Flower bud development in the Concord grape

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FLOWER BUD DEVELOPMENT IN THE CONCORD GRAPE

BY

J. C. Snyder

A Thesis Submitted to the Graduate Faculty for the Degree

DOCTOR OF PHILOSOPHY

Major Subject Horticulture

Approved:

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1932
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INTRODUCTION

The details of flower bud formation in a number of fruits have been studied by horticulturists since the latter part of the nineteenth century. The early workers found that all buds, although vegetative in the earliest stages, are potentially fruit buds. The conditions which control the transition from vegetative primordia to distinct flower primordia are not well understood. A knowledge of the time and character of this differentiation is of value to the horticulturist in order that he may vary cultural practices to govern flower bud production.

The time at which flower bud formation occurs in most of our tree fruits has been determined. Very little is known about this phenomenon in the American grape. The purpose of this problem therefore has been to determine: (1) the time and character of the initiation and development of the clusters and (2) the time and character of the initiation and development of the individual flower in the Concord grape as grown under Iowa conditions. The results include the development of the inflorescence from the time of its initiation to the development of separate pollen grains.
REVIEW OF LITERATURE

Flower bud formation in the apple has been studied by Lazenby (18), Goff (10, 11), Bradford (3), Drinkard (7), and Gibbs and Swarbrick (13). These men agree that flower bud formation is initiated in the apple in late June or early July of the season previous to fruiting. Drinkard (7) found differentiation to occur in the sour cherry and some Japanese plums at the same time as in the apple. According to Drinkard (7), the pear does not differentiate until about July 15th, whereas the peach shows no evidence of floral structures until August 5th. Isbell (16) and Shuhart (24), working with the pecan observed evidence of flower bud initiation in early spring. Abbott (1) reports that buds of the tung oil tree differentiate as early as May 10th.

The work of Goff (10, 11), Schilleter (25), Waldo (26), Darrow (6), Ruef and Richey (20), and Morrow (20), shows that differentiation occurs in the strawberry in September of the year previous to fruiting. The strawberry grower is able to manage his planting more efficiently as a result of this information. The present knowledge concerning flower bud formation in the grape is not sufficient to be of special value to the American viticulturist. Goff (11) states that
"embryo flowers" are discernible during the previous season. Johns (17) reports small masses of flowers forming about October 30th, without visible evidence of floral structures until November 15th.
MATERIALS AND METHODS

Source of Material

Buds for this investigation were obtained from the Concord variety. The vines, grown in sod, without irrigation, were located on the farm of the Department of Horticulture at the Iowa Agricultural Experiment Station and were trained according to the single stem Four Cane Kniffin system. When the shoots were approximately one foot long, a sufficient number of shoots of medium vigor were selected, labeled, and tied to the trellis. All lateral shoots were removed as soon as they appeared (plate XV, fig. 12, LS). Weekly growth records which showed the number of nodes and the length in feet and inches were made throughout the growing season. Beginning June 5, 1931 and extending to September 1st, three to five shoots were collected each week. Beginning September 12th, collections were made once every three weeks until April 1, 1932 after which they were made every week until May 8, 1932.
Preparation for Sectioning

The buds were removed from the shoots and killed in the following killing fluid: (85 per cent alcohol 50 cc., formalin 5 cc., glacial acetic acid 3 cc., and water 42 cc.). In order to facilitate penetration of reagents, the scales were removed and one face of each eye was shaved off until the inner portion of each visible bud within the eye was exposed. All except the primary buds were removed from the swollen eyes collected in the spring. The cutting of these primary buds was further facilitated by removing the bud scales and hairs. As soon as the flower cluster primordia on the primary bud became large enough to be handled without the aid of binoculars, the clusters were removed and kept separate. The material was left in the killing fluid for a minimum of 13 hours after which it was treated in a 52 per cent solution of hydrofluoric acid. Subsequent treatment followed the standard procedure for the paraffin method. The mounted blocks were soaked in warm water for one to eight days before sectioning. Serial sections were made, attached to the slide with a gelatin fixative, (2) and stained in "Fast green" dissolved in 85 per cent alcohol. No counterstain was used. Outline drawings of the indicated magnifications were made by the use of a microprojector.
Numbering of Eyes

The eyes were numbered from the base of the shoot toward the tip, beginning with the first eye subtended by a normal sized leaf, and ending with the last eye which had attained size sufficient for handling. As shown on plate IV, bud number 1 was taken from node 1, represented by 1 on the shoot, fig. 7; bud 2 was taken from node 2, bud 3 from node 3, and so forth.

Selecting Slides

From each shoot in a collection, buds occupying corresponding positions were used for anatomical comparison. For instance, the basal bud of one shoot was compared with the basal buds of the other shoots. This system of comparison was used throughout the basal and middle regions of the shoots. In the apical region, however, selection began with the ultimate bud. Selection similar to that used previously was made from the ultimate and penultimate buds. Obviously, any variation in the number of buds on the shoots in a collection necessitated an omission of some of the buds in the middle regions of all except the shortest shoot. The uniformity of development of the buds in the middle region justified this elimination.
EXPERIMENTAL DATA

In the grape, a group of two to five buds arises at each node. This group is referred to as an eye. Although each bud of an eye may produce a shoot, it is more common for only one shoot to appear at a node. One of the several buds is larger, and structurally more advanced than the others. This bud is referred to as the primary bud. The progressively less developed buds are known as secondary, tertiary, and quaternary buds, respectively (plate VIII, fig. 8, PB, SB, TB, and QB). It is known that under normal conditions the shoots from the primary buds produce the major portion of the crop. In case this shoot is injured or destroyed, one or more of the other buds often produces a fruitful shoot. The investigation involved in this thesis was confined to the primary buds because of their dominant economic importance to the horticulturist. Thus, when the term bud is used the reference is to the primary bud.

