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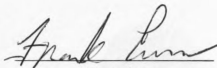
The Development of Cauliflory in Cercis Canadensis (Fabac

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Shirley Ann Owens

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Major professor

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THE DEVELOPMENT OF CAULIFLORY IN CERCIS CANADENSIS (FABACEAE)

by

Shirley Ann Owens

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
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MASTER OF SCIENCE

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ABSTRACT

THE DEVELOPMENT OF CAULIFLORY IN CERCIS CANADENSIS (FABACEAE)

By

Shirley Ann Owens

Cauliflory is defined as flowering on older branches or trunks of woody plants. The development of cauliflory in Cercis canadensis was studied using scanning electron microscopy, light microscopy and macroscopic bud counts. In the leaf axil, a linear series of buds were exogenously initiated before stem elongation was completed. These sequentially matured into first order inflorescences over a five year period. The inflorescence flowered once but second order reproductive buds were formed exogenously in the axils of its basal bud scales. The second order inflorescence could produce third order buds in their bud scales. Along branches and trunks, buds and abscised inflorescences bases formed wens, which are macroscopic swollen areas along the stem. The wens often produced epicormic shoots which were cauliflorous with a linear series of first-order reproductive buds formed in their leaf axils. The shoots usually abscised leaving the first-order reproductive buds at their base. These buds and the sympodial series of higher order buds perpetuate the cauliflorous condition throughout the life of the plant.

To my husband, Miles C. Owens, to my son, Miles B. Owens and to my dear friend and teacher, Lloyd Rodnick.

ACKNOWLEDGEMENTS

The idea for this study came from one of my former students, Stephen Alford, who asked why Cercis canadensis was considered cauliflorous and Weigelia florida was not. Without Steve's question and Dr. Frank W. Ewers interest in cauliflory, this study would not have taken place.

I wish to thank Dr. Frank W. Ewers, my major professor, and the members of my committee, Dr. John H. Beaman and Dr. Karen L. Klomparens for their guidance. A special thanks goes to Shau-ting Chiu, skilled lab partner and friend, who also provided guidance for many parts of my research.

Expressions of gratitude are given to the Center for Electron Optics at Michigan State University and to Dr. Karen Klomparens, Dr. Stanley Flegler, Peggy Hogan and Barry Stein for making the scanning electron microscopy used in this study possible. I also appreciate the vast collection of C. canadensis grown on the Michigan State University campus and thank Dr. Gerard Donnelly, Curator of Woody Plants, for allowing me to sample from the collection.

The list of teachers, family and friends who have supported and helped me throughout my long academic journey are far too numerous to mention in the space allotted. They all have my unpublished thanks.



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INTRODUCTION

In most plants flowering occurs on young leafy shoots. Mildbraed (1922) defined cauliflory as flowering on older leafless twigs, the boughs and the trunks, rather than on young leafy twigs. He also subdivided cauliflory into several categories. The category considered by Mildbraed to be the most primitive is ramiflory, in which flowering occurs on young stems and branches, but not on older branches or trunks. Trunkiflory is the case where flowering occurs only on the trunk, with basiflorous plants flowering only at the base of the trunk. Simple cauliflory is the flowering on all areas of the plant, young, middle-aged and old stems and trunks. In addition to these types, which produce either simple flowers or an inflorescence directly on the parent organ, another type of cauliflory called idiocladanthly involves the production of flowers on stems with scale leaves and long internodes (panicled inflorescences are not included here). These stems can grow upward above the branch or droop downward below the branch. Flagelliflory involves the production of long whip-like flowering branches with scale leaves and long internodes located only at the base of the trunk. The example used by Mildbraed (1922) was Paraphyadanthé flagelliflora which produced long shoots that were primarily buried under leaf debris. This condition is probably the same as the condition that Corner (1978) called geocarpy. Geocarpy as well as basiflory

occurs in several Malaysian species of Ficus (Corner, 1978; Beaman, personal communication). The categories proposed by Mildbraed should be used with caution as there are cases of intermediate types and plants that exhibit more than one type of cauliflory (Richards, 1952).

The classification of ramiflory as a category of cauliflory was problematic for this study. Many temperate plants form axillary buds that mature on leafless stems during the second or third year. Using Mildbraed's definition, these plants would be classified as cauliflorous. This definition of cauliflory is too broad to be of use.

Cauliflory for this thesis will therefore be defined, in the strict sense, as flowering on older branches and stems of woody plants. Thompson (1951) distinguished between cauliflory and ramiflory and defined a cauliflorous plant as one that fulfills the following three conditions: "... one thinks a species can but be a cauliflorous tree when, in it, budding-time for leaf-subtended meristems is long; its spikes have basal buds, with growth retard, from which new ones are always formed: and, first and foremost, flowering is not marked, nor does its vigor reach its peak, until the tree has gained its major height: yet still has dormant buds at many levels on its limbs and boles, despite extensive cork formation." One problem with Thompson's definitive list of conditions is that some plants that are strictly cauliflorous may not be classified as such because they do not reach their potential flowering capacity due to external conditions such as mechanical damage or pathogens.

The cauliflorous condition has arisen independently in many taxonomic lines. In tropical Africa alone, Mildbraed (1922) reported

278 cauliflorous species found in 29 families. World wide, there are about one thousand cauliflorous species (Mildbraed, 1922; Richards, 1952; Walter, 1984). Stebbins (1974) reported that cauliflory is present in species belonging to most of the larger tropical families and that these species, derived from ancestors living in a more open environment, secondarily entered the rain forest.

