds of a given node were placed together and treated as one lot—fifteen buds, accordingly, for each node. All the buds on the canes for the first three collections were used. After the third collection only every other bud was taken above the 4th bud. Since, furthermore, canes of more than twenty buds are rarely retained in the pruning of this variety, no buds were taken from beyond the 20th node.

One week after the last collection of buds (that of March 4, 1934), the first buds began to open. Opening continued about fifteen days. Since the date at which growth begins changes considerably from year to year, it was thought best to include the approximate stage of development of the flower parts by average length measurements of the clusters (table 3) in addition to the date of collection. The dates of the collections of the inflorescences serve to indicate the rate of development of the floral parts. The buds were killed and fixed in Karpechenko's solution. After being washed with tap water, they were passed through alcoholic solutions of increasing concentration up to the 70 per cent solution in which they were stored until used. To facilitate penetration of the killing and fixing

solution, the hairy bud scales were removed, and the buds were put under partial vacuum. Sinking of the buds in the solution was taken to indicate satisfactory penetration.

The buds were then dehydrated with alcohol, cleared in xylene, and infiltrated with and embedded in paraffin. Since the bud scales are rather hard to cut, the embedded buds were soaked in water for one or two weeks before sectioning. A disinfectant was added to the soaking water to prevent the growth of destructive organisms. Delafield's haematoxylin was used for staining, with safranin as a counter stain.

THE MORPHOLOGY OF THE BUD, CLUSTER, AND TENDRIL

Grape buds are generally classified as mixed buds; that is, both leaves and fruit develop from the same bud. They form in the axils of the leaves. The lower buds originate in the axil of the leaf primordia in the previous year's buds (*A* in fig. 4, plate 1, and in fig. 7, plate 2). Inside the scales covering the bud is the growing point with its leaf primordia. Each leaf has two stipules that Barnard[1] calls stipular scales, as large as the leaf primordium or larger. Since they lignify very early, they stain red with safranin and contain many tannin bodies. These stipular scales can be seen on both sides of the base of the petiole of the leaves near the distal end of a growing shoot, whereas only stipular scars remain beside the petioles of the older leaves toward the basal end of a shoot. The arrangement of leaf primordia is distichous. Longitudinal sections through the leaf primordia are shown in figure 4, plate 1 and figure 7, plate 2. Sections at other angles (fig. 8) show only stipular scales. The leaf is initiated as a pointed protuberance from the growing point of the bud (*L* in fig. 2, plate 1, and in figs. 7 and 12, plate 2).

The first initiation of clusters was visible the first week of June. The growing point becomes bilobed; and one of the parts as indicated at *C* in figures 1–6, plate 1, becomes the initial of a cluster, whereas the other continues to be the growing point. It is rather easy to detect whether the new differentiating apex is to be a leaf or cluster primordium, since the leaf forms from a narrow, pointed primordium (*L* in fig. 2, plate 1 and in figs. 7 and 12, plate 2) whereas a cluster of primordium is rather blunt and broad (*C* in figs. 1–6, plate 1). The cluster primordium is always opposite a leaf (*L* and *C* in fig. 2, plate 1 and in fig. 12, plate 2). Thus only sections that are cut in the plane with the growing point and the primordial cluster and leaves will show both these primordia (fig. 4, plate 1; fig. 7, plate 2; and fig. 17, plate 3). Median sections in other planes will show only stipular scales. Nonmedian sections may show clusters (fig. 8, plate 2) and stipular scales but no leaf primordia.

Snyder[14] states that leaf and cluster primordia are alike in the initial stages. Even in this earliest stage of differentiation, however, as figures 1 and 2 (plate 1) will show, the pointed leaf primordium *L* is rather easily distinguished from the blunt cluster primordium *C*. Barnard[1] states that the new organic apex of the bud arises from the apical tissue subtended by a leaf; he interprets this as a sympodial growth, so that the cluster primordium would be terminal. The sympodial origin of the cluster is given general support in the textbooks on viticulture. The rather equal division of the growing point occurring in some buds, the absence of a subtending leaf or stipular scale, and the alternate arrangement of leaves support this idea. A close examination of the growing points of our material revealed, however, that the division of the growing apex to form the cluster primordium in most buds is not equal, which suggests that the cluster may be a lateral rather than a terminal initiation. Further data will be required to support this view.

Goebel[7] states that he does not believe that tendrils are "formed as evident continuations of the internode below them and then only gradually pushed to the side by the stronger growth of the uppermost axillary shoot." Having usually found the tendril primordia situated distinctly laterally on the growing axis, he states: "They either from the first have the leaf-opposed position of the mature condition or . . . proceed from the apex of the axis itself through its unequal division." If the tendrils are not terminal and if, as Goebel points out, they are phyletically derived from inflorescences, it is not unreasonable to accept the possibility of the lateral initiation of cluster primordia, especially since there are many gradations between true cluster and true tendril, a fact that supports their homology. To us this conception appears more tenable than to accept the cluster as terminal and consider it a sympodial growth.

Field studies show that the tendrils occur in a leaf-opposed position the same as the clusters. They are never found below the clusters on the shoot. A tendril primordium (*T*) is shown in figure 9, plate 2, and figure 16, plate 3.