Initiation and Development of the Cluster

The buds arise as lateral protuberances or primordia near the meristematic tip of a shoot. The apical primordium
elongates and produces similar lateral outgrowths which are primary primordia of bud scales, leaves and inflorescences (plate I, fig. 1). By the time there are approximately four such swellings on the axis of the bud, two outgrowths, located alternately on the axis, have elongated and become somewhat pointed. These primordia can be identified at this stage as leaf primordia (plate I, fig. 2, L). As the growing point (G) of the bud elongates, additional lateral primordia appear. Some of these differ from those at the base of the axis in that they are produced in pairs, one on either side. The lobes of each pair, although alike in the initial stage, soon acquire different shapes. One lobe takes on the characteristic shape of a long and pointed leaf primordium described above, while the other becomes obovate in shape. The latter is the first evidence of a cluster primordium (plate I, fig. 3, C1). While this differentiation is taking place, primordia of axillary buds are laid down in the axils of the two previously formed leaf primordia (plate I, fig. 2, A). The appearance of a small, often pointed lobe at the base of the cluster primordium marks the initiation of a cluster bract (plate I, fig. 3, B). Additional lobes soon arise on the cluster beyond the bract. These lobes mark the initiation of secondary clusters (plate I, figs. 4 and 5, SC1).
Figure 5 on plate I is the basal secondary cluster detached from figure 4. Figure 5 represents the secondary cluster after it has redivided and produced three lobes. Each of these lobes originates directly from the main axis of the secondary cluster and is called a tertiary cluster (plate I, fig. 6, SC3). Primordial bracts subtending the groups of tertiary clusters arise soon after the initiation of the tertiary clusters. These are called secondary bracts (fig. 6, B). One or more of the tertiary clusters may redivide to form additional lobes which become quaternary clusters (plate I, fig. 10, SQ3). Occasionally a quaternary cluster redivides and produces additional lobes.

In order to clarify the nomenclature necessary to describe a cluster, a diagram is presented in plate XIV. The inflorescence of the grape forms a racemose panicle. The main axis (a) bears lateral axes of the first order (b) and these in turn bear lateral axes of the second, third, and fourth orders (c and d). The degree of branching decreases toward the apex and the distal part of the cluster bears single axes for the most part. The lateral axes of the first order are longest and most profusely branched. The basal ones are far apart while the distal ones are close together. The cluster of fruit borne by each axis is referred to as a secondary, tertiary, or quaternary cluster according to the order of the axis upon which the fruit is borne. This of course is not true where the
pedicel is attached directly to the rachis. On account of the necessity of referring so frequently to the subdivision of the rachis throughout the entire body of this thesis, the author has chosen to use the term "cluster" in preference to axis; "secondary cluster" being more descriptive and convenient, for example, than "axis of the second order".

Organogeny of the Flower

The first visible evidence of flower formation is a broadening and flattening of the apex of the floral axis. In cross section the calyx appears to be a continuous ring, with no indication of members (plate II, fig. 1, x). Whether the calyx arises as separate sepal primordia which later coalesce, or whether it arises as a continuous sheath is perhaps in some question. However, the smoothness of the epidermal surface of the primordial calyx in all cross sectional planes indicates that it originates as a continuous ridge. It was further definitely determined that the calyx forms a continuous cap over the flower. This is brought about by a proliferation of the tissue in the apical region of the calyx followed by an apparent coalescence (plate III, figs. 2 and 3, x). Before the calyx completely encloses the bud, the petals are evident as definite lobes (plate I, fig. 8, pe). The developing petals
push their way out through the calyx. The mechanism of the rupturing of the fused calyx cap is not known.

As the petals elongate and come nearly into contact with each other, the cells of the apical regions of the petals enlarge rapidly, producing a roughened surface (plate III, figs. 2, 3, and 4, pe). Extensive cell division is initiated in this region, producing a considerable mass of callus at the tips of the petals (plate III, figs. 4 and 5, pe). The callus masses of the petals come into contact; the loose, spongy tissues coalesce and thereby bring about fusion of petals (plate III, fig. 5, pe). The petals remain separate at the base. The most common number of members in the perianth is five, although as many as seven were observed. As far as has been determined the members of each cycle are synchronous in origin and development.

The stamens are evident before the petals are completely coalesced (plate I, fig. 8, st). Archesporial regions appear in the anthers concurrently with the formation of four anther lobes. Progressive enlargement and differentiation occur in the anther until the archesporium becomes clearly delimited. The formation of pollen tetrads and separate pollen grains follows in rapid succession (plate II, fig. 3, PM; fig. 4, Ts, and fig. 5, Pg).
The chronological appearances of tetrads and separate pollen grains were used as diagnostic features in making a study of flower development. In the grape cluster as a whole, anthesis occurs in basipetal succession. For instance basal subclusters develop before other subclusters of the main cluster (plate XI, C1). In individual subclusters anthesis is in acropetal order (plate X, SC1).