Cauliflory is used as a classification character in the taxonomic literature. In recent literature, cauliflory was a characteristic unique to the section Cauliflorae of the genus Clitoria (Fabaceae) (Fantz, 1982). At the species level, cauliflory was one of the main characteristics used to classify Quarabea pumila (Bombacaceae) (Alverson, 1984) and Recchia simlicifolia (Simaroubaceae) (Wendt and Lott, 1985). With the increasing amount of taxonomic work being done in the tropics, the use of cauliflory as a taxonomic character should increase in the future.

The adaptive relevance of cauliflory has long been the subject of speculation. There are three hypotheses; one based upon physiological resources, one based upon mechanical support (for large flowers and fruits), and a third based upon attracting pollinators for cross-pollination. The most feasible physiological hypothesis is that flowers growing on branches and trunks could effectively compete with leaves for minerals and assimilates. Assimilates are stored in the older branches and trunks (Richards, 1952). In tropical evergreen trees that store only enough nutrients for flowering in their lower branches and trunks, cauliflory could represent a more economic means of transporting nutrients. Objections to this hypothesis have been that

this would be more advantageous for large trees whereas cauliflory occurs more frequently in small trees (Mildbraed, 1922; Richards, 1952).

The adaptive significance of cauliflory, based upon Corner's Durian theory, is that large fruits, evolutionarily retained from pachycaulous ancestors, could not be mechanically supported on the more recently evolved leptocaulous trees (Corner, 1949). Ramiflory and cauliflory thus evolved, producing dormant reproductive buds that flower and fruit on branches that provide the appropriate mechanical support.

Attraction to pollinators is another operative hypothesis because cauliflory occurs mainly in the dense tropical shrub layer where flowers can be easily hidden by vegetative leaves. Spatial separation from the leaves make flowers not only more conspicuous to a pollinator but also in many cases more accessible. Animals such as bats, birds, and insects are the primary pollinators in the tropics. An extension of the pollination hypothesis that includes ecological factors was presented by Stebbins (1974) and is as follows: the animal populations in the rain forest, like the plant populations, are in horizontal layers. Competition for pollinators is very high in the dense upper levels but few plants grow in the dimly lit levels toward the ground. This creates a niche of ground level pollinators that can easily be filled by cauliflorous species.

The possible types of cauliflorous development are numerous. The reproductive buds can arise from an axillary or adventitious position. These buds may be of an endogenous or an exogenous origin and can remain dormant or can be initiated anew each flowering season. Axillary buds that remain dormant can form in a linear series when a bud forms



directly below the preceding bud (Thompson, 1946, 1949, 1951) or in a semicircular series when a bud forms in a position lateral to a principle bud (Lent, 1966). Cauliflorous development can change as the plant ages. In young trees of Ficus glomerata, inflorescences develop exogenously in the axillary position but as the tree matures, inflorescences are produced endogenously in an adventitious position (Pundir, 1972).

The density and position of inflorescences can vary among cauliflorous species. Inflorescences of Theobroma cacao mature first on the trunk and sequentially mature in an acropetalous manner up to the one-year-old stems (Lent, 1966). In young trees of F. glomerata, single syconium inflorescences mature on one to three-year-old stems but as the tree matures flowering occurs only on stems that are greater than 3 cm thick and single syconium are replaced by a cauliflorous shoot with many syconia inflorescences. This is an example of basipetal cauliflorous progression (Pundir, 1972). I found that inflorescences mature in C. canadensis in a simultaneous manner on all parts of the tree.

The work done on cauliflorous development consists of nine major works produced by four researchers. Most of these studies were done between 1944-1952 by J. McLean Thompson. I believe the reason for the relative shortage of studies on this topic has to do with the difficulty of interpreting complex three-dimensional relationships from two-dimensional slides. Light microscopy is essential for finding internal vascular connections, but is of limited value in interpreting certain complex bud positions, such as buds forming in the floral bud scales of other buds. Cinematographic analysis, in which successive serial

sections are photographed on videotape (Zimmermann & Tomlinson, 1966), could work, but the difficult (compound) angles formed by the tightly packed buds would pose special problems. Scanning electron microscopy, used in conjunction with light microscopy, proved to be a valuable tool for showing these relationships.

A developmental study of cauliflory can be done in more detail if specimens can be observed and sampled on a frequent basis and if flowering is seasonally controlled. For these reasons, I undertook a study of the development of cauliflory in Cercis canadensis L. var canadensis (Fabaceae), which is one of the few temperate species to exhibit cauliflory (Figures 1, 2). In this species, flowers arise on young stems as well as on old trunks. This taxon is among the few species of the subfamily Caesalpinioideae that have successfully adapted to the temperate region (Wunderlin, Larsen & Larsen, 1987) and is abundantly cultivated on the Michigan State University (MSU) campus.

Scanning electron microscopy (SEM) was used in conjunction with light microscopy and macroscopic observations to answer the following questions: First, do the cauliflorous buds develop in an axillary or adventitious position? Second, do the buds rise exogenously or endogenously? Third, are the future reproductive buds initiated each season or are they dormant buds that were initiated in past seasons? Fourth, how do the vascular tissues of these buds connect with the parent organ and with each other? Fifth, how is the cauliflorous condition perpetuated throughout the life of the plant? This is the first study on cauliflory to involve the scanning electron microscope, which was crucial for many of the interpretations.

