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CERCIS (FABACEAE): EVOLUTION OF CAULIFLORY IN THE GENUS

By

Shirley Ann Owens

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ABSTRACT

CERCIS (FABACEAE): EVOLUTION OF CAULIFLORY IN THE GENUS

By

Shirley Ann Owens

Cercis is a genus with a geographically disjunct distribution in North America, southern Europe and eastern Asia. The architecture of cauliflory (flowering from the lower branch and trunk areas of woody plants) was examined in ten taxa, including nine of the 11 recognized species in the genus Cercis. In each taxon studied, cauliflory was present and the architecture of cauliflory was similar, regardless of geographic distribution. Therefore, cauliflory probably arose only once in Cercis, before the genus radiated from its site of origin.

Stems of Cercis canadensis were pruned to three differently aged segments at three different times during the summer of 1992 to determine the effects of treatment on bud fates (vegetative or reproductive). The development of vegetative and reproductive buds was also microscopically examined on untreated stems. Some buds that would have normally developed into reproductive shoots became vegetative shoots after stems were pruned. Although a change in eventual bud fate occurred in pruned stems, a reversion from the floral to the vegetative state did not occur since all buds are initiated with orthodisticous phyllotaxy and those buds that become inflorescences changed phyllotaxy prior to floral bud initiation. Intermediate shoots were produced on some

experimental stems developed four foliage leaves instead of four bracteose leaves but the flowers on the inflorescence appeared normal. Identification of fossil leaves as Cercis has been questioned based upon the presence or absence of a pulvinus at the base of the lamina (upper pulvinus). The present study indicates that the upper pulvinus degrades at a faster rate than the lamina or the petiole proper. Thus the lack of an upper pulvinus in a fossil leaf that is otherwise similar to Cercis should not constitute a reason for reclassification. However, the pattern left by the degraded cushion of pulvinus tissue or the separated vascular strands at the base of the lamina could used in conjunction with features that are preserved during fossilization.

This dissertation is dedicated to my grandfather, M. K. Heller, for passing on his deep love of learning, my grandmother, L.P. Heller, for passing on her tenacity and my mother D. M. Szacki for passing on her interest in and respect for all things living.

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CHAPTER I

LITERATURE REVIEW

GENERAL INTRODUCTION

This literature review reflects upon the topics addressed in the dissertation and those topics that deserve to be addressed in the future. The literature review is divided into two sections. The first section will consider the literature on the development, ecology and evolution of cauliflory. This section will begin with some general terminology and the use of cauliflory as a taxonomic characteristic.

The second section will be an overview of the systematics of the Fabaceae family. Relevant aspects of the biogeography, paleobotany and relationship of the legumes to the angiosperms as a whole is presented. Since this study deals with relict taxa of the family, emphasis will be on the subfamily Caesalpinioideae and especially on the early genera, Cercis, Gleditsia and Ceratonia.

CAULIFLORY; DEVELOPMENT, ECOLOGY and EVOLUTION

Terminology: In most plants flowering occurs on young leafy shoots but there are exceptions to this flowering position. When these exceptions occur in woody plants, they are

referred to as cauliflory. Mildbraed (1922) defined cauliflory as flowering on older leafless twigs, the boughs and the trunks, rather than on young leafy twigs. He recognized the condition in all growth forms of woody plants; trees, shrubs and lianas. The condition considered by Mildbraed to be the most primitive type of cauliflory is ramiflory, in which flowering occurs on young stems to older branches, but not on main trunks as in Turraeanthus zenkeri. Mildbraed also described several other types of cauliflory. Trunkiflory is the case where flowering occurs only on the trunk (Tetrastemma dioicum, Piptostigma macranthum, Macrolobium lamprophyllum, Cola chlamydantha and Diospyros fragrans), with basiflorous plants flowering only at the base of the trunk (T. sessiliflorum, C. fibrillosa and Chytranthus carneus). Basiflory occurs in several Malaysian species of Ficus (Corner, 1978). Simple cauliflory is the flowering on all areas of the plant; young, middle-aged and old stems and trunks (the Ficus group Fasciculatae, species in the genera Angylocalyx, Drypetes, Diospyros and Omphalocarpum).

In addition to these types, which produce either simple flowers or an inflorescence (with a short axis) directly on the parent organ, another type of cauliflory called idiocladanthie involves the production of flowers on a special stem (inflorescence axis) with scale leaves and long internodes. These stems can grow upward above the branch

(F. mucuso), droop downward below the branch (Annonidium Mannii), or grow predominantly from the trunk (Piptostigma mulitnervium, P. preussii). This does not include a condition called penduliflory in which inflorescences hang down under the crown on thin stalks (Parkia pendula and Coeupia longipendula).

Flagelliflory is the name Mildbraed gave to a special type of idiocladanthie. The plant in this case produces its long whip-like flowering branches with scale leaves and long internodes on the lower part or base of the trunk. The example used by Mildbraed (1922) was Paraphyadanthe flagelliflora which produced long prostrate shoots with scale leaves and long internodes. Most of the shoot was buried beneath litter except near the tips where small white staminate flowers are formed. These runners, which are up to 11 m long, rarely produce roots. This case is similar to the condition that Corner (1978) refers to as geocarpy. Flagelliflory is used in a much broader sense today and refers to the whip-like inflorescences produced on older branches and trunks (Pijl, 1982, Prance and Mori, 1979) rather than just the lower part or base of the trunks (Mildbraed, 1922).

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). Prance and Mori (1979) also found that

inflorescence position in some taxa of the Lecythidaceae is variable and Pijl (1982) reported that in monoecious Artocarpus heterophyllus (Jackfruit) only the female inflorescences are positioned on the trunk.

In addition to the terminology associated with cauline flowering positions (cauliflory, flagelliflory), Pijl (1982) refers to terms which emphasize the resulting fruits (caulicarpy, flagellicarpy). The terminology will be discussed here as it has relevance to some parts of the ecology section of this review. There are two types of caulicarpy recognized by Pijl; functional caulicarpy when seed dispersal in a plant is enhanced by fruit position (bat dispersed A. heterophyllus) or nonfunctionally caulicarpic when fruit drops before dispersal (Durio ziberthinus).

Fruit position can differ from flower position. Arachis has flowers that are not geocarpic but the ovary stalk pushes the fertilized ovary into the soil producing geocarpic fruits. Herbaceous monocots without secondary growth, such as those in the Zingerberaceae and some monocot geophytes also have flowering that could be considered analogous to cauliflory in dicots (Corner, 1949; Richards, 1952). Since the cases above involve the term geocarpy applied to herbaceous plants, geocarpy should not be used as a category of cauliflory. Pijl (1968) used the term basicaulicarpy which better describes the condition for woody plants. In the case of the Ficus species described by

Corner (1978) that have long flowering stems that arise in the base of the tree trunk, basiflagellicarpy might be a term better describing the condition.

Cauliflory as a Classification Characteristic; Cauliflory has been used as a classification character in the taxonomic literature. For instance, 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).

Type of cauliflory has been used as a major classification characteristic for some of the species in two New World tribes of Bignoniaceae (Gentry, 1980). In the Bignoniaceae, inflorescences can be terminal and/or axillary, ramiflorous, flagelliflorous or cauliflorous. Kigelia, a bat pollinated genus, exhibits spectacular flagelliflory (Gentry, 1980). The inflorescence position is constant enough in species of Amphitecna and Parmentiera of the Crescentieae tribe to be used as an important taxonomic character.

Cauliflory has also been used in the classification of some species of actinomorphic flowered New World Lecythidaceae (Prance and Mori, 1979). In this group, cauliflory is common in Gustavia, Grias and Couroupita.

Prance and Mori (1979) found that inflorescence trends in this group changed from the cauline to the terminal position, indicating that cauliflory is the more primitive condition.

Development of Cauliflory

In 1878, Schimper thought that cauliflory was due solely to dormant buds which formed on leaf bearing twigs and rested for years on older branches and trunks areas until they flowered (in Thompson, 1951). Thompson showed that cauliflorous buds could be produced and develop in other ways.

Cauliflorous buds can arise from an axillary or adventitious position. 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 and Stone,1943; Aaron, 1946; Fink, 1983). Axillary buds can be formed 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). 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).

Cauliflorous buds can be of an endogenous (arising in deep seated tissue), or an exogenous (arising in superficial tissue) origin (Esau, 1977; Bell, 1991). They can in addition remain dormant/suppressed or can be initiated anew each flowering season. Eventually buds develop vascular connections to the parent organ. Three methods of vascular connection that can occur in the cauliflorous situation were described by Lent (1966): 1) a direct connection of the vascular tissue of the bud to that of the parent organ, 2) a connection of bud vasculature to the vascular tissue of an old abscised reproductive bud, 3) a connection to the vascular tissue of an abscised vegetative shoot. Confirmation of the axillary origin of buds has sometimes been done using connections of the vascular tissue to the pith. However, 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 (Fink, 1983). Therefore, vascular traces to the pith used alone are not sufficient evidence for axillary origin.

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). Inflorescences of Theobroma cacao mature first on the trunk and sequentially mature in an acropetal manner up to the one-year-old stems (Lent, 1966). In young trees of F. glomerata, synconia are singlely produced 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 the single syconium is replaced by a cauliflorous shoot with many synconia. This is an example of basipetal cauliflorous progression (Pundir, 1972). Inflorescences mature in Cercis canadensis in a synchronous manner on all parts of the tree (Owens and Ewers, 1990).