The divisions of the primordial cluster are first indicated by the appearance of bracts subtending the cluster branches (*B* in figs. 4 and 5, plate 1; and in fig. 11, plate 2). The first bract usually arises from the side of the cluster primordium farthest from the growing point. The first bracts were discernible a week or ten days after cluster initiation. By the middle of July, when the increase in size of the cluster primordia slows down, the lateral surface of the primordial clusters is crowded with branches, each subtended by a bract (fig. 9, plate 2, and fig. 18, plate 3). Although growing less rapidly as the season proceeds, the

cluster primordia divide again and again to give rise to secondary and tertiary cluster branches. When the buds open in spring, they are still in primordial form. The apical part of many clusters is still an undivided mass of meristematic tissue (figs. 16, 17, and 18, in plate 3). As shown in the apical part, *U* of figure 20, plate 4, differentiation continues just before and for a short time after the buds open. After the leafing out, however, it is soon superseded by the very rapid initiations of the flower parts.

THE DEVELOPMENT OF FRUITFUL BUDS

The number of buds found to be fruitful for each position on the fifteen canes taken at each collection is shown in table 1. The columns, except the one at the left that indicates position, represent the fruitful buds

TABLE 1

NUMBER OF BUDS FOUND TO BE FRUITFUL OF THE FIFTEEN COLLECTED FROM VARIOUS POSITIONS ON THE CANES

Position of buds on cane	Date of collection								
	June 7, 1933	June 19, 1933	June 29, 1933	July 11, 1933	July 22, 1933	August 1, 1933	August 22, 1933	December 5, 1933	March 4, 1934
Basal	3	3	5	8	7	8	7	8	9
1	4	5	6	9	9	9	10	8	9
2	4	5	7	11	13	13	13	12	13
3	2	8	8	11	14	15	14	13	14
4	3	6	10	12	14	15	15	15	15
5	3	6	12	14	..	..	..	..	..
6	1	6	11	13	15	15	15	14	15
7	1	5	10	..	..	..	..	..	..
8	1	6	8	13	13	14	14	13	14
9	..	4	8	..	..	..	..	..	..
10	..	4	6	10	12	15	13	15	14
11	..	2	4	..	..	..	..	..	..
12	..	3	4	10	11	13	14	14	15
13	..	2	4	..	..	..	..	..	..
14	..	2	3	7	13	12	12	14	14
15	..	1	2	..	..	..	..	..	..
16	..	..	..	5	10	11	12	11	13
17	..	..	..	..	..	..	..	..	..
18	..	..	..	5	9	9	10	13	14
19	..	..	..	..	..	..	..	..	..
20	..	..	..	4	8	8	9	12	12

collected on the date shown at the top of the column. The number of differentiated buds increases rather rapidly as the season proceeds, up to about August 1. After this date there is a slow but continual increase in the fruitfulness of the buds above bud 12.

The buds on the basal end of a cane differentiate first. As the season advances, however, the maximum differentiation is soon shifted to the

region between the 4th and 12th buds of the cane, where it remains. The figures further indicate that the basal and first buds are the least fruitful of the buds on the part of the canes studied. The fruitfulness of the buds increased up to the 4th bud; from the 4th to the 12th buds it was about the same; from the 12th bud upwards it decreased. This observation closely agrees with crop records at Davis, which indicate that the total weight of crop, weight of cluster, and average crop per node increase from the basal up to the 6th bud. Between the 6th and 10th buds the figures remain about the same, whereas beyond the 10th bud they decline. The basal buds were 45 to 50 per cent fruitful, but the 6th to the 10th buds inclusive were 80 to 100 per cent fruitful. Keffer[9] reports

TABLE 2

A KEY TO THE PHOTOMICROGRAPHS, SHOWING THE STAGE OF DEVELOPMENT OF THE BUDS AT DIFFERENT POSITIONS ON THE CANES

Date of collection	Basal node	1st node	4th node	6th node	10th node	14th node	20th node
June 7, 1933	..	..	..	1*	..	..	..
June 19, 1933	..	..	..	3	2	..	..
June 29, 1933	..	..	..	5	4	..	..
July 11, 1933	6	7	8	9	10	11	12
July 22, 1933	..	..	..	13	..	..	..
August 22, 1933	..	..	..	14	..	..	15
March 4, 1934	..	16	..	17	..	..	18

* These numbers refer to the figure numbers of buds appearing in plates 1 to 3 inclusive.

similar results. He states: "The first buds formed in the spring are less well developed than the following buds; and . . . toward the end of the season buds on the distal end of the cane are not so well developed as those formed earlier in the season."

Table 1 shows the course of differentiation of the buds at a given node on the canes throughout the season. The lower buds on the cane were the first to show cluster initiation. In the buds farther up, other conditions being favorable, cluster initiation more or less paralleled the development of the shoot; that is, when the shoot had attained a given state of development, the buds began to show cluster initiation. The buds on the lower part (bud 4) of the cane reached maximum development before those in the midportion (bud 12) of the cane, the reason being the difference in the time of their formation.