MATERIALS AND METHODS

Light Microscopy: For one year, beginning in September of 1988, monthly samples of reproductive buds were taken from six differently aged C. canadensis and C. canadensis 'alba' trees located on the MSU campus. Trees were all about 3-5 m tall. Buds and the subtending tissue down to the stem xylem were removed with a razor blade from the most currently produced branches, intermediate areas, and trunk or old branch areas. A particular branch was sampled only once every three months. All of the samples were immediately fixed in FAA (formalin-aceto-alcohol), dehydrated in a graduated TBA (t-butyl alcohol) series, embedded in paraffin and microtomed at 8 or 15 μ m using a rotary microtome. The serial sections were then stained with safranin O and fast green (Johansen, 1940). The microslides were examined and photographed on either a Zeiss Photomicroscope III or a Nikon Stereomicroscope.

Scanning Electron Microscopy: Samples of differently aged reproductive areas of C. canadensis and C. canadensis 'alba' were taken during the spring and summer of 1989. These samples were dissected under water with fine beading needles and immediately fixed in a solution of 4% glutaraldehyde in 0.1 M phosphate buffer (pH=7), rinsed twice in 0.2 M sodium phosphate buffer (pH=7), dehydrated in a graduated ethanol series, critical point dried (CO₂) in a Balzers critical point dryer, and coated with 28 nm of gold in an Emscope Sputter Coater. Samples were examined and photographed on a JEOL-35 CF SEM at 10-15 KV. Polaroid 665 film was used for all SEM micrographs.

Macroscopic Bud Counts: After determining that there were different types of buds (first order, second order, etc.) that contribute to the cauliflorous condition in C. canadensis, a study was done to determine what type of buds produced flowers on differently aged stem segments. Order became difficult to determine as the age of the stem increased, therefore in the macroscopic bud counts all buds that were not of the first order were grouped as higher order buds. I also wanted to determine the time sequence for dormancy in first order buds. A bud count was conducted on seven C. canadensis trees growing on the MSU campus. The counts were made during August of 1989 when the reproductive buds for the following spring were macroscopically visible. Trees were selected to vary in age and location. For convenience, only lower branches were selected. For each tree, both reproductive and vegetative buds were counted along the main axis of one representative stem for the current year's and each of the past five years' growth. Ages of the stem segments were determined from pseudoterminal bud scale scars along the branches. In a tree that was completely cut to the ground, these ages were found to equal, in each case, the number of xylem growth rings. Stem segments from the current year were classified as 0. First order versus higher order reproductive bud determinations were made with a hand lens and were based upon serial position, the presence of old bud scales or inflorescence scars, and the position of the floral bud scale with respect to those known to be first order. To determine which type of buds contribute most to the overall flowering condition, the status of every bud on three large branch systems from three separate trees was also determined. The counts on these three

trees included every stem and branch of the shoot system, whereas for the seven trees, only buds along the main branch axis were classified and counted.

RESULTS

The vegetative branching system was sympodial with the distal lateral bud replacing the terminal bud each year. Flowering on Q. canadensis occurred in the spring before the appearance of leaves. Inflorescences matured essentially in a simultaneous manner on the trunk and on all ages of branches and stems. The youngest stem segments to flower were one year old. The two or three distal most lateral buds on the one-year-old stem segments (classified as 0 on counts made the previous summer) developed into vegetative shoots that gave rise to the leaves. Epicormic shoots also developed on some lower branches and trunks. Most of the other nodes produced only reproductive buds. The inflorescence axis abscised after flowering.

To determine whether reproductive buds on older branches (i.e., those without visible leaf scars) arose in an axillary or an adventitious position, it became necessary to determine the phyllotaxy of Q. canadensis. The phyllotaxy was determined from the leaf primordium in the vegetative bud (Figure 3). It follows the orthodistichous pattern of Rutishauser (1982), with alternating leaf primordium forming at approximately 180 degrees from the leaf primordium initiated one node below. Adnate to the leaf primordium were large stipules and intrastipular trichomes (Figures 3, 4). During the early

stages of vegetative bud elongation, buds began forming in the axils of leaf primordia (Figures 4, 5).

Two basic types of reproductive buds were found: first order buds that arose exogenously from the leaf axil, and higher order buds that formed, also exogenously, in the axils of the lower most bud scales of the inflorescence below the abscission zone of the inflorescence axis. Removal of the leaf pulvinus revealed a linear series of up to ten first order buds (Figures 6-8). This series continued to develop basipetally until stem elongation terminated (Figure 6). The first formed buds grew in conjunction with stem elongation as newer buds were formed in the axil (Figures 7, 8). The buds most distal to the pulvinus were the first to have bud scales surrounding their apical dome. The distal buds were later the first to mature into inflorescences.

Second order reproductive buds arose from the axils of bud scales of inflorescences below the abscission zone of the inflorescence axis (Figure 9). At least in some cases, second order buds could be seen before the inflorescence abscised. Some of these second order buds became macroscopic the year after the first order inflorescence had abscised (Figures 9, 10). Both light microscopy (Figure 11) and SEM (Figure 12) showed the scale of a higher order (one that is not first order) bud formed in the axil of floral bud scales that were proximal to the abscission zone of the inflorescence axis. Based upon red staining with safranin O and fast green, the old bud scales were lignified or suberized. The sample for Figure 11 came from an old branch area and showed the vascular connections to the old inflorescence. The outward morphology of a second order bud forming in the axil of a first order

bud scale were also examined (Figure 12).