Wens, macroscopically visible raised and swollen areas along the stem, caused by the cauliflorous condition were described for Ceratonia siliqua and Pleiocarpa mutica (Thompson 1944, 1946, 1949). These are the structures formed by obligatory nodosity ("... the spontaneous congenital disposition appearing on the edges of main or long shoots and side or short shoots of certain Angiospermae lignosae to form nodular swellings with progressive additions of buds."), a counterpart to obligatory cauliflory, reported by Paclt (1985, p. 220) to occur in species of Gleditsia. Up to 40 buds, either vegetative or reproductive, were found on the nodes of older G. horrida

trees. Other legumes with obligate nodosity are Tamarindus indigo and some species of Caesalpinia (Paclt, 1985). This condition was found in C. canadensis, where the wens produced higher order (greater than second order) reproductive buds and in many cases epicormic shoots (Owens & Ewers, 1991). These shoots produced first order reproductive buds on nodes with very short internodes and were also in many cases subtended by a series of reproductive buds. In C. 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).

Development of Cauliflory in Cercis canadensis subsp canadensis: A study on the development of cauliflory in C. c. subsp canadensis produced the following results (Owens and Ewers, 1991): The vegetative branching system in C. c. subsp canadensis is sympodial with the distal lateral bud replacing the terminal bud each year. Flowering 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 C. c. subsp. canadensis. The phyllotaxy was determined from the leaf primordia in the vegetative bud and 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. During the early stages of vegetative bud elongation, buds began forming in the axils of leaf primordia.

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. This series continued to develop basipetally until stem elongation terminated. The first-formed buds grew in conjunction with stem elongation as newer buds were formed in the axil. 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. 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).

Bell (1991) uses the term suppressed rather than dormant for cauliflorous buds. He states that adventitious and preventitious buds "grow a short distance each year in the manner of a short shoot" and therefore can not be dormant. My objection to this in the case of C.c. subsp. canadensis is that the lower buds in the linear series have differentiated bud scales but the actual bud primordia does not differentiate until the year the macroscopic inflorescence bud or macroscopic vegetative bud forms. This could take up to four years in the proximal most buds.

Second order reproductive buds arose from the axils of basal bud scales of inflorescences below the abscission zone of the inflorescence axis. 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. Based upon red staining with safranin O and fast green, the old

bud scales were lignified or suberized.

Floral bud scales had an apical appendage at the tip. These appendages on the floral bud scales of second order reproductive buds were orientated approximately perpendicular to those of a first order reproductive bud. 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. Various orders of buds were observed on the same floral bud stump and some new buds were being formed at the same time that a bud from the previous year showed full development.

In the older branches and trunks, inflorescences arise from wens, which are macroscopically visible raised and swollen areas along the stem. 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.

The wens were in two ranks following the orthodistichous pattern of phyllotaxy established in the vegetative bud. Wens caused by the cauliflorous condition were first described for Ceratonia siliqua and P. mutica (Thompson 1944, 1946, 1949). In C. c. subsp canadensis, the wens produced not only higher order reproductive buds but also in many cases epicormic shoots. Since, 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 in this species (Worthington, 1968), epicormic shoots could easily differentiate when the appropriate physiological cue is given. These epicormic shoots produced first order reproductive buds on nodes with very short internodes and were also in many cases subtended by a series of reproductive buds.

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 and Godman, 1966; Kormanik and Brown, 1969). The epicormic shoots in C. c. subsp 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.

Macroscopic bud counts done by Owens and Ewers (1991) indicated 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.

Data from the entire shoot system indicated that first order reproductive buds produced more of the total inflorescences than did higher order buds. This could be attributed to the high number of current (0) and one-year-old stem segments. 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 versus the quantitative data for macroscopic higher order buds per node, 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 and 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.

Development of Cauliflory in Other Caesalpinioidae: Of special interest is cauliflorous development in two other legume species in the subfamily Caesalpinioidea; Gleditsia triacanthos and Ceratonia siliqua. They are genera from two of the three groups proposed to be archaic for the Fabaceae (Polhill et al., 1981). The development of cauliflory in species of these genera needs to be done as it would establish cauliflory in each of the archaic groups of the legumes; Ceratonia, Gleditsia and Cercis.

Cauliflorous development has been reported for C. siliqua (Thompson, 1944, 1946). He found that a basipetal progression of first order buds was formed exogenously in distal branches. These buds formed inflorescences which abscised after flowering was completed, leaving a stump that may still have superficial buds. These stumps along with the superficial buds became entirely engulfed in cortical tissues. Within these cortical tissues, the first endogenous inflorescences arose. The secondary growth along with the stumps of the original inflorescences and those that were produced later become "warty wens from which

numerous endogenous inflorescences protrude in a chaotic manner during any flowering season." (Thompson, 1944, p. 50).

The term cortical tissue was problematic as most temperate trees such as Ceratonia, whose origin is reported to be in the Mediterranean region, generally lose their cortex after periderm formation. Labels on Thompson's drawings in his 1944 paper show cortex below the cambium and inner cork. Arzee, Arbel and Cohen (1977) reported that C. siliqua formed only a superficial phellogen with cortex persisting beneath until a true periderm formed. The true periderm did not form until the tree was at least 40 years old. The condition produces a smooth bark and usually occurs only in tropical trees. This along with other typically tropical characteristics such as cauliflory, flowering in the autumn and year around cambium activity presents questions about the reported origin of this species (Arzee et al., 1977). They also reported that the superficial phellogen in C. siliqua was at first circumferentially discontinuous, forming first under lenticels, and a complete cork cover took 4-6 years to form. It would seem that Thompson's cambium is actually the superficial phellogen. Delayed development of the true periderm and the longevity of the cortical tissue would better enable endogenous buds to reach the outer surface during growth. It may also protect newly forming buds from

attacks by pathogens or insects.

In 1891 and 1898, Kerner reported the replacement of senescent short shoots in Gleditsia caspica over a ten year period forming swollen nodes which contain the remnants of 20 or more short shoots (in Paclt, 1984). Paclt (1984) reported the presence of obligate cauliflory in Gleditsia that results from obligate nodosity, the term given to the node swelling condition above.

Ecology of Cauliflory

Mildbraed (1922) reported 278 cauliflorous species from tropical Africa. World wide, there are about one thousand cauliflorous species (Mildbraed, 1922; Richards, 1952; Walter, 1971, 1984). Cauliflory is common in rainforest trees, shrubs and lianas. Most of the species that are cauliflorous are found in the understory or shrub layer with few examples found in the canopy layer (Richards, 1952).

The possible reasons for a plant to be cauliflorous are interesting ecological questions. What is the possible adaptive relevance for the plants that exhibit this characteristic? Hypotheses that try to answer this question have been proposed in the past. Four of these are present in the literature; one based upon physiological resources, one based upon mechanical support for large flowers and fruits, a third based upon seed dispersal and predation and

a fourth based upon attracting pollinators for cross-pollination. Because there is such a fine line between seed dispersal and seed predation, they will be combined in this review. A fifth hypothesis will be added; one that considers cauliflory as a means of increasing genetic variability between modules. This hypothesis is based upon meristem mutations (Klekowski, 1988, Tilney-Bassett, 1986) and the concept of individual plants as genetic mosaics (Grant, 1974, Gill, 1986). Since cauliflory is primarily a tropical characteristic, literature on tropical plants and animals was used whenever possible.

Physiological Resources: 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 (in Richards, 1952). In tropical evergreen trees that store enough nutrients for flowering only in their lower branches and trunks, cauliflory could represent a more economic means of transporting and storing nutrients. The objection to this hypothesis has been that this would be more advantageous for large trees whereas cauliflory occurs more frequently in small trees (Mildbraed, 1922; Richards, 1952).

Mechanical Support of Reproductive Structures: The presumed

adaptive significance of cauliflory for mechanical support of reproductive structures is based upon parts of Corner's Durian theory. The theory states that large arillate fruits, evolutionarily retained from pachycaulous (with thick or massive primary construction) ancestors, could not be mechanically supported on the more recently evolved leptocaulous (with thin or slender primary stem) trees (Corner, 1949, 1964, 1978). As examples Corner (1964) uses species in the genus Artocarpus which produce large multiple fruits including breadfruit and jackfruit. Pachycaulous trees such as A. anisophyllus and A. incisus produce fruits on stout twigs. As the leptocaulous tree form evolved in Artocarpus, fruits were either reduced and retained on slender twigs as in A. lanceifolius and A. fulvicortex or fruits were produced on the larger parts of branches and trunks of the trees as in A. heterophyllus (Corner, 1964).

Ramiflory and cauliflory thus evolved, producing dormant reproductive buds that flower and fruit on branches and trunks that provide the appropriate mechanical support. Corner argues that although the species with massive flower and fleshy arillate dehiscent fruits have been replaced in many cases with smaller dry indehiscent fruit types, the massive flowers/ inflorescences or physiological requirements remain in many cases to enforce the cauliflorous condition.

Corner's model for the durian theory are the thirty

species of the genus Durio most of which are cauliflorous. Due to the large spiny fruits and the size of the seeds, seed dispersal was possible only by large mammals. Eames (1977), in his criticism of the durian theory, considered cauliflory to be an adaptation to pollination or seed dispersal by bats and birds and cites that early angiosperms relied upon insects for these functions.

Cauliflory in the early legumes (or legume ancestors) could have evolved to support heavy fruits having seeds with large arils. Corner (1949) considered the primitive legume fruit to be a large red fleshy many seeded (up to 50) pod with black seeds covered with a red aril. If cauliflory evolved early in the history of the legume family, the original selective pressures for the condition may no longer exist. Fruit size reductions and/or the loss of arils probably occurred many times in this large family. This will be discussed because mechanical support could have been the original ecological adaptation for Ceratonia and Gleditsia which produce relatively large fruits on many flowered inflorescences.

Examples of large heavy legume fruits with arils were used by Corner (1949, 1964, 1978) to support his Durian theory. Some taxa in this family produce arils that cover the entire seed. Corner (1949) found two genera in the subfamilies Papilionideae and the Mimosoideae and fourteen genera in the Caesalpinioideae that have species with these

arils. In the genus Acacia, he found species that produce seeds with arils, seeds without arils and many types of seeds with arils that are intermediate to these forms. The arillate condition was considered by Corner (1949, 1964, 1978) to be a relict of the early legume ancestors and the function of attracting dispersal agents has been transferred from the seed itself via intermediate forms to the pericarp of the fruit.