The photomicrographs show the difference in size of primordial clusters at the different positions on the canes and at the different dates of collection. In order to show representative development, the specimens for the photomicrographs were so chosen (table 2) that the differentiation of a bud at a given position could be followed through the season,

as well as the differences in size of the primordial clusters in the buds at different positions on the canes for a given date. For the first purpose the 6th bud was selected and followed from the earliest collection showing cluster initiation until the next spring, to show the stages of growth of the primordial cluster. For the latter purpose the canes that were collected on July 11 were chosen. Such an arrangement of the buds reveals that for the 6th bud, the increase in size of the primordial cluster is rather rapid until the middle of July, then slows down gradually; after August the increase is relatively slow (figs. 1, 3, and 5 in plate 1; 9 in plate 2; 13, 14, and 17 in plate 3). The buds farther up on the cane, which developed later, were also later in differentiation and followed the 6th bud in this respect at each date of collection until after August 1. The most rapid increase in differentiation in these buds also came somewhat later in the season than that of the 6th bud. The uppermost buds examined were the latest in development in all respects. Not until the end of the season did their development begin to equal that of the 6th bud. In the upper buds of the canes, however, the development never did attain equality. A comparison of the 20th bud on the August 22, 1933 (fig. 15, plate 3) and March 4, 1934 (fig. 18, plate 3) collections will show that there was a marked increase in size during this period. The great increase in size, however, occurred prior to the October 6 collection. There was no perceptible change between the December 5 and March 4 collections.

Since the differentiation of buds on a cane starts from the base and proceeds upwards, a difference in the size of the primordial clusters in the same direction would be expected. An examination of the buds collected on July 11, 1933 (fig. 6, plate 1, and figs. 7–12, plate 2), shows that, although the first three buds are earlier in time of differentiation than the 4th to 10th buds, their primordial clusters are smaller. The 4th to 8th buds have the largest primordial clusters. Beyond the 8th bud the size of the primordial clusters decreased gradually, until in the 20th bud only the beginning of differentiation was visible. The trend of development in the buds of the August 22, 1933, collection was similar to that described above. The cluster primordia in the basal buds were smaller than those of the first and second buds. Their size increased gradually up to the 4th bud, became about constant from the 4th to the 10th bud, and above the 10th bud decreased again. By the time the buds were ready to open in spring these differences diminished. The differences that persisted, however, though small, were in the same direction as in the younger buds (figs. 16, 17, and 18, plate 3). The findings of Colby and Tucker[6] with Concord closely agree with these figures.

SEQUENCE AND RATE OF DEVELOPMENT OF THE INFLORESCENCE

Our observations on the sequence of the development of the floral parts of *Vitis* agree with those of Sartorius,[13] Baranov,[2] and others—namely, that it is regular. The calyx, corolla, stamens, and pistil are differentiated in the order named. Each flower primordium pushes out from the axis, to which it is attached, as an undifferentiated, rather roundish mass of meristematic tissue (*Uf* in fig. 20, plate 4). The calyx (*S* in figs. 20 and 21, plate 4) first appears as a protuberance on either side of this meristematic surface in the longitudinal sections. The initiation of the corolla (*P* in fig. 21, plate 4) primordium follows the calyx in similar manner. As the calyx grows, the lobes bend inward, come in contact with each other, and give the impression of a coalescence. Snyder,[14] having observed a similar condition in *labrusca,* reports the case as an actual coalescence, while Sartorius[13] states that the end cells of the sepals are simply held together with a sticky substance in *Vitis vinifera.* Barnard and Thomas[3] could not find this condition in Sultanina. As the corolla lobes grow upward they separate the sepals (figs. 22 and 23, plate 4). During their upward growth the petals bend inward and come in contact with each other to form the so-called calyptra (*P* in fig. 22, plate 4).

According to Snyder[14] extensive cell division occurs in the parts of the petals that touch, and a considerable mass of what he terms "callus" is formed at their tips. This was not the case in our material. Usually the epidermis of petals has an irregular outline, and the cell walls bulge out. When the petals come together, the projecting cells of one intermesh into those of the other, and thus interlock the petals. This agrees with the findings of Sartorius.[13] The red-staining cuticle layer clearly shows the line of meshing; and the fact that the petals separate from each other at the base along this line when the calyptra is shed indicates the lack of actual union of the cells. Snyder's mass of "callus" cells is, in fact, a portion of the posterior lobe, which in sectioning has been left in the same plane with the two lateral lobes. The same red-staining substance aids in identifying the cells as belonging to the epidermal tissue. In this case the petal tissue is cut tangentially.

Before the calyptra is completely formed, the primordia of the stamens are discernible as definite lobes (*St* in figs. 21 and 22, plate 4).

The primordia of the carpels appear soon after the meshing of the petals (*Cp* in fig. 23, plate 4). They arise from the meristematic apex in a manner similar to the other parts. At this stage of development the stamens show no evidence of differentiation into anthers and filaments.

Figure 24, plate 4, shows the further development of the carpels; the stamens show the differentiation into anthers (*An*) and filaments (*F*). The primary sporogenous tissue is discernible in the anthers.