Floral bud scales had an apical appendage at the tip (Figure 13). These appendages on the floral bud scales of second order reproductive buds were orientated approximately perpendicular to those of a first order reproductive bud (Figure 13). The change in orientation of the shoot was clearly marked by these appendages. However, no morphological difference was found between first order and second order reproductive buds once they were removed from the plant.

Second order reproductive buds also gave rise to buds in the axils of bud scales. These could be called third-order buds, which can give rise to fourth-order buds, and so on. An example of the complexity of the bud orders is shown in Figure 14. A first order inflorescence scar was seen with two abscised second order buds, one of which is producing a third order bud in its bud scale axils. A magnification of one of these third order buds (Figure 15) shows the position of the third order bud with respect to the inflorescence axis and bud scales of the abscised second order inflorescence. Various orders of buds were observed on the same floral bud stump (Figure 16). Some of the new buds were being formed at the same time that a bud from the previous year showed full development (Figures 13, 17).

In the older branches and trunks, inflorescences arise from wens, which are macroscopically visible raised and swollen areas along the stem (Figure 18). Wens became quite distinct by the time the stem segment was six years old, corresponding with maturation of some of the higher order buds. The buds grew in conjunction with the stem such that buds with active meristems were never engulfed by secondary growth. New

buds originated each year in the axils of old bud scales and the wen increased in surface area over time. The sympodial series of inflorescences on a wen resulted over the years in a complex network of vascular tissue between the buds, old and new, on the wen (Figure 19). The vascular network traced back to the first order vascular tissue next to the pith.

The wens were in two ranks following the orthodistichous pattern of phyllotaxy established in the vegetative bud (Figures 3, 20). Some of the wens also produced epicormic branches (Figure 20) which were themselves cauliflorous with many basal first order buds (Figure 21). These shoots were also subtended by a linear series of buds (Figures 21, 22). The epicormic shoots often abscised and later became covered with periderm.

Macroscopic bud counts of differently aged stem segments showed that the first order reproductive buds flower during a five-year period (Figure 23). The highest mean number of first order buds per age class was produced on the one-year-old segments. Higher order reproductive buds appeared on one-year-old segments but were most frequent on three-year-old segments. Five-year-old stem segments had only higher order buds: first order buds were not observed. The mean number of vegetative buds on the currently produced stems was 2.4. These were produced only on the distal nodes.

The three whole shoot bud counts showed similar results to one another but since one shoot system of *Q. canadensis* 'alba' could be clearly counted back eight seasons, only the data from this shoot are shown here (Table 1). A total of 429 first order and 168 higher order

reproductive buds were produced on the eight-year-old shoot system. There were 23 current year stem segments producing 173 first order and 0 higher order reproductive buds. The 14 one-year-old stem segments produced 175 first order and 2 higher order reproductive buds. The segments that were six or more years old produced only higher order buds. With advancing stem age, reproductive bud production changed from a first order to higher order source, but there were no stem segments lacking reproductive buds altogether. The number of higher order buds per node generally increased with the age of the stem segment and was greatest (3.60) on the eight-year-old stem segment.

A summary of cauliflorous bud development in C. canadensis appears in a schematic representation (Figure 24).

TABLE 1. The number of macroscopic first order and higher order reproductive buds in a shoot system of Cercis canadensis 'alba'.

Age ^a of Segment	NS ^b	First Order	Higher Order	Number of Nodes	First Order per Node	Higher Order per Node
0	23	173	0	195	0.89	0.00
1	14	175	2	95	1.84	0.02
2	4	54	2	36	1.50	0.06
3	2	15	12	16	0.94	0.75
4	2	11	41	27	0.41	1.52
5	2	1	28	15	0.07	1.87
6	1	0	23	18	0.00	1.28
7	1	0	24	11	0.00	2.18
8	1	0	36	10	0.00	3.60

Note: Reproductive buds were counted during August of 1989 and produced flowers during the spring of 1990.

^a 0 - current years growth.

^b NS= Number of stem segments of each age on the stem segment.



Both Figures are of Cercis canadensis 'alba'.

Figure 1. Cauliflory observed macroscopically. A large branch in flower.

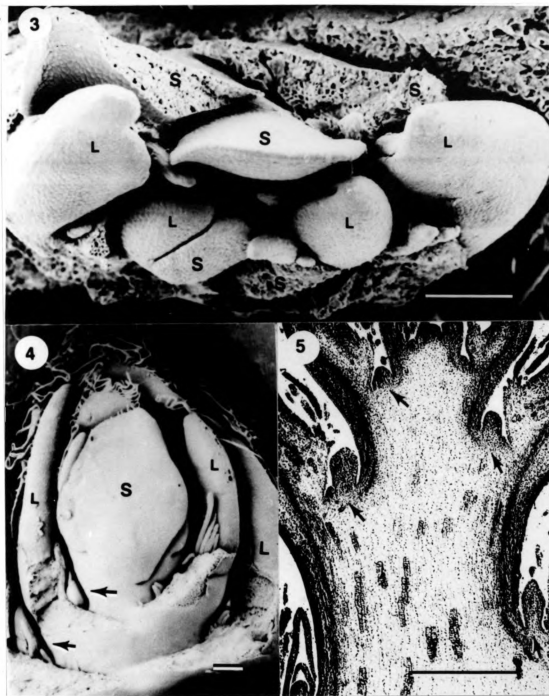
Figure 2. Several cauliflorous inflorescences and a vegetative shoot. These were growing out of two epicormic shoot scars at the base of a trunk.