Criticism of this argument came from Pijl (1982) who criticized the loose interpretation of an aril which Corner used in the ecological sense "..... for anything juicy near the seed, using only incidentally (for placental appendages) a morphological criterion. When meeting morphological discrepancies, he (Corner) rather freely invokes a process indicated by him as a 'transfer of function' defying homology." (Pijl, 1982, p. 139). The juicy part near the seed could be the sarcotseta (a fleshy outer integument), an aril (an outgrowth of the funicle) an arilloid (a term used by Pijl and Ridley (1930) for the intermediate forms between a sarcotesta and an aril), or the pulpa (an outgrowth of the endocarp). Corner and Pijl also disagreed on the origin of the sarcotesta: Corner thought that it was derived from a combination of the aril and seed and Pijl found it to be fundamental, found in cycads and Ginkgo, criticizing Corner for lack of consideration of the angiosperm connection to the gymnosperms. Obviously Corner took the criticism

seriously and by 1978 had reduced the number of listed genera possessing arils in the Fabaceae.

The use of the term aril vs arilloid is still controversial in the Fabaceae. Gunn (1981) suggested limiting the use of the term aril until anatomists clearly establish the origin of all legume arils.

Mechanical support is a plausible ecological adaptation for cauliflory in some legumes. Gleditsia produces indehiscent fruits with endocarp pulpa and Ceratonia produces semifleshy indehiscent drupes (Pijl, 1982). These structures could be transitions from the arils that Corner (1949) proposed for the earliest legume fruits. In addition, both genera produce fruits on many flowered inflorescences so it is possible to have many of these relatively heavy fruits on one inflorescence axis. This would further increase the need for mechanical support.

Seed Dispersal: Another plausible hypothesis for the adaptive relevance of cauliflory is seed dispersal. Fruits that have been selected for by or have evolved to attract seed dispersers (frugivores) can be divided into two categories: 1.) fruits that are eaten by animals that feed opportunistically and perform low-quality dispersal and 2.) fruit adapted to relatively specialized frugivores that perform high quality dispersal (McKey, 1975). Opportunistic frugivores eat other things besides fruit and use fruits as

a source of water and carbohydrates. They will choose succulent sugar rich fruits with small (easy to pass through the digestive system) seeds, obtaining protein and lipids from other sources. Specialized frugivores are totally dependent on fruit as an energy source and choose fats and protein rich fruits (Snow, 1962, McKey, 1975). Fats and proteins are generally associated with providing nutrients for developing embryos in large often non-dormant seeds which are harder for the frugivore to digest. Often the nutrient material is digested away from the seeds and the seed is regurgitated.

If frugivores, both opportunistic and specialized, can not physically obtain fruits they do not get dispersed. Therefore, another factor for successful dispersal is fruit position including all types of cauliflory. If the cauliflorous condition is primitive within a plant group, we would expect seed dispersal to be done first by reptiles (saurochory) (Takhtajan, 1964) and then by mammals. Early basicaulicarpous buds may have been saurochorous (Pijl, 1982).

Bats are important seed dispersers in the tropics. Pijl (1982) reported that fruit bats are nocturnal and color blind, with a good sense of smell preferring musty, rancid odors. They have blunt molars used for pressing the juice out of fruits. The fruit and the seeds are then discarded. This enables them to have the small, simple gut necessary to

maintain a low body weight. Fruits that attract them are drab in color, have a butyric acid smell and large juicy seeds (Pijl, 1982).

Old World fruit-bats with their weakly developed sonar-apparatus have problems flying through dense foliage. Caulicarpic and flagellicarpic species of Ficus, Lansium and Artocarpus are chiropterochous (seeds dispersed by bats) and have fruits positioned away from the foliage (Pijl, 1982). One interesting example reported by Pijl (1982) is Swartzia prouacensis, a legume, which produces large black seeds with white arilloids that are suspended on funicles that can be up to three meters long. He calls this flagellispermy. Tropical caulicarpic species that have seeds dispersed by bats are found in the Palmae (caulicarpy is organizational), Moraceae, Chrysolbalanaceae, Annonaceae, Sapotaceae, Anacardiaceae and Fabaceae (Pijl, 1982).

Seed dispersal by birds (ornithochorous) is important for plants in tropical areas. Although caulicarpy occurs in many tropical understory trees, it is not considered to be a part of the ornithochorous syndrome. Perhaps it has been overlooked.

Morton (1973) reported that the majority of neotropical adult birds are at least partially frugivorous. Nestlings are usually fed insects which nutritionally produce faster growth. This is a selective advantage in the tropics where there is a high rate of nesting predation. In general,

fruit is more abundant year around in the tropics than insects which are widely dispersed or abundant only during specific times of the year (Morton, 1973, McKey, 1975). Frugivorous birds can be specialists or opportunistic fruit eaters. Most birds that are specialized frugivores are large while opportunistic birds are small. Morton (1973) attributes this to the fact that the specialists eat fruits with fewer but larger seeds that can not be digested by the small birds.

Fruit position is probably as important for birds as the size of the seed. If the fruit is not accessible, it does not get eaten/dispersed. Tropical birds which are at least partially frugivorous are specialists and opportunistic feeders of variable sizes (Morton, 1973). In order to obtain fruit, they usually have to either perch, hover next to fruits, or else snatch fruit while in flight. Large birds that perch to obtain fruit would need the support of larger branches and hovering and fruit snatching birds would find fruit to be more assessable without obstructions such as small branches and leaves. Although there have been few studies that consider position of the fruit (flagellicarpy and caulicarpy) as a part of the syndrome for seed dispersal by birds, this would seem to be an important factor that has been overlooked. Ridley (1930) reported many tropical plant species that are ornithochorous. Finding out which of these species are also

caulicarpic could become an interesting study for the future.

Predation: It is hard to determine when seed dispersal actually turns into seed predation (Janzen, 1971). In addition, adaptations that attract seed dispersers, also attract predators. Seed predation is especially intense in the tropics and is the selective factor behind the immediate germination of the seeds of many primary forest species as soon as they hit the ground (Sarukhan, 1980). Predator satiation could be achieved by increases in fruit or seed production. Woody plants with certain types of cauliflory, such as simple cauliflory, produce relatively more fruits and seeds than it would if it were not cauliflorous.

Cauliflory might be especially adaptive in the legume family because of predation. Bruchid beetles (in the family Bruchidae) are predators that feed mainly on the seeds of species in the Fabaceae (Janzen, 1969, Johnson, 1981). They feed only on seeds and are generally host specific.

Solbrig and Cantino (1975) studied seed production in three species of Prosopis from the United States and Argentina. They found that of the 220-240 flowers produced per inflorescence for each species, at most two fruits developed to maturity. Bruchid beetles laid eggs on the developing fruit surface and hatched larvae penetrated the seeds damaging up to 25% of the seeds while they are still

on the tree. Reinfection of the seeds occurs after they have fallen from the tree. Only those seeds that pass through seed dispersers escape, and of those, only around 50% on the average germinated. Solbrig (1981) estimated that it would take 100,000 flowers to produce one germinating seed.

Studies done by Janzen (1969, 1976) compared species of perennial woody legumes from Central America and found similar differences between those that are hosts to bruchid beetles and those that are not. He also reported (1969) an unpublished study done by J.E. Mathwig on two northern latitude species; Gleditsia triacanthos (honey locust) and Gymnocadus dioca (Kentucky coffee tree). Thirty to 50% of the 10,000 seeds produced by the honey locust tree were destroyed by the first bruchid beetle generation. Fruits were removed from the tree and the upper valves (not the seeds) were eaten by fox squirrels. The uneaten parts of the fruits were then thrown on the ground where other bruchid generations ate 90-100% of the remaining seeds. The Kentucky coffee tree of the same age and size produced 400 seeds which were not destroyed by bruchid beetles probably due to a toxin in the seed.

Although this may be immaterial, a cost factor that was not reported for this study was the dioecious condition in Gymnocladus. Gleditsia triacanthos flowers are often functionally unisexual but the species is not dioecious. A

comparison between these two species should take into account that it took at least part of a strictly pollen donating tree to produce the 400 Gymnocladus dioca seeds.

Several strategies against predation by bruchid beetles were favored by Janzen (1976). They include selection for larger and fewer seeds with chemical deterrents. Flowering sequences that are more than a year apart would also be effective as the predators would not have a dependable food source and plant resources would be greater when flowering and fruiting does occur. Another strategy would be an increase in the number of seeds for predator satiation. Certain types of cauliflory would make this possible. An increase in seed production was not a strategy favored by Janzen (1976). He suggested that selection for an increase in seed number would not necessarily decrease the percentage of seed mortality but admitted that this hypothesis had not been tested. His studies also indicate that the beetles are host specific and able to produce only one generation per year in the lowland deciduous forest of Guanacaste Province on the Pacific Coast of Costa Rica.

An obvious argument to this reasoning is that even if the percentage of seed mortality remains the same, there should still be more seeds to take a percentage of with an increase in seed production. Simple cauliflory would be a strategy for increasing the number of seeds and there are probably tropical cauliflorous legumes with and without seed

predation by bruchid beetles that could be used to test the hypothesis.

Those genera of beetles that are seed predators associated with genera relevant to this study are the following: Amblycerus, Bruchidius and Bruchus (Gleditsia); Bruchus, Caryedon, Mimosestes, and Pseudopachymerus (Ceratonia); and Gibbobruchus (Cercis) (Johnson, 1981).