The Chronological Development of the Cluster

The first collection of buds was made June 5, 1931, when the growing shoots were approximately one foot long. At this time each bud consisted of a growing point and one to several leaf primordia (plate IV, fig. 1, G and L). Cluster initiation therefore had not yet occurred. All buds on the shoots collected June 5th showed this condition.

The shoots collected June 13th, although still succulent were 18 inches long. Each shoot had developed eight eyes, the basal six of which were large enough to be handled. Most of the buds on each shoot had developed three nodes, as was determined by the difference in size and shape of nodal and internodal cells (plate XVIII, figs. 1 and 2). In buds of the middle region of the shoot, two cluster primordia are evident (plate IV, figs. 3 and 4, C1 and C2). The basal cluster primordium (C1), originating at node 3, and hereafter referred to
as cluster 1, shows the initiation of a bract (B). The primordium for cluster 2 (C₂) is evident by the time the bract is visible in cluster 1. The middle region shows considerable advancement over the collection of June 5th. The buds of the apical and basal regions of shoots collected June 13th are not much advanced over the collection of June 5th. Evidently the development of apical and basal buds lags behind the development of buds of the middle region.

The shoots collected June 20th were approximately two feet six inches long and bore eight suitable eyes, the buds of which had developed approximately five nodes each. The presence of a secondary cluster in bud 3, (plate V, fig. 3, SC₃) and pointed bracts in buds 3 and 4, (figs. 3 and 4, B) indicate that the greatest development had occurred in the middle regions of the shoots. A primordial second cluster was evident in bud 3, (plate V, fig. 3, C₂). The evidence of greatest development in the basal region was a bract subtending the basal cluster in bud 2, (plate V, fig. 2, B). The buds in the apical region were less advanced, as indicated by the absence of bracts subtending the cluster (plate V, figs. 7 and 8). The buds collected June 20th therefore, with the exception of those in the apical regions, were more highly developed than those collected June 13th. Greatest advancement occurred in the middle regions where the first visible evidence of a secondary cluster appeared.
The shoots collected June 27th were approximately four feet long and most of them bore eleven eyes, nine of which were sectioned. The most advanced buds occurred in the middle region of the shoots and had developed six nodes. The basal clusters in buds 3, 4, 5, and 6 are subtended by bracts (plate VI, figs. 3, 4, 5, and 6, C1 and 8). These clusters have re-divided to form secondary clusters (SC1). In bud 4 the basal secondary cluster is subtended by a bract (plate VI, fig. 4, B). In several of these buds, cluster 3 is subtended by a bract (figs. 3, 4, and 6, B). There is evidence of a second cluster in bud 2 (fig. 2, C2) while bud 1 shows evidence of one cluster only (fig. 1, C1). The buds in the apical and basal regions show identical stages of development.

The shoots collected July 17th were six feet long and commonly bore 18 eyes, 14 of which were sectioned. Buds 4 and 5 were omitted from plate VII because they were in the same stage of development as bud 3. Several of the buds in the middle region of the shoot contain three clusters, the basal one having numerous secondary clusters (plate VII, fig. 4, C1, C2, and C3 and fig. 3, SC1). The secondary clusters in most of these basal clusters are subtended by bracts. Cluster 2 (C2) contains fewer secondary clusters (SC1) than does cluster 1. In most of these buds there is evidence of a third cluster (plate VII, figs. 5, 6, and 8, C3). It is evident that in
the buds of the middle region, the development of the three clusters is in basipetal order.

Cluster 1 in the basal region is nearly as advanced as cluster 1 of the middle region, whereas clusters 2 and 3, in the basal region, when present, are in the form of simple protuberances (plate VII, figs. 1 and 2, \( C_1 \) and \( C_2 \)). In the apical region the ultimate bud shows only one cluster (plate VII, fig. 12, \( C_1 \)). The penultimate bud is in practically the same stage as bud 2 in the basal region (plate VII, fig. 11).

The above data indicate that on July 17th the buds in all except the apical regions were more advanced than they were on June 37th. There seems to be a tendency for the buds on a shoot to reach a stage of equal development at this time. The important feature of development of the buds at this time is the presence of: (1) secondary clusters in cluster 3; (2) bracts subtending secondary clusters in cluster 1.

The shoots collected September 13th were approximately 10 feet long and the tips were still in a growing condition. These shoots had approximately 41 eyes each, 34 of which were sectioned. Examination of the sectioned buds indicated that all those in the middle regions had reached the same stage of development. For this reason, buds 14 and 22, shown on plate VIII, figs. 3 and 4 were selected to represent the buds in this region. The buds in the middle region contain three clusters.
The basal cluster shows numerous secondary clusters, many of which are subtended by bracts (plate VIII, figs. 3 and 4, SC₁ and B). Some of the secondary clusters have divided and produced tertiary clusters (plate VIII, fig. 4, SC₂).

Cluster 2 in this region, although smaller than cluster 1, shows numerous secondary clusters, some of which are subtended by bracts (fig. 4, B). Cluster 3, having secondary clusters with no evidence of bracts, shows less development than cluster 2.

In the basal region of the shoot, cluster 1 is in the same stage of development as cluster 1 in the middle region although the former is smaller. Cluster 2 in the basal region shows evidence of several secondary clusters, while cluster 3 is in the form of a simple protuberance (plate VIII, figs. 1 and 2, SC₁). The buds in the apical region are less developed than those in the basal region. From July 17th to September 12th of this season, considerable development occurred in all except the apical regions of the shoots. By September 12th the secondary clusters in all main clusters were more numerous than in the previous collection. Tertiary clusters in cluster 1, and secondary clusters in cluster 3, represent advancements over the buds of the previous collection.