The further increase in size of carpels is associated with the development of the ovules. The ovules, their structures, and the sequence of their development were described in some detail by Berlese[4] as early as 1892. His descriptions have been confirmed and expanded by Sartorius,[13] Baranov,[2] and others. The sequence and rate of development of the structures of the ovule are described in greater detail by the latter workers. We have attempted to correlate the development of the individual flower and its parts with cluster size and time (table 3). The

TABLE 3

LENGTH OF CLUSTER AND DEVELOPMENT OF FLOWER PARTS ON THE DATES ON WHICH THE INFLORESCENCES WERE COLLECTED

Length of cluster, inches	Date* of collection	Figure numbers (plates 4 and 5) showing average development for each group
¼- 1	March 18	19, 20
1 - 2	April 1	19, 21
2½	April 8	22
2½- 3	April 13	23
3 - 4	April 21	24, 25
4 - 5	April 25	26, 27
7 -10	May 1	28, 29, 30

* Vine development was almost three weeks earlier than usual during this period of development in the 1934 season.

rate of development of both the flowers and the cluster is influenced, however, by climatic and seasonal conditions.

Although the number of carpels in *Vitis* is two, it is not unusual to find three. Two ovules arise in each carpel. The ovule primordium (*Nu* in fig. 24, plate 4) first appears as a protuberance. It continues to increase in size until it completely occupies the ovarian cavity (fig. 25, plate 5). The placentation is axile. A ring of tissue, arising near the tip of the nucellar tissue, forms the inner integument (*I* in fig. 26, plate 5), which in turn is followed by the formation of a second ring of tissue outside the first, which develops into the outer integument (*O* in fig. 27, plate 5). Approximately a week after the outer integument is initiated, the macrospore mother cell has passed through the second meiotic division to form a tetrad. Since *Vitis* species have anatropous ovules, these structures must move through a considerable arc (figs. 26–29, plate 5). This growth begins soon after the inner integumentary ring becomes dis-

cernible (figs. 26 and 27, plate 5). At this stage the macrospore mother cell can be seen. The bending of the funiculus continues until the ovule tip is directed downward toward the placenta (fig. 29, plate 5). The inner integument has now grown to enclose the nucellus entirely, leaving only the micropylar opening at the lower end. In the Sultanina the development of the inner integument is abnormal, so that its tubular tip is distorted and presses against the ovary wall toward the funiculus (fig. 30, plate 5). Pearson,[11] who observed a similar condition, states that the outer integument is abnormally short. By the time the stage of development shown in figure 30 is reached, the egg cell is ready for fertilization.

During these stages of megasporangial development the primary sporogenous tissue in the anthers divides to form microspore mother cells. About the time the first integumentary ring appears in the ovule, the microspore mother cells enter the prophase of the first meiotic division. At the stage of development shown in figures 28 and 29 (plate 5) each member of a tetrad rounds off and separates to form a microspore. By the time the ovule has reached the stage of development shown in figure 30, the microspores have become mature.

SUMMARY

A histological study of the Sultanina was undertaken in order to determine the time of differentiation of the fruit buds and the course of development of the primordia.

Cluster primordia begin to be initiated during the first week of June. They appear as blunt, rather broad outgrowths of the growing point of the bud. The leaf primordium, on the contrary, appears as a pointed outgrowth from the growing point and is readily distinguished from the cluster primordium.

The most productive part of the canes is the portion between the 4th and 12th buds. The basal and distal buds on a cane are the least productive. The primordial clusters in the basal and apical buds of the canes do not become so large as those in the buds in the middle of the canes.

The differentiated cluster primordia increase rapidly in size during the early season and then slow down. There is no perceptible increase during the dormant period.

The formation of a bract is the first indication of the division of the primordial cluster. Bract formation is discernible a week or 10 days after cluster initiation. Lateral cluster branches arise in the axils of these bracts. By the end of the season the lateral surface of the primordial cluster is a mass of bracts and branch primordia.

Tendril primordia form later in the season than primordia of the clusters.

The development of the flower is regular. The parts follow each other in rapid succession in their development. Six to seven weeks after leafing out, the development of parts is complete.

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EXPLANATION OF PLATES

PLATE 1

Photomicrographs of longitudinal sections through the buds from the collections of June 7, 19, 29, and July 11. (× 26.) Compare figures 1, 3, and 5 with figure 9, plate 2, and with figures 13, 14, and 17 of plate 3, to note the influence of time on stage of development; and compare figure 6 with figures 7–12, plate 2, to note the influence of position of the bud on the stage of development of the cluster primordium.

Fig. 1.—Bud from the 6th node, June 7 collection. *C*, Early stage in the development of the cluster primordium. *L*, Leaf initial.

Fig. 2.—Bud from the 10th node, June 19 collection. *C*, Early stage in the development of the cluster primordium. *L*, Early stage of leaf development.

Fig. 3.—Bud from the 6th node, June 19 collection. *C*, Cluster primordium. *A*, Buds in the axils of the primordial leaves.

Fig. 4.—Bud from the 10th node, June 29 collection. C_1, Early stage in the development of the upper (second) cluster primordium. *C*, Lower (first) cluster primordium. *B*, Initial stage of a bract on the primordial cluster. *A*, Buds in the axils of the primordial leaves.

Fig. 5.—Bud from the 6th node, June 29 collection. *C*, Cluster primordium. *B*, Initial stage of a bract on the primordial cluster.

Fig. 6.—Bud from the basal node, July 11 collection. *C*, Cluster primordium.