Some stipules were removed for the SEM micrographs. L, leaf primordium, S, stipule.

Figure 3. SEM, polar view of phyllotaxy. This showed the orthodistichous phyllotaxy of leaf primordia in a vegetative bud. Bar = 100 μm .

Figure 4. SEM, longitudinal view of bud initiation. Elongating vegetative shoot showed buds initiated exogenously in the axils of leaf primordium. Bar = 100 μm .

Figure 5. Light microscopy, longitudinal section of bud initiation. Elongating vegetative axis showed buds initiated exogenously in the axils of the leaf primordium (arrows). Bar = 500 μm .



The tops of the figures below are distal to the leaf axil.

Figure 6. SEM, linear series of first order reproductive buds. The series of buds were initiated exogenously in the leaf axil. The distal most bud was dissected and the pulvinus of the mature leaf was removed. Bar = 1 mm.

Figure 7. SEM, longitudinal section through linear series of buds. This showed the basipetal formation of the first order reproductive buds on an elongating stem. Bar = 100 μ m.

Figure 8. Light microscopy, longitudinal section through linear series of buds. This showed the basipetal formation of the first order reproductive buds on an elongating stem. Arrow indicates undifferentiated meristematic tissue. Bar = 500 μ m.

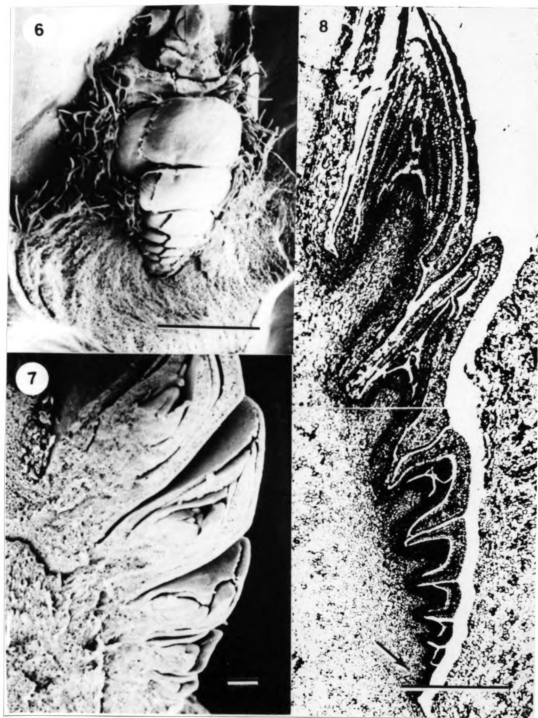
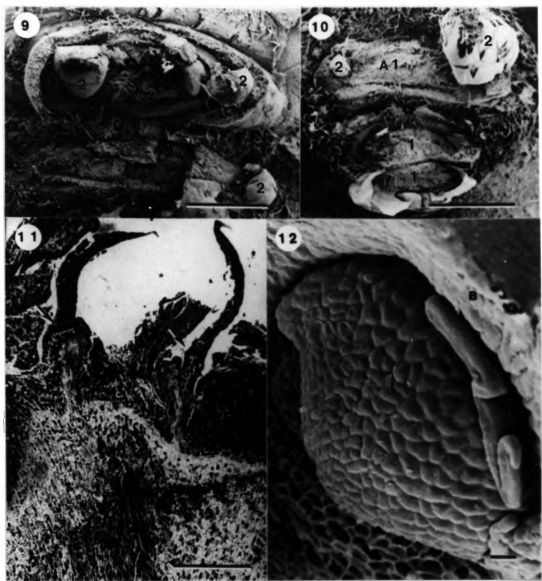


Figure 9. SEM, second order reproductive buds. Two first order inflorescence scars with second order reproductive buds (2) forming in the axils of the floral bud scales (B). Bar = 1,000 μm .

Figure 10. SEM, second order reproductive buds. Second order (2) buds formed in the axils of the bud scales of a newly abscised first order bud. The two lower first order buds (1) were removed. Bar = 1,000 μm .

Figure 11. Light microscopy, longitudinal section of buds forming in bud scales. Section through a wen showed two higher order (those that are not first order) buds initiated in bud scales. Arrows indicate demarcation of the bud scale staining. Bar = 500 μm .

Figure 12. SEM, outer morphology of a bud forming in a bud scale. A second order bud forming in a first order bud scale (B). The inflorescence axis and the tip of the first order bud scale were removed to obtain the micrograph. Bar = 10 μm .



- Figure 13. SEM, a five-year old node. A first order (1) and second order (2) reproductive buds on a five-year-old stem segment with the floral bud scale appendages (arrows). Bar = 1 μm .
- Figure 14. SEM, complexity of ordered buds. A first order floral bud scales (B1) with two abscised second order inflorescences (A2) giving rise to a third order reproductive bud (3). Bar = 100 μm .
- Figure 15. SEM of third order bud. A higher magnification of the third order bud indicated by the arrow in Figure 14 showed the position of the bud (3) in relation to the second order floral bud scale (B2) and the second order bud abscission scar (A2). Bar = 10 μm .
- Figure 16. SEM, higher order buds from an older stem. Higher order buds from an older stem segment formed in the floral bud scales of an abscised inflorescence. Bar = 100 μm .
- Figure 17. SEM, higher order buds from a wen. This showed that higher order buds formed in the axils of floral bud scales. Bar = 100 μm .