Pollination: Attraction to pollinators is another operative hypothesis because cauliflory occurs mainly in the 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 foraging for nectar and/or pollen, are the primary pollinators in the tropics. An extension of the pollination hypothesis 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 need by ground level pollinators that can easily be filled by cauliflorous species.

Bats are the pollinators that are most frequently associated with cauliflorous tropical plants. Pollination by bats is called chiropterophily. There are two suborders

of the Chiroptera: the Old World Megachiroptera (frugivorous) and the Microchiroptera (mainly insectivorous but a few New World frugivorous species). Both suborders have a few species that can pollinate flowers which they feed on (Start and Marshall, 1976). Faegri and Pijl (1971) reported that the most primitive group of Megachiroptera, the Pteropinae, are fruit eaters and the more derived Macroglossinae have adaptations for feeding on nectar and pollen

Bats can be effective vectors for cross pollination. Start and Marshall (1976), in a study of three species of Malaysian bats, found that the bats probed rapidly for nectar, visiting many inflorescences on the same or different trees. Pollination occurred when pollen dusted onto the bats was deposited onto receptive stigmas during foraging.

Flower position is an important part of the chiropterophily syndrome for bats such as those in the Megachiroptera that have an inefficient sonar-system. Woody plants that are flagelliflorous and penduliflorous position their blossoms in open spaces. In some Mucuna species, the stems bearing flowers are 10 m long and in many genera of Mucuna and Kigelia cauliflory and flagelliflory occur together (Faegri and Pijl, 1971). Faegri and Pijl (1971) consider some members of the Cactaceae to be cauliflorous and report that they along with Durio and night blooming

flagelliflorous Marcgravia species are pollinated by bats. Corner (1964) reported chiropterophily in Cereus (Cactaceae), Kigelia and Durio.

Chiropterophily occurs in all three subfamilies of the legumes but most (50%) occurs in the New World Caesalpinioidae (Arroyo, 1981). An example used was Eperua with flagelliflorous inflorescences (Arroyo, 1981) and sticky, coarse, warty pollen grains (Graham, 1981).

Pollination by birds (Ornithophily) is another consideration for cauliflorous species. Although pollination is performed by sun-birds, nectar-eaters, honeycreepers, hummingbirds, sugar-birds and even parrots (Arroyo, 1981), the focus here will be on the hummingbirds. Hummingbirds are not only important pollinators in the tropics but much of the literature suggests that they would be attracted to cauliflorous plants. For example, Snow and Snow (1972) in their study of nine species of hummingbirds in the Arima Valley, Trinidad, reported that the only plants that were adaptive to hummingbird pollination were found in the understory. In an unpublished study by F. G. Stiles, California hummingbirds were found to forage from beneath a plant rather than from the top (in Frankie, 1973). In addition, hummingbirds are able to hover (Faegri and Pijl, 1971) enabling them to collect nectar and pollen from flowers that arise on lower branches and trunks.

Grant and Grant (1968) found that a number of tropical

American plant groups have bat flower and hummingbird flower taxa in the same genus or in genera of the same family. They suggest that the systematic distribution of the bat pollinated flowers indicates that they were derived from bird pollinated taxa. Taxa in these groups would be good candidates for the study of cauliflory in relation to ornithophily. Skutch (1952) in a study of the Costa Rican Passiflora vitifolia found that the large red flowers of this liana were pollinated by the hummingbird, Phoethornis supercilious. Vegetative leaves are located as high in the canopy as this liana grows but the flowers are borne on special shoots produced near the ground.

Insects are other possible pollen vectors for cauliflorous species. Pollination by bees has been reported for some cauliflorous species of Couroupita (Prance and Mori, 1979). Midges have been reported to be the pollinators of Theobroma cacao (Faegri and Pijl, 1972). Accidental pollination by ants was suggested by Mildebraed (1922). Butterflies, hawkmoths and beetles are other possible pollen vectors.

In conclusion, Bawa and Beach (1981) view "... the ecological interactions among individuals that mate with each other, as being the result of the coevolution between sexual partners and also between flowers and pollinators.". Cauliflory in some species is an integral part of this coevolution. It also plays a role in seed dispersal which

may ultimately result in the continuation of a plant lineage.

Genetic Variability Between Modules and the concept of genetic mosaics: Genetic variability between different shoot units in a plant (particularly in woody plants) is the last hypothesis considered as having adaptive relevance for cauliflory. It is probable that the genetic diversity among gametes formed on some cauliflorous plants would increase since reproductive structures are formed at different times and on different parts of a plant. The hypothesis is based upon plants as a metapopulation of modules, upon meristematic mutations in plants, and upon another hypothesis, that of genetic mosaics. An introduction will be provided to each of these topics and a discussion on how this pertains to cauliflory will follow.

Plants as Metapopulations: Classical thought has been that the underlying mechanism for evolutionary change is natural selection with the individual organism as the fundamental unit of this selection (Lewontin, 1970). Although some change is possible directly through mutations, the major evolutionary changes are thought to be brought about by genetic recombination through sexual (meiosis or conjugation) reproduction, resulting in high genetic diversity upon which natural selection can act. Evolutionary thought along these lines is based upon

Weismann's doctrine of developmental determinism of phyletic distribution (Buss, 1983). Genetic recombination in plants, according to this line of thought, implies cross pollination (xenogamy) of individuals (Stebbins, 1974). Also implied is the genetic uniformity of individual plants; the pollen and ovary bearing individuals involved in cross pollination must be independent. Any other method of sexual or asexual reproduction in plants is often considered to be incapable of producing progeny that are genetically diverse enough for significant evolutionary change.

Evolutionary theory based upon these assumptions is problematic for plants (and other organisms such as fungi and many invertebrates). The major problem is in the definition of an independent individual as the basic unit of natural selection (White and the references therein, 1970, Harper and White, 1974, Solbrig, 1980, Gill, 1986). Would a tree with many orders of branches (modules) be considered to be the basic unit of natural selection or would the individual modules themselves be considered the basic units?

A system of architectural models based upon a secession of modules was derived for trees (Halle et al., 1978, Prevost, 1978). White defined a module as an axis whose meristem creates all the differentiated structures of a shoot from inception to flowering (1980) and proposed that a plant should be considered as a metapopulation of individual modules (1979).

Modules have a demography, experiencing birth, fecundity and death (White, 1970, Harper and White, 1974, Solbrig, 1980). Maillette (1982) used this concept in a study of the structural dynamics of Betula pendula, silver birch. She considered the individual tree as a population of repeated units (buds) suitable for a demographic study. The buds could die or become long vegetative shoots, short vegetative shoots or reproductive shoots all with different levels of needs competing for limited amounts of resources. Ultimately the fate of these buds determines the shape of the tree (Fisher and Tomlinson, 1973).

Mutations in Plants: Stratified meristems (those with a tunica-corpus organization) have independently evolved in many plant groups (Romberg, 1963, Tilney-Bassett, 1986, Klekowski, 1988). The tunica is defined as the peripheral layer(s) of the shoot apical meristem distinguished by cells that divide in the anticlinal plane (Esau, 1977). The corpus, located beneath the tunica, is comprised of layers of cells that divide periclinally and anticlinally. The genetic consequences of stratified meristems is clearly understood: because component meristems in such apices are almost autonomous, somatic mutations often lead to the development of periclinal mutations. (Klekowski, 1988). Periclinal mutations are mutations that occur in entire layers of the meristem. Unlike embryotyic animal growth in which certain layers give rise to certain tissue, apical

meristem initials are not predetermined. Initials from the tunica give rise to epidermal layers and if multilayered, can also add to tissue below the epidermis. The corpus can give rise to provascular tissue and also to ground tissue.

Mutations can occur in any of the meristem layers. The location of the mutation determines the phenotypic and genotypic differences between modules. For a complete review of meristem mutation types and the history and work done with plant chimeras see Tilney-Bassett (1986). The tunica-corpus can be divided into an LI (outer layer of the tunica), LII, LIII, etc. as the layers progress into the center of the corpus (Grant, 1974). These layers are going through many anticlinal and/or periclinal divisions and mutation in these cells get reproduced into subsequent L layers. As leaf primordia, stem tissue and axillary buds are formed from these layers, mutations are passed on and also change depending on where the mutations was when organs were initiated.

The mutation process is nicely illustrated in chimeras with leaf variegation such as Mentha arvensis 'Variegata' (in Klekowski 1988). At least one of the L layers in this plant produces cells that are incapable of photosynthesis (white cells formed). Other layers produce cells that do photosynthesize and produce normal green cells. If the white cells occur in the layers of the leaf where they are not masked by the green cells, the area appears white.

Ploidy level mutations have been discovered in the shoot apex of a number of periclinal chimeras of Datura stramonium, jimson weed (Avery et al., 1959). The chimeras have diploid and polyploid meristem layers. These kinds of mutations have also been induced with colchicine to produce larger flowers or fruits (Grant, 1974, Tilney-Bassett, 1986). Since an increase in ploidy level produces an increase in cell size, these mutations have been used to determine the fate of the layers of the tunica and corpus in fruits of thorn apple (Satina and Blakeslee, 1943; Satina, 1945; Dermen, 1947; Blaser and Einset, 1950)) and peach (Dermen and Stewart, 1973). They determined that the germ cells are formed in these species from subepidermal tissue (usually LII layers). Pollen and embryo sac mother cells in potato were also found to be derived from the LII layer (Howard, 1970)

In woody plants, branching patterns are often developmentally determined and thus have a genetic basis (Klekowski, 1988). Branching also affects the distribution of somatic mutations in the plant. Klekowski did some mathematical modeling with branching systems and determined that the most important characteristic for determining mutation accumulation is the branching system (1988). The branching system determines the biological age of apical initials by the number of cell divisions that have occurred since zygote formation. Plants with a lot of branching have

apical initials that have undergone fewer cell divisions from the zygote than a plant with similar biomass that has less branching. Genetic stability is greater in apical meristems that have gone through fewer mitotic divisions. Other factors which affect the frequency of somatic mutations are growth rates and deaths of branches within a plant, whether a plant has monopodial or sympodial branching and the formation of long and short shoots (Klekowski, 1988).