The shoots collected December 23rd were approximately 10 feet long and bore an average of 31 buds which were not
winter killed. Cluster 1 in the middle region shows an increase in the number of bracts subtending secondary clusters (plate IX, figs. 4 and 5, B). The secondary clusters show more tertiary clusters than were present on September 12th. Practically no advancement is evident in cluster 2 of this region (plate IX, figs. 4 and 5, C2). In cluster 3, however, there seems to be a slight increase in the number of secondary clusters (plate IX, figs. 4 and 5, C3). The clusters in the basal region, although smaller, are in the same stage of development as those in the middle region, (plate IX, figs. 1 and 2). The apical region of the shoot was winter killed.

These data indicate that slight development occurred between September 18th and December 23rd and that all the buds on the shoot had reached practically the same stage of development by December 23rd.

Between April 1st and May 8th nearly all buds of each collection were in the same stage of development. Because it is possible to represent the entire collection by the use of one bud, bud 13, from a cane 13 feet long, was selected to represent the collection made April 9, 1932 and is shown in plate IX, fig. 6. In the basal cluster of this bud, tertiary clusters were more common at this time than they were in the most advanced bud of the December collection. An increase also occurred in the number of secondary clusters subtended
by bracts in clusters 2 and 3 (plate IX, fig. 6, C₂ and C₃). Evidently, in April, the basal cluster is slightly more advanced than either of the other two clusters. The bud as a whole seems to show greater development than was evident in the most advanced bud of the December collection.

Bud number 26 from a cane approximately 10 feet long was selected to represent the buds collected April 24th. In the basal cluster (C₁) of this bud, secondary clusters are numerous throughout the length of the cluster. In the apical region they are in the form of simple protuberances without bracts (plate X, SC₁). The secondary clusters are progressively larger toward the base of the main cluster, and these enlarged secondary clusters are subtended by prominent bracts (plate X, B on C₁). Further development of the secondary clusters occurs concurrently with the appearance of secondary bracts (plate X, B₂ on C₁). At this stage the secondary cluster subdivides to form tertiary clusters (plate X, SC₂ on C₁). Note that one of these subdivisions is flattened at the apex, this flattening being the first evidence of flower differentiation. One or more of the tertiary clusters may subdivide and form quaternary clusters (plate X, SC₃ in C₁). On one of the secondary clusters (SC₁), a quaternary cluster (SC₂) shows evidence (x) of flower differentiation.

In cluster 2, the development of the apical region is practically identical with the condition found in the
corresponding region of cluster 1. In the remainder of cluster 2 the secondary clusters have redivided to form tertiary clusters (plate X, SC2). The tertiary clusters in each secondary cluster show a noticeable variation in size, the central one being the largest. The appearance of an unusually large central cluster protuberance indicates a prequaternary condition (plate X, SC2 in SC2). Many of the tertiary clusters in cluster 1 had formed quaternary clusters indicating that cluster 2 lags behind cluster 1 in development. Cluster 3 is slightly less advanced than cluster 2. The data indicate that the development of each cluster, as well as the development of the expanding shoots, occurs in basipetal order.

In the grape, tendril and cluster primordia arise opposite leaf primordia. At the node above cluster 3 there is a definite leaf primordium (L). Opposite this leaf primordium there is a lobed structure (T). Since the latter structure bears no resemblance to cluster primordia described previously it may be safely inferred that (T) is a tendril.

It will be noted that there are two tendril lobes (TL) and a bract (B) on this tendril. Arising from the node beyond this tendril there is another tendril primordium showing evidence of bract formation (B). The bud figured in plate X shows two distinct developments not evident in any previous collection: (1) a flattening and broadening of the apex of
a floral axis, which is the first indication of flower bud formation; (2) unmistakable evidence of tendril formation.

The eighteenth bud from a cane approximately 13 feet long was used to represent the buds collected May 1st. In the apical region of the basal cluster there are only a few secondary clusters in the form of simple protuberances (plate XI, S9). In the basal and middle regions of the main cluster, the secondary clusters have not only formed tertiary and quaternary clusters, but many of the resulting axes have developed rudimentary calyx lobes (plate XI, x). In cluster 2 not only do fewer inflorescences show calyx lobes, but the lobes are less prominent, whereas in cluster 3 no calyx lobes are evident (plate XI, x). In cluster 3, however, there is a noticeable variation in the size of the tertiary clusters, indicating that some of the tertiary clusters are in the process of forming quaternary clusters. A tendril with a prominent bract and two tendril lobes is also evident in this bud (plate XI, T and TL). The bud as a whole seems to show considerable advancement over those collected April 24th.