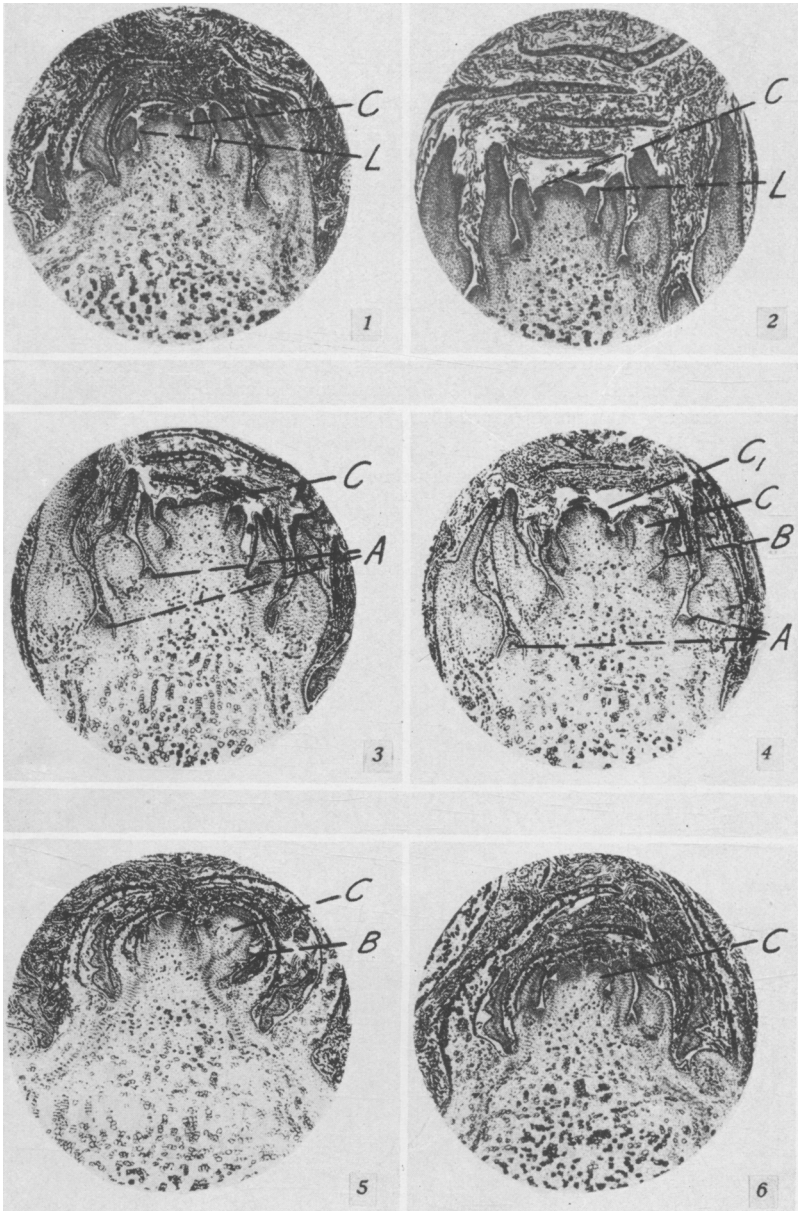

C
L
1
C
L
2
C
A
3
C1
C
B
A
4
C
B
5
C
6

PLATE 2

Photomicrographs of longitudinal sections through buds from different positions on the canes from the collection of July 11. (× 26.) Compare figures 7–12 with figure 6, plate 1.

Fig. 7.—Bud from the 1st node. *C*, Cluster primordium. *L*, Early stage of leaf development. *A*, Buds in the axils of the primordial leaves.

Fig. 8.—Bud from the 4th node. *C*, Cluster primordium. *Cb*, Branches on the cluster primordium.

Fig. 9.—Bud from the 6th node. *C*, Cluster primordium. *Cb*, Branch on the cluster primordium. *T*, Early stage of development of a tendril. B_1, Bract on the branch primordium. *B*, Bract subtending the branch primordium.

Fig. 10.—Bud from the 10th node. *C*, Cluster primordium. *B*, Bract subtending the branch primordium.

Fig. 11.—Bud from the 14th node. *C*, Cluster primordium. *B*, Initial stage of a bract on the primordial cluster.

Fig. 12.—Bud from the 20th node. *C*, Cluster primordium. *L*, Early stage of leaf development.