Mutations from the vascular cambium can be passed on through adventitious buds (Tilney-Bassett, 1986, Klekowski, 1988) and adventitious cauliflory (Klekowski, 1988). There is a lack of data on the mutation rates of the fusiform initials and how these mutations affect genetic diversity in adventitious reproductive structures.

Somatic mutations in modules are often transformed to the reproductive structures that they produce. Based upon the type of cell divisions in the apical meristem, germ cells of dicots are usually formed from the LII or LIII layers (Gill, 1986). This eliminates LI layer mutations from being sexually reproduced. Other mutations will be lethal or reproductively unsuccessful. Some mutations though will be reproductively successful and thus, those mutations will be heritable.

Genetic Mosaics: Grant (1974) defines a mosaic as an individual consisting of genetically different cells. Gill

(1979) defined an hypothesis based upon genetic mosaics in plants. He looked at large extensively branched plants as colonies of many heritable genotypes and estimated that a plant can have between 10,000 to 1,000,000 modules depending on species. The genetic diversity among these modules comes from developmental mutations of meristems. Since the modules produce reproductive as well as vegetative shoots, some of these mutations are heritable. The assumptions of the hypothesis are 1) the plant architecture is modular with modules gaining developmental independence over time, 2) the existence of significant phenotypic differences between modules, 3) the phenotypic differences confers differentials in fitness among modules and 4) geitonogamy (within plant pollination) effectively recombines genetic variation within self-compatible plants (Gill, 1986). Gill has used the hypothesis of genetic mosaics to answer some of the biological questions concerning the co-evolution of certain plants and their herbivores. He also looked at the impact this hypothesis has upon genetic recombination in a geitonogamous plant breeding system. The latter will be discussed in this review.

The consequences of genetic differences among modules has profound effects on the reproductive success of woody plants with many modules. Breeding systems and pollination strategies in plants are variable. Types of breeding systems include autogamy (within flower, self compatible),

facultative autogamy, geitonogamy (within plant, compatibility between different flowers), xenogamy (between plant, self incompatible) and facultative xenogamy (Cruden 1976, Lloyd, 1980).

A consideration about autogamous breeding systems, is that even self compatible plants do not necessarily favor self-fertilization. In self compatible Phlox drummondi, Levin (1986) reported that after applying only one type of pollen (all self or all cross), seed set was the same regardless of self or cross pollination. He also found that when pollen of both types was applied to stigmas, the pollen from cross pollination germinated on the stigma several hours earlier than the pollen from self pollination, suggesting that the breeding system in this self-compatible species favors cross pollination (Levin, 1986).

Cross pollination (xenogamy) is thought to be facilitated by the behavior of certain pollinators. Territorial bee behavior has been reported to occur in the tropics (Frankie and the references therein, 1975). Males of four Centris species set up territories in the crowns of flowering trees and chase out intruders. The intruder can then go to another part of the tree or leave the tree altogether. Frankie and Baker (1974) reported aggregates of from 15-300 individuals of anthrophorid bees foraging on certain legume trees with large crowns and abundant flowers. This may drive foragers that are not part of the aggregation

to leave the tree for another and increase the probability of outcrossing. Although the examples of pollinator behavior have been reported primarily for bees, they are probably also practiced by hawkmoths, bats and hummingbirds (Janzen, 1971, Baker, 1973).

Floral characteristics may also influence the chances of outcrossing. Pollinator rewards that are produced daily over a long period of time indicates that pollinators have to visit many flowers to get enough of the reward. This has been proposed as an effective strategy increasing the likelihood of cross pollination by certain solitary bees capable of long distant flight (Janzen, 1971). Floral morphology in some plants may also promote cross pollination. Darwin (1877) described many types of flowers with heterostyly that have anthers and gynoecium positioned such that cross pollination is prevented. Temporal isolation such as protogyny and protandry also prevent self fertilization. Plant sexual systems which include monecism, andromonecism, gynomonecism, dioecism, androdioecism, and gynodioecism promote cross pollination and also optimize maternal and paternal reproductive success (Bawa and Beach, 1981).

An important and often overlooked characteristic of breeding system/pollination analysis is the number of flowers of a species that open at the same time (Cruden, 1977) and a decrease in plant density (Levin, 1986; Lloyd,

1980). These factors increase the probability of the movement of pollinators among flowers on the same plant (geitonogamy) (Frankie, 1975, Arroyo, 1976, Hessing, 1988).

From marked recapture studies, Frankie (1975) showed that many solitary bee species that are associated with Andira inermis (Fabaceae) remain on the same tree for at least a day (20-38%). Only 1-2% of the bees moved to adjacent conspecific trees. Levin, Kerster and Niedzler (1971) showed that bees have a directional rather than a random foraging pattern and created a carry-over model in which a pollinator deposits most of the pollen picked up on one plant to the first three plants visited (70%). This model was based upon a study of Lythrum salicaria, a herbaceous perennial with far fewer modules than most woody plants. Hessing (1988) devised a model in which exclusive geitonogamy occurs when consecutive visits to a plant equal or exceed twenty-one.

Outcrossing rates for mass flowering species is low (Gill, 1986; Bawa and Beach, 1981). Mass flowering would therefore be very expensive for a plant because geitonogamous pollination requires the same investment in pollen and nectar without the benefit of cross pollination. Fraegri and Pijl (1971) discuss allogamy, with its two classifications, geitonogamy and xenogamy, in relation to pollination. They point out that both of these classes also require the same amount of work by the pollinator. The

adaptive relevance of mass flowering according to the genetic mosaic hypothesis would be an increase in the number of ways to acquire genetic recombination; through xenogamy and geitonogamy (Gill, 1986). Gill points out that this would only work with self compatible species. He should narrow this down as this excludes plants with temporal isolating mechanisms such as protandry and protogyny which may otherwise be self compatible.

Genetic mosaics and Cauliflory: Certain types of cauliflorous plants would be ideal for testing a genetic mosaic hypothesis. In some taxa, cauliflorous reproductive structures are formed at different times and on different parts of the plant. Various forms of short shoots and long shoots are also produced. Ceratonia siliqua , Couroupita giganensis, Ficus glomerat, F. pomifera, Artocarpus integrifolia, and Swartzia shomburgkii have adventitious cauliflory. There is a good chance that many of the modules in these plants mutate and produce genetic mosaics which are passed on through gametes.

Mass flowering also occurs in some tropical cauliflorous species. This also increases the chances of geitonogamy. It has been found that small numbers of flowers that opened at the same time maximizes cross pollination in self incompatible plants (Cruden, 1975). It has also been found that after 8-10 pollinator visits to one

plant, geitonogamy becomes the mode of pollination (Levin, 1978). Temperate cauliflorous species such as C. c. subsp. canadensis, which exhibit both ramiflory and cauliflory, have a seasonal type of mass flowering. The trees produce vast numbers of flowers on different modules that are open at the same time during a short flowering period. It would be reasonable to expect that they are at least partially geitonogamously pollinated. If this is combined with xenogamous pollination, there would be more chances for pollination especially during times when pollinators are scarce.

This hypothesis would also seem to be relevant for some cauliflorous species because they are primarily understory trees found in the tropics where outcrossing species are spatially far apart. Cauliflorous conditions such as reproductive modules produced on differently aged sections of the same or other branches or trunks would increase the probability of mutations that lead to mosaics. Some of these mosaics will produce progeny through sexual reproduction.

The problem with this hypothesis is the difficulty in testing. Determining the sexual system of the plant, the choice of modules for geitonogamous pollination, testing for viable pollen and receptive stigmas and anther removal to eliminate the probability of self fertilization are just a few of the difficulties. After pollination experiments,

tests for seed viability and heritable mutations would take many years to complete.

General Ecological Conclusions: The ecology of cauliflory is as diverse as the plants that exhibit the condition. Corner's problem was that he tried to fit all cauliflorous species into his durian theory. Selective advantages of cauliflory are not necessarily mutually exclusive. For example, adaptations for seed dispersal by bats may also have evolved into bat pollination in some species (Pijl, 1982). Mass fruiting (flowering) to satisfy seed predators could also increase genetic diversity among different-aged modules for geitonogamous pollination. Mechanical support of heavy fruits could place the fruits in a position that enhances the chances of pollination and seed dispersal.

In species in which cauliflory is the primitive condition, the selective pressures which originally made cauliflory adaptively relevant may no longer exist. Dispersal of fruits by reptiles that are currently rare or extinct would be an example of this. Floral or fruit characteristics could have changed without a change in position.

The last part of this discussion will address some of the possible ecological advantages for cauliflory in Cercis canadensis subsp. canadensis. Pseudopapiliod flowers in the genus are adapted to bee pollination and fruits are few

seeded with dry, indehiscent valves which indicates wind dispersal (Wunderlin et al., 1981). Although seed dispersal by wind could also be facilitated by the cauliflorous position of the fruits, I chose to do pollination studies (unpublished).

Observations of foraging by many species of bees indicated that at least some of the pollination was geitonogamous. The trees observed produced so many flowers that opened within a few weeks that the insects primarily foraged within the same tree. Bagged inflorescences did not produce fruits but fruits were produced on others that were not bagged. Observations on the sexual system suggest that this taxon is protogynous. For these reasons, C. c. subsp canadensis could be used for future testing of the genetic mosaic hypothesis.