The twelfth bud from a cane nearly 11 feet long was used to represent the buds collected May 8th. These buds had produced shoots from one-fourth to three-fourths of an inch long, on which the clusters were quite visible to the naked eye. The clusters were removed from the axis of the
young shoot and sectioned separately. In clusters 1 and 2 the visible floral structures are slightly less advanced in the apical than in the basal and middle regions of the clusters (plate XII, figs. 1 and 2, x, pe, st). In the latter regions the floral parts show very little variation in development. In cluster 3 the most advanced flowers are in the same stage of development as the flowers in the apical region of clusters 1 and 2 (plate XII, fig. 3, x, pe, st). The flowers in the apical region of cluster 3 are somewhat less advanced than the basal flowers. It seems, therefore, that at this time the flowers in the three clusters in a bud have reached approximately the same stage of development. At this time all the flowers in a bud show definite perianth and stamens.
DISCUSSION

A thorough knowledge of flower bud formation is essential for intelligent cultural practices. Cultural practices in the grape have been based upon practical experience and experiments dealing with fertilizing and pruning, without a knowledge of the development of the inflorescence. Horticul
turists have known from gross observation that in the grape, inflorescence primordia arise during the season previous to flowering. However, the grape differs from some other fruits that have been studied. In the apple, inflorescences are initiated and floral organs are developed during the same growing season. In the grape there is an extended and pro­gressive period, from June to the dormant period, during which initiation of inflorescence occurs, but, contrary to possible inferences from the report of Johns (17) and Goff (11), floral organs do not appear during this period. The initiation of definite floral structures occurs in the spring at about the time the buds begin to break, following a rather definite second period of subdivision. During the dormant period very little visible structural change occurs.

In order to increase the yield it is necessary to in­crease either the number or the size of clusters or both. It is known that in some fruits, flower bud initiation for the
following year may be controlled by proper fertilizing. Colby (5) found that nutritional conditions which bring about the formation of clusters on the more distal nodes also increase the size of the proximal clusters. He does not state, however, when these conditions must obtain. Partridge (21) states that the size of the cluster depends entirely upon the nutritional conditions in the growing primordia in the spring.

The present work has shown that normally the number of clusters borne by a shoot arising from a dormant bud is determined before that bud reaches the dormant condition. Consequently, measures taken to increase the number of clusters must be applied before the buds on the shoot become dormant. Since cluster initiation occurs in the growing region of the shoot, such measures as early cultivation and fertilizing which lengthen the growing period may be effective in increasing the production of cluster primordia. In view of the fact that the cluster primordia laid down this first season subdivide during this season as well as during the subsequent spring, there are two periods during which the size of the cluster may be influenced: first, the growing season during which the clusters are initiated; and second, the growing period in the following spring before the initiation of definite floral structures occurs.

In the apple, conditions which favor excessive vegetative growth are not conducive to the initiation of flower buds.
Since excessive vegetative growth is not likely to occur in the grape, the viticulturist has considerable latitude in attempting to control the production of flower buds.

The foregoing discussion has been limited to primary buds developed under normal conditions. Winkler found that with some European varieties the secondary buds produced nearly a normal crop after the primary buds had been killed by frost. It was determined in the present study that the secondary buds rarely contain more than two primordial clusters and that these clusters are much smaller than those in the primary buds. Obviously, a production of a normal crop from secondary buds as reported by Winkler would be impossible without further subdivision of the already existing primordial clusters in the secondary buds. The author did not find any evidence of initiation of additional clusters in the spring, but he did not study secondary buds sufficiently to be assured that such a phenomenon is impossible. Partridge (21) found that the buds which normally blossom the following spring can be forced into bloom during the current season by pinching off the ends of the shoots and removing the laterals in midsummer. Clusters resulting from such practices, however, possess fewer flower buds than do average sized spring clusters. Apparently the subdividing of the primordial clusters is inhibited by this practice. The results of the work of both Partridge (21)
and Winkler (27) demonstrate quite positively that a certain amount of artificial control of cluster formation is possible. In view of this fact it is not impossible to hope that means may be devised whereby the primordial clusters in the Concord grape may be induced to subdivide still more frequently and subsequently produce larger clusters than are normally produced.
SUMMARY

1. A morphological study of the development of the buds of the Concord grape was made. The study embraces the chronological development of the flower clusters through an entire year. The development of the gynoecium and the details of the development of the androecium are not included.

2. Cluster initiation begins as soon as the buds are formed and continues throughout the growing season in the newly forming buds.

3. The first evidence of cluster initiation occurs in buds 3 and 4 on the shoot. The buds in the middle region of the shoot show advancement over those in the basal and apical regions throughout the growing season.

4. Toward the latter part of the growing season there is a tendency for the buds on a shoot to reach the same stage of development. The buds on a shoot are in practically the same stage of development during the dormant season and during the following spring.

5. The number of clusters borne by a shoot arising from a bud formed the previous growing season is determined before the bud reaches the dormant condition in the fall.
6. Of the three clusters known to occur in each of the early primary buds, clusters 1 and 2 are evident in early June, while cluster 3 does not appear until the latter part of the month.

7. Cluster initials subdivide and form subclusters. The production of subclusters is rapid following cluster initiation, and decreases progressively toward the beginning of the dormant season. Following a period of reduced activity, development is resumed with great rapidity about April 1st of the following spring.

8. The first evidence of flower formation was observed on April 24th in the basal cluster. At this time cluster 3 shows evidence of flower initiation while cluster 3 lacks such evidence.

9. On May 1st, calyx primordia are evident in cluster 1. Cluster 2 shows indications of flower initiation, whereas in cluster 3, distinct flower primordia are not evident.

10. On May 8th, calyx, petals, and stamens are present in each of the three clusters of a bud. These structures are more advanced in clusters 1 and 2 than in cluster 3.

11. The basal cluster is initiated earlier and develops faster than the other two clusters of the bud. The initiation and rate of development of the other two clusters are in basipetal order.
12. At the beginning of the dormant season the basal cluster is largest and the other two clusters are smaller in basipetal order. This size relationship is maintained throughout the development of the clusters.