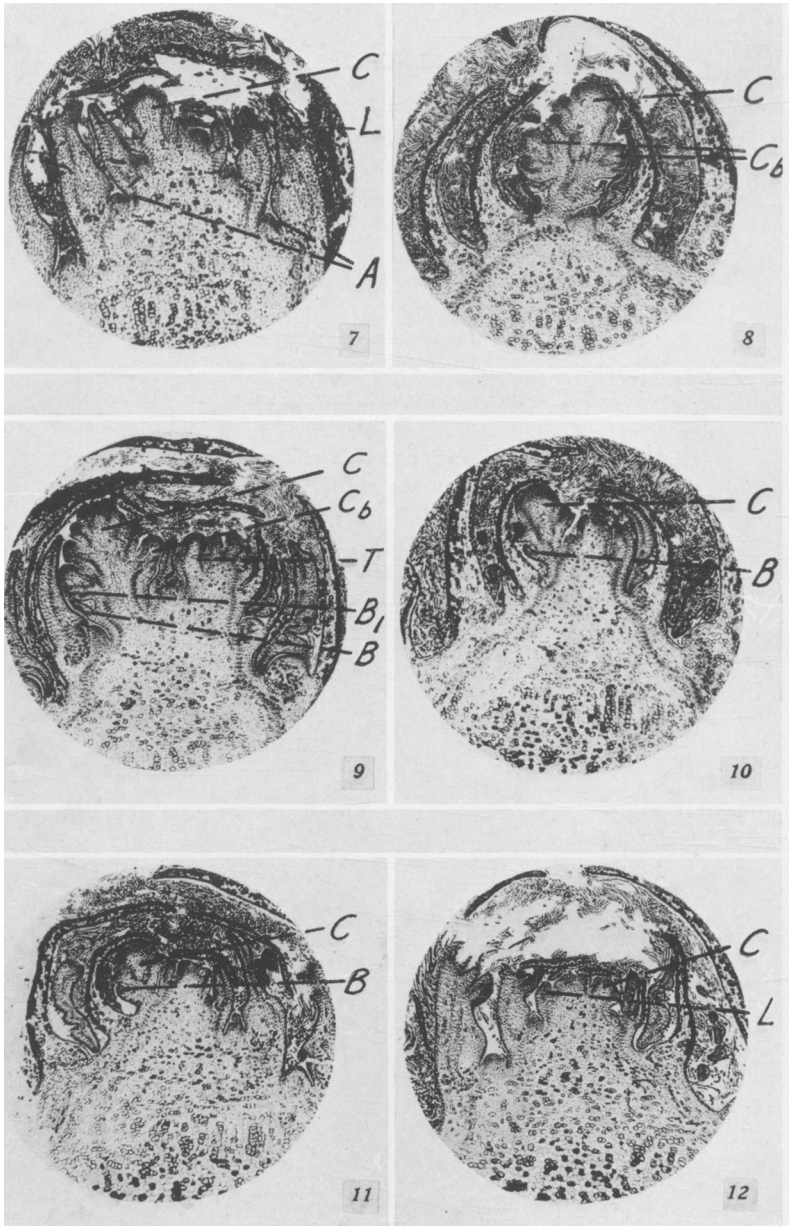

C
L
A
7
C
C_b
8
C
C_b
T
B_1
B
9
C
B
10
C
B
11
C
L
12

PLATE 3

Photomicrographs of longitudinal sections through buds from the collections of July 22, August 22, and March 4. (×26.)

Fig. 13.—Bud from the 6th node, July 22 collection. C_1, Upper cluster primordium. *C*, Lower cluster primordium. *Cb*, Branch on the cluster primordium. *B*, Bract subtending the branch primordium.

Fig. 14.—Bud from the 6th node, August 22 collection. *C*, Cluster primordium.

Fig. 15.—Bud from the 20th node, August 22 collection. *C*, Cluster primordium. *B*, Bract subtending the branch primordium.

Fig. 16.—Bud from the 1st node, March 4 collection. *C*, Cluster primordium. *T*, Early stage of development of a tendril.

Fig. 17.—Bud from the 6th node, March 4 collection. *C*, Cluster primordium. *Cb*, Branch on the cluster primordium. *B*, Bract subtending a branch primordium.

Fig. 18.—Bud from the 20th node, March 4 collection. *C*, Cluster primordium. *Cb*, Branch on the cluster primordium. B_1, Bract on the branch primordium. *B*, Bract subtending a branch primordium.