Evolution of Cauliflory

Evolutionarily, Mildebraed (1922) considered ramiflory to be the most primitive condition and this was probably followed by simple cauliflory, trunkiflory, and the more specialized basiflory, and flagelliflory. Corner thought that cauliflory was the primitive condition. His durian theory, in part, was that large arillate fruits, evolutionarily retained from pachycaulous ancestors, could not be mechanically supported on the more recently evolved leptocaulous trees (Corner, 1949, 1964, 1978). Ramiflory

and cauliflory thus evolved, producing dormant reproductive buds that flower and fruit on branches and trunks that provide the appropriate mechanical support.

Eames (1977) thought that cauliflory was a derived condition that attracted bats resulting in seed dispersal and pollination. If this was a primitive condition, according to Eames, it would have been insect pollinated. Stebbins (1974) reported cauliflorous species were derived from ancestors living in a more open environment and secondarily entered the rain forest. Prance and Mori (1980) concluded that inflorescence trends in New World Lecythidaceae change from the cauline to the terminal position indicting that cauliflory is the more primitive condition for that group of plants.

Pijl (1982) thought that cauliflory in relation to seed dispersal was a specialized condition. The term specialized does not really tell anything about the evolution of cauliflory in general but it may better describes the evolution of the condition in specific plant families.

The cauliflorous syndrome evolved many times in different taxonomic lines. It may be primitive in some taxa and highly specialized in others.

SYSTEMATICS and PALEOBOTANY of the FABACEAE

Fabaceae (Legume family) is the third largest angiosperm plant family with 650 genera and 18,000 species (Polhill et al., 1981; Dickison, 1981). Legumes are distributed over much of the terrestrial habitats of the world with the greatest diversity occurring in areas with seasonal climates and variable topography (Polhill et al., 1981). As with any plant family of this size and importance, there are problems with phylogenetic relationships at most taxonomic levels. Extinctions leave unfilled gaps between extant taxa. Some of these problems have been addressed in recent studies of legume systematics and paleobotany.

The systematics section of this literature review concerns the origin and the adaptive radiation of the legume family, the biogeography of the early legumes, the phylogeny of the legumes in relation to other angiosperms and to each other, the classification of the Caesalpinioidae, of some of the tribes therein, and of the genus Cercis.

Systematics of the Fabaceae

The Fabaceae consists of three subfamilies; the Caesalpiniodeae, the Mimosoideae and the Faboideae /Papilionoideae. The Caesalpinioideae are the first subfamily in the fossil record followed by the Mimosoideae

and the Faboideae. Within the Caesalpinioideae, some have claimed that there are three groups of archaic woody genera; Gleditsia-Gymnocladus, Ceratonia-Zenia and Cercis (Polhill et al., 1981, Dickison, 1981, Cowan, 1981). Recent paleobotanical work by Herendeen (1990, 1992) and Wheeler and Baas (1992) suggests that perhaps these basal groups should be reevaluated.

Cauliflory has been reported in Cercis (Owens and Ewers, 1990) and Ceratonia (Thompson, 1944) and part of this dissertation deals with cauliflory in Gleditsia triacanthos. Although cauliflorous development may be quite different in these three genera, the condition appears to occur in all three of the basal groups and may be primitive for the legumes. A comparison on the development of cauliflory for most (ca. 9) of the species of Cercis was done as part of this dissertation. Establishing when the species radiated from the site of origin was a necessary consideration for this study. The early fossil record of the legumes is therefore relevant to this dissertation. A review of early paleobotanical literature will include reports of fossil pollen, fruits, reproductive structures and wood.

Origin and Adaptive Radiation: Reviews of fossil pollen (Muller, 1981) and wood (Baretta-Kuipers, 1981; Wheeler and Baas, 1992) indicate that the oldest record of legumes is from the Cretaceous (65-70 m.y. BP). Diversity of the legumes is thought to have been the result of major pulses

of thermal changes during the Cenozoic (Axelrod, 1992). By the Eocene, the Mimosoidae and the Caesalpinioidae were established and widely distributed. Polhill, Raven and Stirton (1981) defined three major periods of adaptive radiation for the legumes. These periods were distinguished by functional components that became uniquely fixed, such as Cercis like leaves, pollen shed in tetrads or other polyads, and Papilionoid flowers (Polhill, et al., 1981). First, the early Caesalpiniodeae (Caesalpinieae, Cassieae, Cercideae) became established during the late Cretaceous and early Tertiary. Seed structure, nectaries and types of leaves were established during this period. Surviving members of this group are distributed mainly in north temperate or subtropical areas of the world (Polhill, et al., 1981).

Second was the radiation of woody tropical genera from all three subfamilies during the Paleocene. Biotic and chemical defense mechanisms, nitrogen fixation, elaborate and/or zygomorphic flowers and systems that produced and controlled dormancy in seeds evolved during this period of radiation. The less advanced genera were scattered on the intercontinents, disjunct from near relatives, while the more advanced genera concentrated in continental Africa and South America with little representation in Asia and Australia (Polhill, et al.,.1981).

Finally, a surge of adaptive radiation occurred in the more advanced genera of the Papilionoideae while genera of

the other subfamilies continued in their radiation. This began with climatic changes in Oligocene and is associated with the Neogene. Evolution during this radiation was characterized by radical diversifications in both ecology and morphology. The advanced Papilionoideae genera formed regional cores. Some genera of the other groups went through periods of accelerated proliferation which created the large present day genera of Acacia, Bauhinia, Caesalpinia and Cassia (Polhill, et al., 1981).

Biogeography: Africa and Eurasia were still in contact during the Cretaceous and this contact represented the only reasonable route for plant migration between the southern and northern hemispheres (Raven and Polhill, 1981). Legume groups that originated during this period probably radiated via this route. By the middle Eocene, direct connections existed between Europe and North America. This route remained open with few short distance water gaps during the Miocene (Raven and Axelrod, 1974). Laurasia and Africa were also connected during early legume evolution. Although South America and Africa were probably separated by 800 km during the late Cretaceous, numerous islands along the Mid Atlantic Ridge facilitated migration of plants between the two continents. By the early Eocene when the main groups of legumes were differentiating, South America was separated by 1200 km from both Africa and North America (Raven and

Axelrod, 1974). Geographical relationships during the early evolution of the legumes suggest that the primary site of tropical legume evolution was Africa (Raven and Polhill, 1981).

Africa, Madagascar and South America contain the most legume diversity, perhaps due to early establishment in the ecosystem (Raven and Polhill 1981). Although the African flora has been depleted, the legumes are still relatively diverse when compared to other taxa. Madagascar, the "museum of African flora" (Stebbins, 1974), has a legume flora which includes genera that are archaic and endemic along with genera that are considered to be more recently derived. Archaic genera of legumes are also relatively more abundant in the Old World suggesting that early legume evolution took place in Africa (Raven and Polhill, 1981).

Legumes colonized North America during the Tertiary from South America and from Eurasia. Tropical North American legume floras are apparently derived from South American ancestors while temperate and subtropical floras are thought to be Eurasian in origin. The climatic conditions after the Oligocene caused the extinction of many genera in Europe and North America. In other areas, tropical Asia, New Zealand and Australia, the legumes were unable to successfully move into established ecosystems once they had the opportunity to do so and are poorly represented in tropical Asia even today (Raven and Polhill, 1981).

The hypothesis discussed above implies that South American legumes with a diversity center and a Tertiary fossil record in North America and a pantropical distribution radiated into tropical North America. An alternative boreotropics hypothesis is that the tropical South American legumes fulfilling the conditions above came from North American legumes. These legumes had migrated to North America from Eurasia. The proponents of the boreotropics hypothesis contend that South America was geographically isolated during the early Tertiary and that migration of taxa primarily took place between North America, Africa and Eurasia which were still connected (Wolfe, 1975; Tiffney, 1985 a, b; Lavin and Luckow, 1993). Lavin and Luckow (1993) pointed out that the two hypotheses discussed above are not mutually exclusive; that North American tropical legumes were derived from many different sources and migration events.

Phylogeny of the Fabaceae: The phylogeny of the Fabaceae is problematic due to the size and the morphological/anatomical diversity of the family. Another compounding factor is that few dicots, including the legumes, have recent ancestors among extant genera. The three phylogenetic problems within the legumes that will be discussed are their affinities with other groups of angiosperms, classification of the three groups of legumes and tribal classifications within the

Caesalpinioideae.

Historically the legumes have been placed in the order Rosales. Based upon new evidence, recent workers have reconsidered this position and have shown closer phylogenetic relationships between the legumes and the Sapindaceae (Thorne, 1983, 1992, Dickison, 1981). Historical classification background is given by Dickison (1981). His review of the systems of legume classification showed that the legumes have been assigned as an advanced member of the Rosales near the Connoraceae, Rosaceae and Chrysobalanaceae since Bentham and Hooker classified them in 1862. Hutchinson, in 1926, was the first to classify them as the sole family in their own order (Leguminosales). By 1964, he had split the order into three separate families; the Caesalpiniaceae, the Mimosaceae and the Papilionaceae (Fabaceae) and retained his contention that the legumes were derived from the Rosaceae.

Current systematists such as Takhtajan (1973) and Cronquist (1988) have placed the legumes into their own order, the Fabales in the subclass Rosidae. Dahlgren (1977) placed the family into its own order but found this order to have a closer relationship to the Sapindales. Thorne (1976) first classified the Fabaceae under the Rosales. He later found that the legumes were closer related to the Sapindales and reclassified the legumes under his super order Rutanae, order Rutales (Sapindales), suborder Fabineae (Thorne, 1983,

1992). Dickison (1981) found that the legumes differ from taxa in the Rosales because, among other differences, they have vestured pits in secondary xylem.

Support for a closer relationship with the Sapindaceae comes from wood anatomy. There is a similar level of evolutionary advancement in the wood anatomy and wood structure of the two families (Baretta-Kuipers, 1981). Other similarities between the legumes and the Sapindaceae include phytochemical (tannins and the rare ellagic acid), leaf, trichome and floral morphologies (glandular tapetum, ephemerous middle cell layer in the anthers, one nucleate tapetal cells, two nucleate pollen grains, crassinucleate and bitegmic ovules), seed coats and embryology (Polygonum type embryo sac, nuclear endosperm and chloroplasts in the embryo) (Dickison, 1981). Although there are questions about affinities with the Sapindaceae, most angiosperm classification systems show close affinities between the Connaraceae and the legumes.