13. The initiation of distinct floral parts occurs in all three clusters at approximately the same time, while the rate of development decreases in the three clusters in basipetal order.

14. In main clusters the differentiation of subdivisions is in basipetal order, whereas in the secondary cluster of a main cluster, the development of flowers is in acropetal order.

15. The initiation of floral parts in each flower occurs in basipetal order.
EXPLANATION OF PLATE I

Outline drawings showing the development of the inflorescence from the first visible evidence of the bud to the initiation of stamens. Magnification X 40 unless otherwise specified.

Fig. 1. A very young bud showing growing point (G) and bud scales (BS).

Fig. 2. An older bud showing growing point (G), leaf primordium (L), cluster primordium (C1), and axillary bud (A).

Fig. 3. A more advanced bud showing cluster primordium (C1) and cluster bract (B).

Fig. 4. A primordial cluster showing secondary clusters (SC1).

Fig. 5. The basal, secondary cluster detached from figure 4.

Fig. 6. A secondary cluster after it has produced three tertiary clusters (SC2) and two secondary bracts (B2).

Fig. 7. A group of tertiary clusters, the middle one showing calyx (x).

Fig. 8. A group of tertiary clusters containing an inflorescence in which calyx (x), petals (pe), and stamens (st) are evident.

Fig. 9. Inflorescences showing continued development of calyx, petals, and stamens.

Fig. 10. A secondary cluster containing two tertiary clusters (SC2) and three quaternary (SC3).

Figs. 11, 12, and 13 showing the secondary cluster shown in figure 10 in progressive stages of development.
EXPLANATION OF PLATE II

Outline drawings of flowers in cross section showing the development from the time of stamen initiation to the formation of separate pollen grains. X 30.

Fig. 1. A flower showing a very early stage of the stamens (st). The petals (pe) and calyx (x) show considerable development.

Fig. 2. A later stage of the flower showing the anthers (an) in a four lobed condition.

Fig. 3. A flower showing prominent anther lobes and pollen mother cells in the archesporia.

Fig. 4. A flower showing the tetrad condition of the pollen grains.

Fig. 5. A flower showing separate pollen grains.
EXPLANATION OF PLATE III

Outline drawings of flowers showing the coalescence of calyx and corolla. X 55.

Fig. 1. A flower before the proliferation of calyx (x) or petals (pe) is evident.

Fig. 2. A flower in which the calyx (x) is somewhat proliferated. Note that the stamens (st) are evident.

Fig. 3. A flower in which the calyx shows considerable proliferation and the petals are nearly in contact at their apices.

Fig. 4. A flower showing a slight coalescence of calyx (x) and petals (pe).

Fig. 5. A flower showing the calyx (x) after it has been erupted by the petals. The petals (pe) show considerable coalescence.
EXPLANATION OF PLATE IV

Outline drawings of longitudinal sections of buds collected June 13, 1932 and a shoot collected June 10th. Magnification X 60 unless otherwise stated.

Fig. 1. Bud 1 showing growing point (G) and leaf primordia (L).

Fig. 2. Bud 2 showing leaf primordium (L) and basal cluster primordium (C1).

Fig. 3. Bud 3 showing bract primordium (B), basal cluster primordium (C1), and leaf primordia (L).

Fig. 4. Bud 4 showing axillary buds (A), basal cluster primordium (C1), bract primordium (B), and second cluster primordium (C2).

Fig. 5. Bud 5.

Fig. 6. Bud 6.

Fig. 7. A portion of a fruiting cane (Ca) bearing tendril (T). Opposite the tendril was a bud from which arose the fruiting shoot (S). Buds 11, 21, 31, 41, 51, and 61, correspond to the positions from which the buds represented by figs. 1, 2, 3, 4, 5, and 6 respectively were taken. Clusters 1, 2, and 3 are represented by (C1), (C2), and (C3) respectively. Opposite cluster 1 is a petiole (P) from which the leaf was removed. X 0.3.
EXPLANATION OF PLATE V

Outline drawings of buds collected June 30th. Magnification X 60.

Fig. 1. Bud 1 showing early evidence of a bract (B) on the basal cluster (C₁).

Fig. 2. Bud 2 showing a basal cluster (C₁) subtended by bract (B).

Fig. 3. Bud 3 showing a basal and a second cluster (C₁) and (C₃). Cluster 1 has developed a pointed bract (B) and a secondary cluster (SC₁).

Fig. 4. Bud 4 showing a basal cluster (C₁) with a pointed bract (B).

Fig. 5. Bud 5.

Fig. 6. Bud 6 showing cluster 1 (C₁).

Figs. 7 and 8. Buds 7 and 8 each showing a basal cluster (C₁).
Outline drawings of buds collected June 27th and a growing shoot. X 40 unless otherwise stated.

Fig. 1. Bud 1 showing a basal cluster (C₁).

Fig. 2. Bud 2 showing a basal cluster (C₁) with a suggestion of a bract (B) and a secondary cluster (C₂).

Fig. 3. Bud 3 showing a basal cluster (C₁), a second cluster (C₂), and evidence of a third cluster. Cluster 1 shows a secondary cluster (SC₁) and cluster 2 shows a bract (B).

Fig. 4. Bud 4 showing a basal cluster with several secondary clusters (SC₁), one of which is subtended by a bract (B). Cluster 2 (C₂) is subtended by a bract (B).