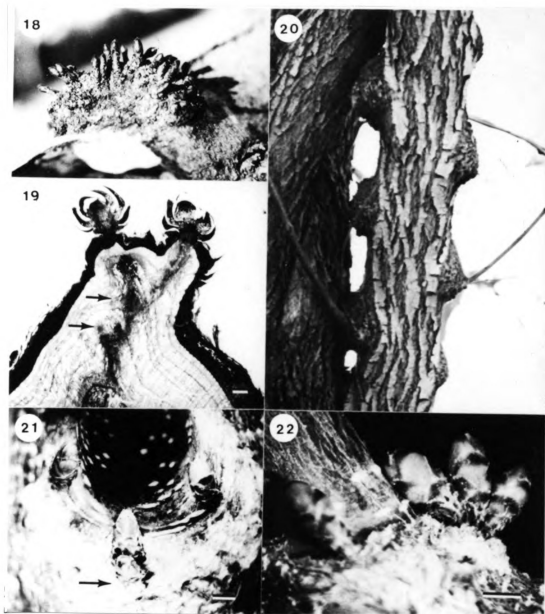
Figure 18. Wen from a twelve-year-old stem segment. Wen with many higher order reproductive buds. Bar = 1 cm.

Figure 19. Light microscopy, longitudinal section through a wen. Two buds with vascular connections to other buds and the parent organ. Arrows indicate the vascular branching to other buds that are not in the plane of the section. Note the pattern of secondary growth. Bar = 1 mm.

Figure 20. Wens on an older branch. Wens, some with epicormic shoots, followed the same orthodistichous phyllotaxy established in the vegetative shoot.

Figure 21. Base area of an epicormic shoot. Note the two linear series of first order buds on the shoot and the linear series of buds subtending the shoot (arrow). Bar = 1 mm.

Figure 22. Side view epicormic shoot base. Side view of the linear series of buds subtending the epicormic shoot. Bar = 1 mm.



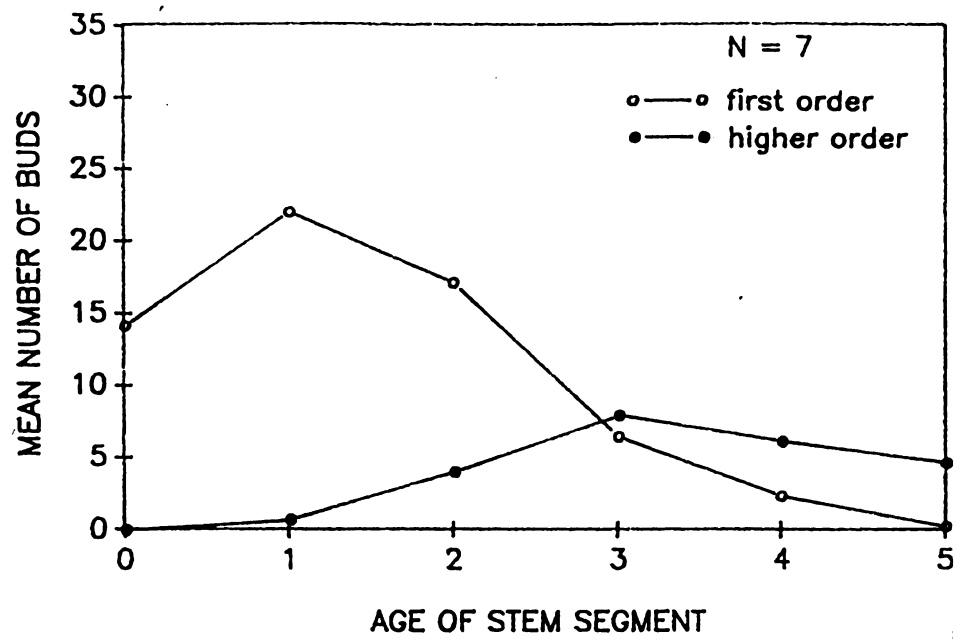


Figure 23. The mean number of first order and higher order buds for differently aged stem segments.

Figure 24. Schematic summary of the development of cauliflorous reproductive buds in Cercis canadensis. First order buds (1) form in a linear series in the axil of a leaf. LS - leaf scar. First order buds sequentially mature over a five-year period. The buds flower once and abscise (A1) but in the axils of reproductive bud scales (B1), second order (2) reproductive buds are formed. These second order buds also flower once and abscise (A2). Third order buds (3) are formed in the axils of the second order reproductive bud scales (B2). The sequential initiation of higher order buds can continue indefinitely.

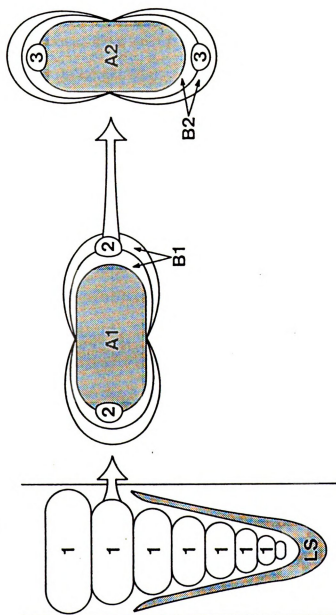


Figure 24

DISCUSSION

In C. canadensis, first order buds form exogenously in the axils of vegetative leaves and higher order buds form, also exogenously, in the axils of floral bud scales. Even on trunk areas, wens correspond with the original phyllotaxy (Figure 21).