The legumes have been classified as one family, the Leguminosae/Fabaceae, with three subfamilies (the Caesalpiniodeae, the Mimosoideae and the Faboideae/Papilionoideae) or three separate families (Caesalpiniaceae, Mimosaceae and Fabaceae/Papilionaceae). The differences in classification are in the weight given to differences between the three groups. Most current workers support a one family, three subfamily classification since

there are so few clear differences between extant members of the three groups and so much diversity within the groups (Polhill et al., 1981; Takhtajan, 1973; Dahlgren, 1975). Thorne (1992) used a four subfamily classification with the addition of the subfamily Swartzioideae. Cronquist (1988) classified the three groups as three separate families because he considered the treatment to be more in harmony with the customary definitions of families in angiosperms. The classification used for taxa in this dissertation will follow the three subfamily format.

The Subfamily, Caesalpinioideae: The Caesalpiniodeae is considered to be the most primitive group within the family. Some evidence in support of this comes from studies of comparative wood anatomy, the Caesalpiniodeae has the least specialized wood in the family (Baretta-Kuipers, 1981; Wheeler and Baas, 1992). Floral development has also been used to argue for primitiveness in this subfamily, since it includes taxa with variable features of floral development. These features are stable in taxa of the other two subfamilies (Tucker, 1989, 1991, 1992). The other two subfamilies are considered to have branched off from the early Caesalpiniodeae (Baretta-Kuipers, 1981; Tucker, 1989), with the Mimosoideae arising from the Dimorphandra group and the Papilionoideae arising from the Sclerolobium group (Raven and Polhill 1981).

South America, Africa and Southeast Asia are the main geographic regions of current Caesalpinioideae distribution. This suggests that ancestors of this subfamily evolved in the late Cretaceous when Africa and South America were close together (Cowan, 1981). Connections between Africa and Southeast Asia were not severed until the late Tertiary. The Caesalpinioideae are poorly represented in temperate regions but the existence of archaic genera in these areas suggest that ancestors were represented in temperate as well as tropical environments (Cowan, 1981).

The Caesalpinioideae are mostly tropical woody plants: large trees, understory trees, shrubs and lianas. The subfamily is currently composed of five tribes; Caesalpinieae, Cassieae, Cercideae, Detarieae and Amherstieae.

Pettigrew and Watson (1977) did an analysis of the genera in the Caesalpinioidae based upon 71 morphological traits and 45 other features that included chemistry and pollen ultrastructure. The conclusions of their analysis were that there were two main groups in the subfamily. Group 1 included the tribes Caesalpinieae, Cassieae and Cercideae, while group 2 consisted of the Detarieae-Amherstieae. They concluded that the Cercideae in group 1 and Swartzieae were the only readily defensible taxonomic assemblages (Watson, 1981). Swartzieae is now thought to be one of the early papilionoid tribes, near the Sophoreae

(Cowan, 1981; Watson, 1981). The analysis does not support most of the tribal classifications in use but alternate groupings did not emerge from the analysis.

The Tribes of Caesalpinieae, Cassieae and Cercideae: One of the findings of the Pettigrew and Watson (1977) study was that Hutchinson's classification of the Caesalpinioideae was inferior to updated versions of Bentham's. Tribal monographs reflect this finding (Cowan, 1981; Irwin and Barneby, 1981; Wunderlin et al., 1981, 1987; Polhill and Vidal, 1981).

Probably due to extinctions, transitions are no longer apparent between the Cercideae, the Cassieae and the early Caesalpinieae (Polhill et al., 1981). Caesalpinieae may be the base group for the other subfamilies as it is basal to the Dimorphandra group, proposed to be ancestral to the Mimosoideae and the Sclerolobium group, proposed to be ancestral to the Faboideae (Polhill and Vidal, 1981; Polhill et al., 1981). Cassieae includes the ditypic (Ceratonia) and the monotypic (Duparquetia) which have no known contemporary kinship within the family (Irwin and Barneby, 1981). Unisexual flowers that lack petals make Ceratonia unique. A recent floral development study done by Tucker (1992) confirms the lack of characters needed to show affinities with an early ancestor of other Cassieae. She considers the large number of variable characteristics of the flowers to be a primitive rather than a specialized

state.

The Cercideae may have branched off from ancestors of the Caesalpiniodeae early based upon certain characteristics such as palmate venation in leaves, independent nyctitropic leaf movement (from a single pulvinus) for each half of the leaf, the position of the lens on the same side of the hilum as the micropyle and the lack of hour glass sclereids in the hypodermis of the seed coat (Wunderlin et al., 1981, 1987). In addition, the Caesalpinieae, the Cercideae and a few of the Cassieae (species in the subtribes of Dialiinae, Duparqueriinae and Labicheiinae) are the only groups in the legume family without vestured pits in their wood anatomy (Quirk and Miller, 1985). Cercis is the only diploid (2n=14) in the family (Goldblatt, 1981; Polhill et al., 1981).

Tribal affiliations and distribution of certain genera of importance to this dissertation are as follows: Caesalpinieae includes Gleditsia, Cassieae includes Ceratonia and Cercideae includes Cercis. Gleditsia L. has about 14 species: two to three in Eastern North America, one in southern South America, one around the Caspian Sea, the rest from India to Japan (Polhill and Vidal, 1981). Ceratonia L. has two species; C. siliqua, the carob, thought to have originated in the East Mediterranean but widely planted in the seasonally dry tropical and subtropical areas of the old and new world and C. oreothauma, a newly

described relict species found in SE Arabia and the Horn of Africa (Irwin and Barneby, 1981). Cercis L. is a small genus in the Cercideae with six (Wunderlun,et al, 1981, 1987) to 11 (Huang and Yang, 1985) species depending on the systematic treatment. Distribution is disjunct in the warm temperate northern hemisphere with taxa native to eastern and western North America, to southern Europe and to eastern Asia.

The Genus Cercis: The genus Cercis is thought to have originated in the Mediterranean area during the Paleocene and from there, migrated to Asia and North America (Wunderlin et al, 1987). Cercis is a genus containing six (Wunderlun et al, 1981, 1987) to 11 (Huang and Yang, 1985) species. C. siliquastrum, native to the Mediterranean is the only species without numerous synonyms. The rest of the taxa are divided between North America and Eastern Asia (Table 2). For a complete review of the classification schemes for the North American taxa, see Ballenger (1992).

In a revision of North American Cercis, Ballenger (1992) recognized six taxa, most at the subspecies level. Enzyme electrophoretic and morphological analysis were used for the revision. The eastern redbud complex within North America was not distinguishable using enzyme data, but morphological differences, especially in leaf modifications, distinguished three taxa. The western redbud complex was enzymatically distinguishable but showed little

morphological diversity.

Classification of Asian species of Cercis is variable depending on the treatment. Li (1942) recognized 5 species of Cercis from Eastern Asia; C. racemosa, C. Chuiana, C. chinensis, C. Chingii and C. pauciflora. Huang and Yang (1985) describe all of the species above in addition to C.yunnanensis and C. gigantea. Recent communication with Dianxiang Zhang, who works on Cercis at South China Institute of Botany, Academia Sinica, indicates that most chinese botanists recognize 5 species of Cercis native to or cultivated in China (Table 2). C. yunnanensis was reduced to a synonym of C. glabra which H.L. Li later reduced to a synonym of C. chinensis (Zhang, per. comm. 1993). Personal observations of the Cercis collection at North Carolina State University Arboretum suggests that in the future the Eastern Asian complex will be revised especially for those taxa lumped into C. chinensis. There are greater morphological differences between the Asian taxa than Ballenger found between the North American taxa used for her reclassification.

Paleobotany of the Fabaceae

Legume Fossil Pollen: The basic pollen type for extant legumes is the tricolporate tectate-reticulate single grain (Guinet, 1981 a) but as expected in a family this large, there is a great deal of diversity. In addition, pollen can

be dispersed from the anthers in the form of monads, tetrads or polyads. Much of the material presented in this section is based upon a review of fossil pollen of extant taxa (Muller, 1981).

Caesalpiniodeae: The earliest legume fossil pollen found is the Sindora type from the Maastrichtain of Siberia (in Muller, 1981). The Crudia type from the Paleocene of South America-Nigeria and Maniltoa grandiflora from Texas have been reported (Elisk, 1968). The Caesalpinia type from the lower Eocene has been found in Venezuela and India (Germeraad et al., 1968). The oldest and the most diverse Caesalpinia type fossil pollen comes from India, suggesting an Indian ancestor for genera with this type pollen (Muller, 1981). Brachystegia type pollen was more common in the Oligocene. Eperua types from the Miocene of Guyana and Cassia type from the Pliocene of the Sahara complete the early fossil pollen record of Caesalpiniodeae.

Representative extant genera for fossil pollen types for the Caesalpinioidae are from the tribes Detarieae, Cassieae and Caesalpinieae. Extant genera of this subfamily have 3-colporate pollen which occur as monads (Cowan 1981).

Mimosoideae: The basic pollen characters for this subfamily had evolved by the Eocene and all of the early fossil pollen was found in West Gondwannaland (Guinet 1981 b). The arrangement for fossil pollen in this large group is by tribe.

Parkiae tribe: The Pentaclethra macrophylla type from the upper Eocene of Cameroon are monads with indistinct colpi and endopores. Four irregular tetrads formed the polyads of the Parkia type from the upper Eocene of Cameroon (Guinet and Salard-Cheboldaeff, 1975).