Fig. 5. Bud 5 showing cluster 1 (C₁).

Fig. 6. Bud 6 showing cluster 1 (C₁) and cluster 2 (C₂). Cluster 2 shows a secondary cluster (SC₁) subtended by a bract (B).

Fig. 7. Bud 7 showing cluster 1 (C₁).

Fig. 8. Bud 8 showing cluster 1 (C₁) subtended by bract (B).

Fig. 9. Bud 9.

Fig. 10. A growing shoot with buds 1₁, 2₁, 3₁, 4₁, 5₁, 6₁, 7₁, 8₁, and 9₁, corresponding to the positions from which the buds shown in figures 1, 2, 3, 4, 5, 6, 7, 8, and 9 were taken. The basal, second and third clusters are shown also (C₁, C₂, C₃). X about 0.2.
Fig. 9. Bud 11 showing two clusters. Note that cluster 2 is in the form of a simple protuberance.

Fig. 10. Bud 12 showing two clusters. Cluster 2 had developed a bract (B).

Fig. 11. Bud 13 showing cluster 1 (C_1) with bract (B) and secondary clusters (S_C_1). Cluster 2 (C_2) is in the form of a simple protuberance.

Fig. 12. Bud 14 in which there is only one cluster. Note that it is subtended by a bract.
Outline drawings of buds collected July 17th. X 40.

Fig. 1. Bud 1 with cluster 1 \((C_1)\) subtended by bract \((B)\) and a secondary cluster \((SC_1)\) subtended by bract \((B)\). Cluster 2 \((C_2)\) is in the form of a simple protuberance.

Fig. 2. Bud 2 showing cluster 1 \((C_1)\) subtended by bract \((B)\) and cluster 2 \((C_2)\) in the form of a simple protuberance.

Fig. 3. Bud 3 showing clusters 1 and 2 \((C_1)\) and \((C_2)\) each subtended by bracts \((B)\). Note that cluster 2 \((C_2)\) as well as cluster 1 \((C_1)\) has developed a secondary cluster \((SC_1)\).

Fig. 4. Bud 6 showing three clusters, \((C_1, C_2, \text{and} C_3)\) each of which is subtended by bract \((B)\). Note that cluster 2 \((C_2)\) has developed several secondary clusters \((SC_1)\).

Fig. 5. Bud 7 showing three clusters, \((C_1, C_2, \text{and} C_3)\).

Fig. 6. Bud 8 showing three clusters, \((C_1, C_2, \text{and} C_3)\).

Fig. 7. Bud 9 showing clusters 1 and 2, \((C_1 \text{ and} C_2)\), each subtended by bracts \((B)\).

Fig. 8. Bud 10 showing clusters 1, 2, and 3, \((C_1, C_2, \text{and} C_3)\). Note that the only secondary lobe on cluster 2 is bract \((B)\) and that cluster 3 is in the form of a simple protuberance.
EXPLANATION OF PLATE VIII

Outline drawings of buds collected September 12th.
X 40 unless otherwise stated.

Fig. 1. Bud 1 showing clusters 1, 2, and 3 ($C_1$, $C_2$, and $C_3$). Note the secondary cluster ($SC_1$) in cluster 2.

Fig. 2. Bud 2 showing cluster 1 ($C_1$) with several secondary clusters subtended by bracts. Lobing in cluster 2 ($C_2$) suggests the initiation of secondary clusters. Cluster 3 ($C_3$) is in the form of a simple lobe.

Fig. 3. Bud 14 showing three clusters ($C_1$, $C_2$, and $C_3$), each with secondary clusters ($SC_1$). Note the initiation of a tertiary cluster ($SC_2$) in cluster 1 ($C_1$).

Fig. 4. Bud 22 showing structures similar to those in bud number 14.

Fig. 5. Bud 32 showing three clusters. Note the bract (B) subtending cluster 2.

Fig. 6. Bud 33 showing clusters 1, 2, and 3 ($C_1$, $C_2$, and $C_3$).

Fig. 7. Bud 34 showing one cluster.

Fig. 8. A complete eye showing primary, secondary, and quaternary buds (PB, SB, TB, and QB) respectively. Magnification X 30.
EXPLANATION OF PLATE IX

Outline drawings of buds collected December 23, 1931 and April 9, 1932. Figures 1 - 5 represent buds collected December 23rd. X 30. Figure 6 represents a bud collected April 9th. X 60.

Fig. 1. Bud 1 showing cluster 1 ($C_1$). Note that the basal cluster in this bud is smaller than the basal cluster in buds farther out on the shoot.

Fig. 2. Bud 2.

Fig. 3. Bud 17 showing cluster 1 and 2 ($C_1$ and $C_2$).

Fig. 4. Bud 23 showing clusters 1, 2, and 3 ($C_1$, $C_2$, and $C_3$). Note the prominent tertiary cluster ($C_{32}$) in cluster 1, and the numerous secondary clusters ($C_{31}$) subtended by bracts (B). Cluster 3 ($C_3$) shows a secondary cluster ($C_{31}$).

Fig. 5. Bud 30 showing structures similar to those in bud 23, figure 4.

Fig. 6. Bud 13 showing clusters 1, 2, and 3 ($C_1$, $C_2$, and $C_3$). Note the prominent tertiary clusters $C_{32}$ in cluster 1. One of the tertiary clusters is subtended by a bract (B).
EXPLANATION OF PLATE X

Outline drawing of bud number 26 on a cane collected April 24th. X 40.