There are two possible positions from which a bud could develop: axillary or adventitious. An axillary bud is defined as a bud which forms in the axil of a leaf. These buds on a segment of stem would follow the normal phyllotaxy of the tree. An adventitious bud arises from mature tissue in areas other than those of the normal phyllotaxy or from callus tissue anywhere on the plant (Stone & Stone, 1943; Aaron, 1946; Fink, 1983). Incidents of axillary cauliflory have been reported to occur in Cercis siliquastrum, Pleiocarpa mutica (Thompson, 1946, 1949) and Theobroma cacao (Lent, 1966), while incidents of adventitious cauliflory were reported for Ceratonia siliqua (Thompson, 1944), Couroupita giganensis (Thompson, 1952; Fink, 1983), Ficus glomerat, F. pomifera (Pundir, 1972, 1975), Artocarpus integrifolia, and Swartzia shomburgkii (Fink, 1983).

In C. canadensis, the linear sequence of first order buds (Figure 7, 8) showed decreasing stages of meristematic development terminating at the leaf axil with meristematic tissue showing little differentiation. This is consistent with results for C. siliquastrum and P. mutica (Thompson, 1946, 1949). These first order buds remain in a dormant state before maturing in a basipetal series over several years. Dormancy is used here as the general term for all instances in which a

tissue predisposed to elongate (or grow in some other manner) does not do so (Doorenbos, 1953; Romberger, 1963).

{ The macroscopic bud counts indicate that the microscopic first order reproductive buds sequentially mature during a five-year period and that new first order buds were not formed on those stem segments after this time. } Perpetuation of the cauliflorous condition over the life of the plant came primarily from higher order reproductive buds that formed in the axils of floral bud scales. Second order buds matured anytime after the second year (Figures 9, 10). The data from the entire shoot system indicated that first order reproductive buds produced more of the total inflorescences than did higher order buds. This can be attributed to the high number of current (0) and one-year-old stem segments. { The seven and eight year old stem segments produced more reproductive buds per node than younger stem segments. All of these buds were also higher order buds. Based upon the high number of newly developing higher order microscopic buds in the micrographs (Figures 11-15) versus the quantitative data for macroscopic higher order buds per node (Table 1), it appears that higher order buds can also go through a period of dormancy. } A similar situation was reported to occur in vegetative collateral buds formed on epicormic shoots of Liquidambar styraciflua (Kormanik & Brown, 1969). These first order vegetative buds produced second order vegetative buds in the axils of the bud scales. The second order buds remained suppressed and were eventually engulfed in periderm.

Buds of plants must eventually develop vascular connections to the parent organ. Lent (1966) described three methods of vascular connection that can occur in the cauliflorous situation. One case was the direct

connection of the vascular tissue of the bud to that of the parent organ. The second was the connection of bud vasculature to the vascular tissue of an old abscised reproductive bud, while the third was a connection to the vascular tissue of an abscised vegetative shoot. Connections of the vascular tissue to the pith are sometimes used to confirm the axillary origin of buds. Fink (1983), however, found that endogenous adventitious buds in Tilia platyphyllos have vascular traces to the pith because differentiating vascular strands of newly formed adventitious buds attach to old adjacent axillary buds. For this reason, used alone, vascular traces to the pith are not sufficient evidence for axillary origin.

In the case of C. canadensis, the vascular connections were consistent with the observed axillary origin of all reproductive buds. Branching of vascular tissue shown in a wen of C. canadensis (Figure 20) indicates a continuum of vascular connections between reproductive buds through time. The vascular tissues came strictly from reproductive structures, as vegetative stumps were not found in this segment. Since all reproductive buds arise ultimately from first order buds, as expected, the vascular traces to the inflorescences could be followed all the way back to the pith (Figure 20).

Wens caused by the cauliflorous condition were first described for C. siliqua and P. mutica (Thompson 1944, 1946, 1949). In C. canadensis, the wens produced not only higher order reproductive buds but also in many cases epicormic shoots (Figs. 2, 20). These shoots produced first order reproductive buds on nodes with very short internodes (Fig. 21) and were also in many cases subtended by a series

of reproductive buds. In Q. canadensis there is no difference in size, shape or organization of the shoot apex of a vegetative shoot versus a reproductive shoot until initiation of the floral apex (Worthington, 1968). Undifferentiated buds in the linear series may be induced to grow into vegetative shoots. For this reason, epicormic shoots probably originate from those dormant buds that subtend or are at the base of an abscised vegetative shoot.

In Acer saccharum and L. styraciflua, many epicormic and lateral branches are short lived and the dormant buds on the bases of these shoots become engulfed in periderm (Church & Godman, 1966; Kormanik & Brown, 1969). The epicormic shoots in Q. canadensis, due either to abscission or pruning, are also short lived. Although first order basal buds from epicormic shoots were not found embedded in periderm, they continued in their sequential development and also produced second order reproductive buds in their bud scales. These buds, along with the telescoped sympodial series of higher order reproductive buds, perpetuate the cauliflorous condition throughout the life of the plant.

The cultivated trees used in this study often had greater wen development than occurs in nature. However, wens were not present on all trunks of trees observed for this study. Lack of wens on trunks may be the result of mechanical or pathological damage to the meristematic areas. Once the meristematic areas are destroyed, new buds do not form since inflorescences can form only from axillary buds. Adventitious cauliflory was not observed in this species.

Most of the previous work done on the development of exogenous cauliflory was done before the development of SEM as a research tool.