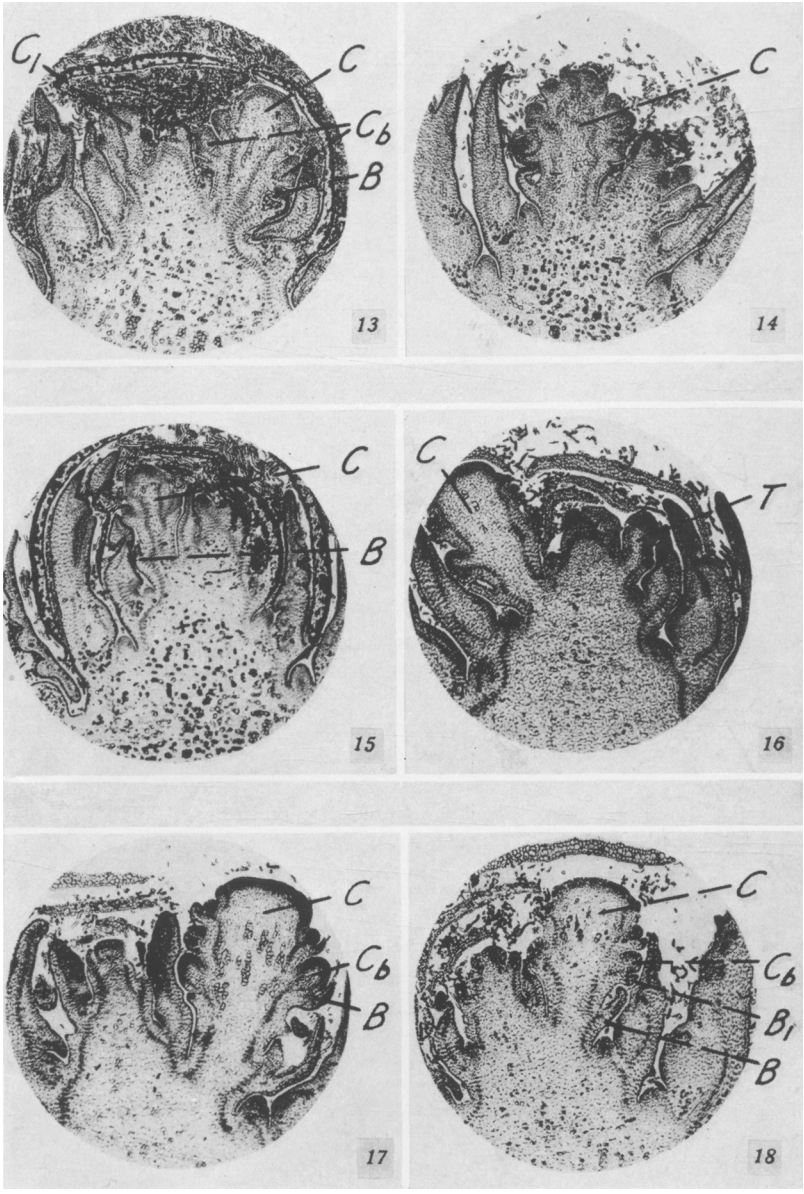

C1
C
Cb
B
13
C
14
C
B
15
C
T
16
C
Cb
B
17
C
Cb
B1
B
18

PLATE 4

Photomicrographs of longitudinal sections through cluster branches, showing the initiation and development of the flower parts.

Fig. 19.—Cluster branch about two weeks after leafing out. (× 26.) *K*, The coming together of the petals to form the calyptra. *B*, Bract subtending an individual flower. *R*, The coming together of the sepals, which occurs early in the development of the flower parts.

Fig. 20.—Cluster branch about one week after leafing out. (× 100.) *U*, Undifferentiated mass of meristematic tissue from which several more flowers may arise. *Uf*, Undifferentiated mass of meristematic tissue from which the flower parts will arise. *S*, Beginning of calyx differentiation.

Fig. 21.—A flower about two weeks after leafing out. (× 100.) *S*, The lower line shows an early stage of calyx development, while the upper line points to a later stage of development of the calyx. *P*, Early stage of corolla development. *St*, Initiation of stamen differentiation.

Fig. 22.—A flower about three weeks after leafing out. (× 100.) *S*, Calyx; the sepals still appear coalesced. *P*, Corolla; the petals are coming together above to form the calyptra. *St*, Initiation of stamen development.

Fig. 23.—A flower three to four weeks after leafing out. (× 100.) *S*, Calyx. *P*, Corolla. *St*, Stamen. *Cp*, Initiation of carpel development.

Fig. 24.—A flower about four weeks after leafing out. (× 100.) *P*, Calyx. *S*, Corolla. *An*, Anther. *Cp*, Carpel. *F*, Filament. *Nu*, Nucellus.