C1. Cluster 1 showing: (1) primordial secondary clusters SC1 at apex of the cluster; (2) secondary clusters subtended by secondary bracts (B3); and (3) tertiary clusters SC3 with evidence of calyx (x).

C2. Cluster 2 showing: (1) primordial secondary clusters (SC1) at apex of cluster; (2) group of three tertiary clusters (SC2), the central one of which (CSC6) is larger than the other two.

C3. Cluster 3 showing a secondary cluster (SC3) and a secondary bract (B3).

T. Tendrile (T), the basal one showing bract (B) and tendril lobes (Th).

L. Leaf primordia.
EXPLANATION OF PLATE XI

Outline drawing of bud 18 collected May 1st. X 30.

C₁. Cluster 1 showing numerous quaternary clusters with prominent calyx lobes (x).

C₂. Cluster 2 showing evidence of calyx formation (x).

C₃. Cluster 3 showing a variation in the size of the tertiary clusters, in a secondary cluster, the central one being the largest.

T. Tendril with tendril lobes (TL) and a bract.
EXPLANATION OF PLATE XII

Outline drawings of the 3 clusters from bud 12 collected May 8th. X 25.

Fig. 1. Cluster 1 showing calyx, petals, and stamens in basal and apical flowers (x, pe, st). Note that primary and secondary bracts (B) and (B₂) are numerous.

Fig. 2. Cluster 2 showing calyx, petals, and stamens (x, pe, st) and primary and secondary bracts (B) and (B₂).

Fig. 3. Cluster 3 showing calyx, petals, and stamens (x, pe, and st) in the basal and apical regions of the cluster.
EXPLANATION OF PLATE XIII

Outline drawings of the clusters on a shoot showing their chronological development from June 5, 1931 to May 1, 1932. These drawings are intended to show the progressive development of the clusters in relation to each other. The clusters represented by the first eight collections are of the same magnification whereas those in the last two collections are of a lower magnification. Irrespective of the degree of magnification, the drawings represent the new developmental failures as they occurred.
PLATE XIII

Cluster 1

June 9

July 9

August 9

September 9

October 9

Cluster 2

Cluster 3
EXPLANATION OF PLATE XIV

A diagramatic drawing of a grape cluster showing:
(1) the main axis or rachis (a); (2) the secondary axis (b); (3) the tertiary axis (c); (4) the quaternary axis (d); (5) the secondary cluster (SC₁); and (6) the tertiary cluster (SC₂).
EXPLANATION OF PLATE XV

Photographs of shoots collected June 8th.

Fig. 12 showing a lateral shoot (LS). X 0.15.
EXPLANATION OF PLATE XVI

Photomicrographs showing the progressive development of the buds from the precluster condition up to and including the initiation of calyx. X about 50.

Fig. 1. A bud showing no evidence of a cluster (C). 
Fig. 2. A bud showing cluster primordium (C), growing point (G), and leaf primordium (L).

Fig. 3. A bud in which cluster 1 \((C_1)\) shows evidence of a bract. Note the growing point (G) and leaf primordium (L).

Fig. 4. A bud collected June 27th in which cluster 1 \((C_1)\), shows several secondary clusters \((SC_1)\), some of which are subtended by bracts (B).

Fig. 5. A bud collected July 17th showing cluster 1 \((C_1)\), cluster 2 \((C_2)\), and axillary bud (A).

Fig. 6. A bud collected April 24th showing cluster 1 \((C_1)\), tendril lobe \((TL)\), bract \((B)\), subtending a tendril, growing point \((G)\), and definite nodal cells \((N)\).

Fig. 7. A portion of a basal cluster collected April 24th showing evidence of calyx \((x)\).
EXPLANATION OF PLATE XVII

Fig. 1. A basal cluster (C₁) showing secondary cluster (SC₁). A secondary cluster near the apex of the main cluster is subtended by a bract (B) and has subdivided to form tertiary clusters (SC₂). X 40.

Fig. 2. A bud with a basal cluster in which the tertiary cluster has subdivided to form quaternary clusters (SC₃). X 35.
EXPLANATION OF PLATE XVIII

Fig. 1. A bud showing basal cluster (C₁), axillary bud (A), tendril (T), leaf primordium (L), and growing point (G). Note the difference in the size and shape of the nodal and internodal cells. X 30.

Fig. 2. A longitudinal section of an expanding shoot showing six definite nodes and growing point (G). The portion of the cluster included in this section bears flowers in which petals (pe), and calyx (x), are evident. X 20.
EXPLANATION OF PLATE XIX

Fig. 1. A flower in cross section showing the initial stage of the stamens (st). Note the petals arranged opposite the stamens and the calyx (x) forming a continuous ring. X 30.

Fig. 2. A flower in cross section at the stage when the pollen grains are separate. Note the proliferation of the cells of adjoining petals in a stage previous to coalescence (co). The anthers (an) are four lobed and the filament (fi) is evident. X 30.
LITERATURE CITED


ACKNOWLEDGMENTS

The writer wishes to express his deep appreciation to those members of the Departments of Horticulture and Forestry and of Botany who aided in making this investigation. Special credit is due Professor B. S. Pickett, Head of the Department of Horticulture and Forestry, for making it possible to carry out the problem, and to Dr. J. E. Sass for his splendid cooperation and helpful suggestions during the progress of the problem. Grateful acknowledgment is rendered to Professor H. W. Richey for suggesting the problem.