Considering the special features associated with cauliflory in C. canadensis (i.e., serial first order buds, second order buds in the bud scales of an inflorescence), future SEM studies in other taxa may reveal very complex and variable patterns of cauliflorous development.

{ Since C. canadensis comes from a subfamily of primarily tropical species and is itself one of the few cauliflorous species in temperate regions, this study may be of use in future interpretations of the cauliflorous condition in other taxa, both temperate and tropical. }

Results of the research done on cauliflorous development in C. canadensis could result in future studies that follow four possible directions. First, the development of cauliflory could be studied in more detail in C. canadensis. Second, since all species of the genus Cercis are cauliflorous, a comparative study could be done on the development of cauliflory in the genus. Third, cauliflorous development could be studied in other legumes. Finally, studies could be done on cauliflorous development in unrelated taxa

Cauliflorous Development in Cercis canadensis: The present study did not interpret the development of the inflorescence itself. A study such as this would give further insight into the interpretation of cauliflory. Tucker (1987) states that the inflorescence type of C. canadensis, is a raceme with flowers initiated and usually maturing acropetally on the inflorescence. Thompson (1946), in a discussion on inflorescence development in relation to cauliflory in C. siliquastrum, found that an inflorescence producing second order reproductive buds often produce them at the same time as the flowers are produced. When this is the case, flowers often mature acropetally while the lateral

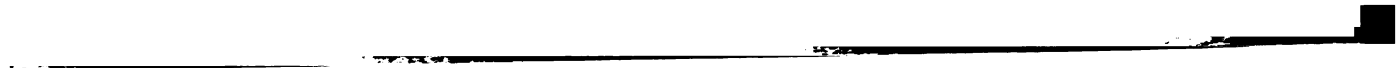
second order reproductive buds initiated below the flowers mature in a basipetal sequence. He refers to this as a cymose type of inflorescence. It appears as though Thompson was considering the entire reproductive shoot with the terminal inflorescence maturing first and the second order buds formed in the floral bud scales maturing in subsequent years. Therefore, he considers this to be a compound inflorescence; a cyme of cymes or racemes that will mature over several years. Preliminary studies using SEM and light microscopy indicate that this condition may occur in the inflorescences of C. canadensis and the present study showed that at least some of the higher order buds became microscopically visible before the inflorescence had abscised (Figures 12, 13). This raises at least one major question: Are the inflorescences racemose or cymose?

Other questions arise about the formation of epicormic shoots on wens. Detection of photoperiod in the leaves of a plant stimulates florigen, the flower inducing hormone (Salisbury and Ross, 1985; Roberts and Hooley, 1988). Epicormic shoots produce leaves and the leaves on these shoots may play a role in producing both products of photosynthesis and florigen for the cauliflorous buds produced on older branches and trunks. Epicormic shoots probably arise from the linear series of first order buds formed laterally at the base of an abscised or pruned vegetative shoot (Figures 21, 22). Since reproductive buds on the epicormic shoots contribute to the cauliflorous condition, a study of these shoots may be of value to the nursery trade for increasing flower production of this important ornamental.

Cauliflorous Development in Other Species of Cercis: Cercis is a small genus consisting of six species (Wunderlin, Larsen & Larsen, 1981, 1987). Although small, the genus has a disjunct distribution within the northern temperate regions with species in eastern Asia, southeastern Europe, eastern North America and southwestern United States down to northern Mexico (Li, 1944). Comparison of cauliflorous development within the genus would be of taxonomic value due to this discontinuous distribution and also because all of the species grow in temperate regions. Conservation of cauliflorous development is to be expected in species that are growing on the same continent and taxonomically classified as a different species because of recent speciation (i.e., C. canadensis and C. occidentalis from North America) but what about the taxa that have long been geographically separated (i.e., C. canadensis, C. siliquastrum from the Mediterranean and C. chingii from China)?

Sampling of most of the other species of Cercis has been done at the North Carolina State University Arboretum and macroscopic observations indicate that cauliflorous development might be conserved within the genus. Further microscopic studies are necessary to test the macroscopic observations.

Cauliflorous Development in Other Legumes: Many other legumes are cauliflorous. The list includes Adenolobus, from western African, another member of the tribe Cercideae (Wunderlin, et. al., 1987). Since this small genus, consisting of two species, closely resembles Cercis (Brummitt and Ross, 1975), a comparison of cauliflorous development may be of taxonomic importance.



Gleditsia triacanthos, a temperate member of the subtribe Caesalpinioideae, also appears to be cauliflorous. Preliminary sampling, done in the fall of 1989 and the spring of 1990, indicates that cauliflorous buds develop subordinately (in a semicircular pattern) and that they may arise endogenously in the axils of leaves. The superposed buds and thorns found in G. triacanthos will make interpretations of cauliflorous developmental in this species especially challenging.

Cauliflorous Development in Taxa Unrelated to Cercis: The staggering number of tropical species that exhibit cauliflory (Mildbraed, 1922, Richards, 1952, Stebbins, 1974) and the meager amount of work done on cauliflorous development indicate endless research possibilities. Comparisons of the development of cauliflory in different growth forms could also be done since cauliflory occurs on lianas, shrubs and trees (Mildbraed, 1922, Richards, 1952).

Unrelated temperate species that exhibit cauliflory are rare. Thompson (1946, 1951) reports that ramiflory occurs in species of Forsythia. Although preliminary observations indicate that second order buds are not formed on the Forsythia plants growing on the MSU campus, developmental studies using SEM may add to our knowledge of the differences between ramiflory and cauliflory.

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