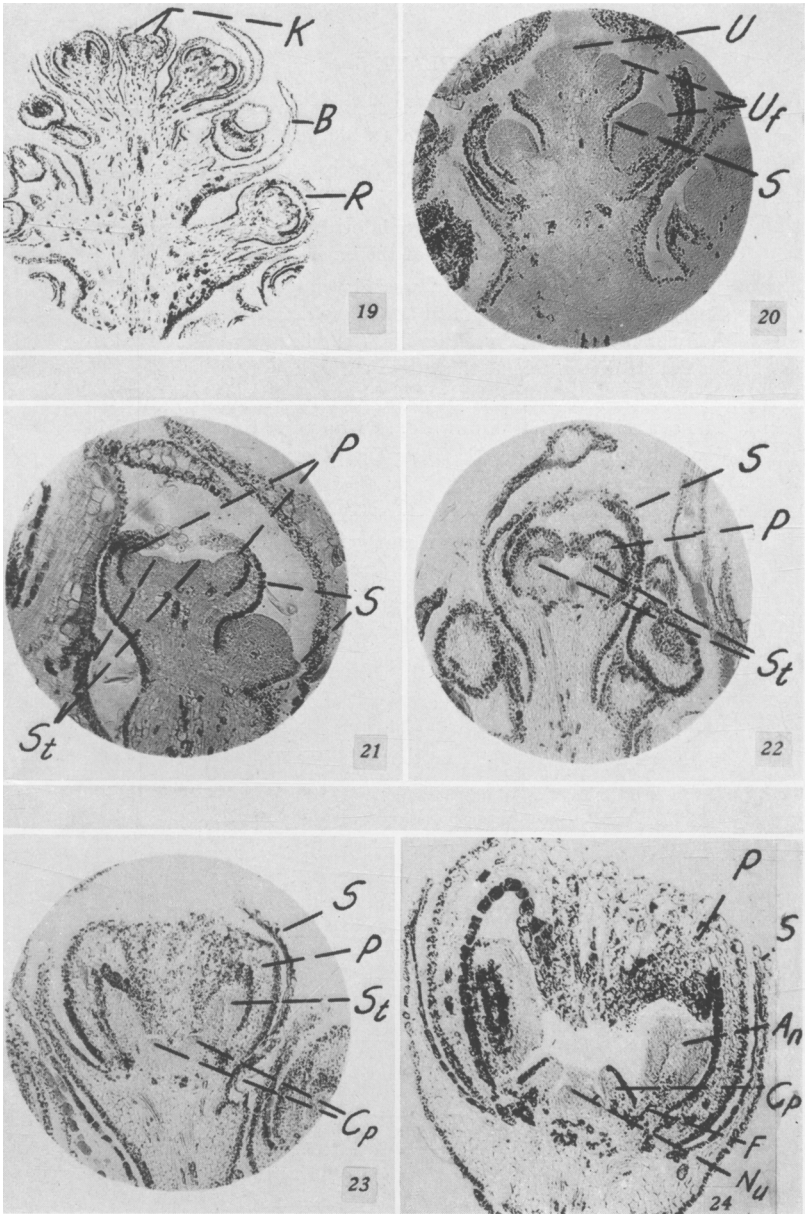

K
B
R
19
U
Uf
S
20
P
S
St
21
S
P
St
22
S
P
St
Cp
23
P
S
An
Cp
F
Nu
24

PLATE 5

Photomicrographs of longitudinal sections through flowers, showing the development of the parts. (×100.)

Fig. 25.—A flower four to five weeks after leafing out. *Ov*, Ovary. *Nu*, Nucellus. *F*, Filament.

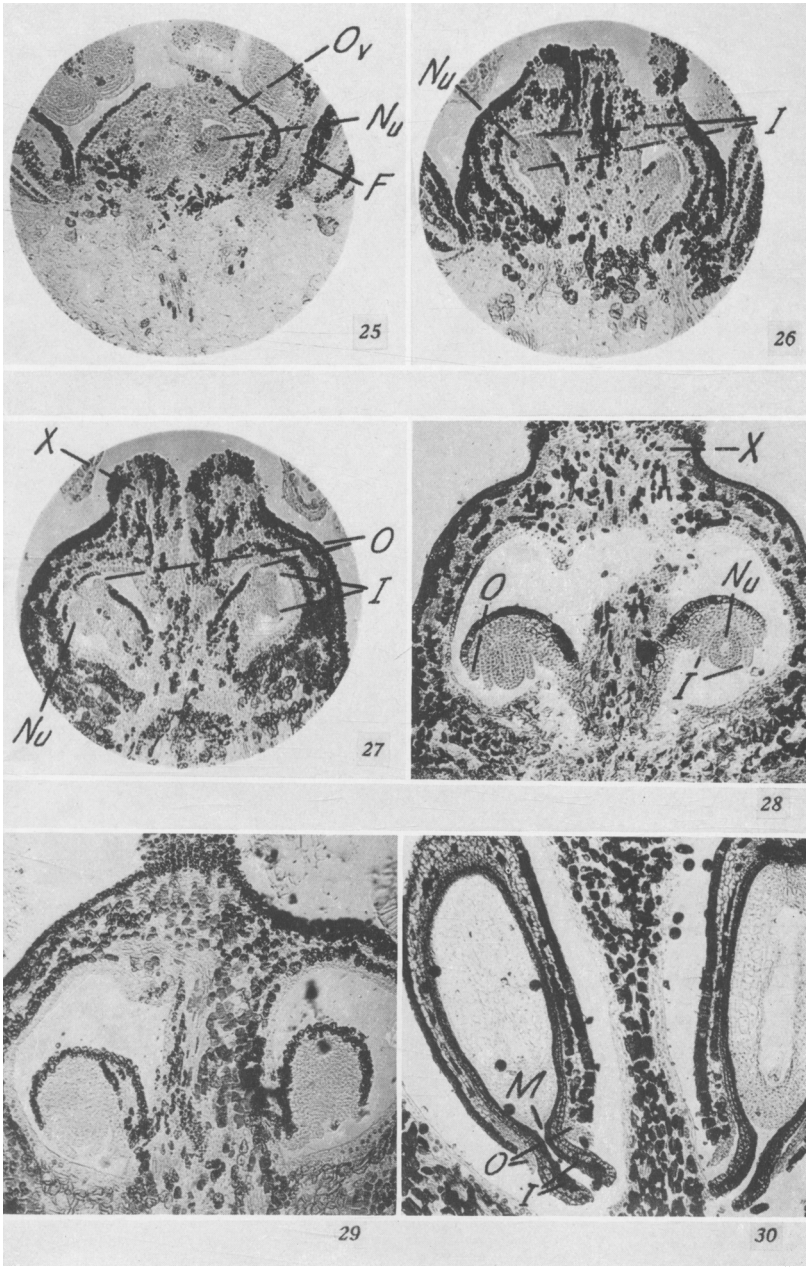
Fig. 26.—A flower several days later than that shown in figure 25. *Nu*, Nucellus. *I*, Initiation of the inner integument.

Fig. 27.—A flower about a week later than of figure 25. *X*, Early stage in the development of the style. *O*, Outer integument. *I*, Inner integument. *Nu*, Nucellus. (The bending of the funiculus is first discernible at this stage.)

Fig. 28.—A flower several days later than that of figure 27. The ovule is pointing downward, and its parts have advanced in development. *X*, Style. *O*, Outer integument. *Nu*, Nucellus. *I*, Inner integument.

Fig. 29.—A flower five to six weeks after leafing out. The flower parts are approaching maturity.

Fig. 30.—The mature megasporangium. The inner integuments elongate abnormally, so that the micropyle may be contorted. *M*, Micropyle. *O*, Outer integument. *I*, Inner integument.


Ov
Nu
F
25
Nu
I
26
X
O
I
Nu
27
X
O
Nu
I
28
29
M
O
I
30