Piptadenieae tribe: The Filaeopsis type from the Oligocene of Cameroon were tetrads of reticulate exine, tricolpate grains. From the upper Eocene, the Calpocalyx ngouniensis type with reticulate exine and colporate apertures, the Pseudoprosopis sericeus type with areolate tectum and syncolporate apertures and the Adenenthera type with fine areolate tectum and simple apertures were all found in regular polyads (Guinet and Salard-Cheboldaeff, 1975).

Adenanthereae tribe: The Amblygonocarpus type of regular polyads with areolate sculpture and simple costate porate apertures (Guinet and Salard-Cheboldaeff, 1975) and the Prosopis juliflora type with tricolporate tetrads with perforated tectum (Piel, 1971) are reported from the Oligocene of Cameroon and Canada respectively.

Eumimoseae tribe: Eumimosoidea plumosa type from the middle Eocene was actually isolated from a fossil inflorescence (Crepet and Dilcher, 1977). The pollen was in tetrahedral tetrads. The Leuceana type of tricolporate monads with long colpi are reported from the Oligocene of Cameroon (Salard-Cheboldaeff, 1978). From the Miocene,

Desmanthus type tricolpate pollen has exine with striations (Graham, 1976).

Acaciaene tribe: Acacia type from the upper Eocene are all polyads with grains having more than one morphology. For a detailed survey of fossil pollen from this tribe, see Guinet and Salard-Cheboldaeff, 1975.

Ingeae tribe: Albizia type from the Miocene of France were grains with finely areolated exine (Caratini and Guinet, 1973).

The fossil pollen record of the Caesalpinioideae agrees with the chronological order of evolution of the tribes that was derived from comparisons of the morphology of present genera (Guinet, 1981 b). An interesting feature is that many of the fossil pollen types are characterized by compound grains in polyads or tetrads. Pollen shed in this manner might be a selective advantage for pollination in any plant that produces more than one ovule per ovary.

Faboideae: The only reliable early pollen record are of Indigofera and Astragalus from the Pliocene of the Sahara (Beucher, 1975).

Legume Fossil Fruits: The diversity of fruit types in the legumes is thought to have evolved from a single basic fruit type, the legume or pod, that is common to the Fabales (Dudik, 1981). One fruit or more than one fruit (apocarp) per flower are produced depending on the taxon. Legume is generally applied to a fruit derived from a superior ovary

with a single carpel, that dehisces along two sutures. The fruits of the legume family are, however, highly variable and differ in types of dehiscence, in seed number, in adherence of the seed to the pericarp, in the development of a septa or in pericarp consistency (Dudik, 1981). Early fruits were few seeded follicles like those of Gymnocladus (Polhill, et al., 1981). Winged fruits, common in the Caesalpinioideae, are found in the fossil record for legumes from the Eocene of North America and Europe (Polhill, et al., 1981).

Recent analysis of fossil legumes from several sites in North America was done by Herendeen (1990) and Herendeen and Dilcher (1991). They used fossil legumes from the Middle Eocene Claiborne Formation from the Mississippi Embayment in western Tennessee, western Kentucky and northern Mississippi, the Eocene Green River Formation in Wyoming, Oligocene Catahoula Formation of eastern Texas and the Miocene Whitebird sediments of Idaho.

Comparisons using venation of the wings and valves, number of ovules and shape and measurements of the pods and seeds were made with herbarium specimens of extant taxa. The number of specimens examined appear in brackets following the scientific nomenclature.

Caesalpiniodeae: Crudia grahamiana Herendeen and Dilcher [2] was placed in the extant pantropical genus Crudia. Caesalpinia claibornensis Herendeen and Dilcher

[18] and C. flumen-viridensis Herendeen and Dilcher [2] were place in the extant C. subgenus Mezoneuron. This represents the only reliable fossils of this subgenus (Herendeen and Dilcher 1991). Legumes of Erythrophlem [4], Leguminosites phyllocarpoides [4], Acrocarpus [1], Caesalpinia [9], Senna [1], Gleditsia? mississippiensis [5] and Stemonocoleus / Aubrevillea [1] were also found.

Mimosoideae: Eliasofructus catahoulensis Herendeen and Dilcher [approx. 15] and E. claibornensis Herendeen and Dilcher [3] fossil legumes were reported for this subfamily.

Papilionoideae: Diplotropis claibornensis Herendeen and Dilcher [2] was placed in the extant tropical South American genus. Swartzia [5], Cladrastis [4], Ormosia [9] and Sophora [1] fossil legumes were also represented.

Fossils of Legume Inflorescences and Flowers: The Fabaceae is diverse in floral morphology. Inflorescences are commonly racemes of bisexual flowers (Tucker, 1987). Actinomorphic flowers are considered to be more primitive and the zygomorphic flowers are a derived state (Polhill et al., 1981). Most flowers are five-merous with an androecium consisting of ten (rarely five) stamens and a gynoecium with a single carpel. Fossil Mimosoideae inflorescences and flowers were found from the Middle Eocene Claiborne Formation (Crepet and Dilcher, 1977, 1986). Papilionoid fossil flowers do not appear in the fossil record until the

Paleocene (Crepet and Taylor, 1985).

Mimosoideae: Eomimosoidea plumosa, six separate fossil spicate inflorescences from the Claiborne Formation (Middle Eocene) had flowers alternately arranged with very short pedicels. The actinomorphic perianth consisted of a small calyx and a four-merous corolla. The androecium consisted of ten exerted stamens with two chambered anthers that dehisced longitudinally. Pollen was found in the anthers and on the stigmas of some flowers. Pollen grains were tricolpate with tectate, reticulate, baculate exine (Crepet and Dilcher, 1977). In situ evidence indicates that they remained in tetrahedral tetrads after dispersal. The gynoecium had one carpel with trichomes on the style and stigma. A comparison with extant taxa places these fossils in the Mimosoideae but as form genera.

Protomimosoideae: The compressed inflorescences (2) and flowers (49) studied came from the Paleocene-Eocene Buchanan, Puryear and Warman areas of western Tennessee (Crepet and Taylor 1986). The inflorescence was a raceme of small, actinomorphic bisexual flowers alternately arranged. The perianth consisted of a cup shaped calyx and a five merous corolla of valvate petals. Stamens were free. The superior ovary had one carpel with a short pubescent style. Fruits were pods. Pollen grains, shed in monads, were tricolporate with semi-tectate exine. Saggitate anthers, uneven stamen length and pollen were characters shared with

the Diamorphandra (Caesalpinioideae) group. This evidence, coupled with the characters showing the affinities that classify the fossils as Mimosoideae, suggest that the Mimosoideae were derived from the Caesalpinioideae (Crepet and Taylor 1986).

Papilionoideae: Crepet and Taylor (1985) show two zygomorphic papilionoid flowers from Paleocene-Eocene sediments. Although there were a few Caesalpinioideae species with papilionoid like flowers, they differ considerably in development and thus the position of the petals. In the Papilionoids, the standard is formed before the wing petals and is located outside of these petals while in the Caesalpiniodeae, the standard is formed with the wings and is located inside of these petals. The fossils had papilionoid flower morphology and were also the first zygomorphic flowers in the fossil record (Crepet and Taylor 1985). Extant papilionoid flowers also have sculptured wing petals with striations on the proximal areas (Stirton, 1981). One of the fossil flowers also had sculptured wing petals (Crepet and Taylor, 1985).

The significance of these fossil flowers is the implication of adaptations to a more specific pollinator. Bee pollination is closely associated with zygomorphic flowers and is also associated with papilionoid legumes (Arroyo, 1981). In addition, sculptured wing petals vary considerably (Stirton, 1981) and are thought to have evolved

to aid specific pollinators (ie. footholds, attractants, etc.). The fossils are the earliest evidence of bee pollination in legumes (Crepet and Taylor, 1985).

Legume Fossil Wood: Although there is more fossil wood assigned to the Fabaceae than to any other angiosperm family (Wheeler and Baas, 1992), there are few early fossil woods known. There are only 100 reliable records of dicot fossil wood from the Cretaceous and only 40 from the Paleocene (Wheeler and Baas, 1991, 1992). Most records are from the Late Tertiary and most of the work has been done on collections from North African or Indian localities (Wheeler and Baas, 1992).

The legumes have advanced wood structure in the sense of Bailey (Wheeler and Baas, 1992). Simple perforation plates on short vessel elements with alternate intervessel pits, homocellular rays or rays with few upright cells occurring in margins, abundant axial parenchyma frequently in a aliform-confluent arrangement and storied wood are present or frequently present.

Identification of fossil woods is problematic because parallelism and convergent evolution in wood anatomy have occurred in many plant families (Wheeler and Baas, 1992). Except for the Cercidae, and some groups of the Cassieae (Quirk and Miller, 1985) and Caesalpinieae, the legumes have vestured pitting which makes separation from other groups

possible. However, in fossils, vestured pitting is hard to detect. Deposition of secondary metabolites in heartwood and bacteria in pit membranes can look like vestured pits (Quirk and Miller, 1985). In addition, mineral deposits can be interpreted as vesturing in pits (Wheeler and Baas, 1992). Without the identification of vestured pits in fossils, it is hard to distinguish between different plant families and different legumes, especially those in archaic groups.

Early Fossil Record for Cercis, Ceratonia and Gleditsia: Evidence from the fossil record indicates that species of Cercis were scattered between North America, Armenia and Asia by the middle Oligocene. To date, fossils of Cercis are not known from the Eocene of Southeastern North America (Herendeen, 1992), but it has been reported from the Florisant Formation (MacIntyre, 1953) and the Creede flora (Axelrod, 1985) of the early Oligocene. Guo and Zhou (1992) report that although legumes from the Oligocene of China are rare, there are reliable fossils consisting of two Cercis fruit impressions from this epoch. Wood of C. blacki from the Quaternary and leaves and fruits of C. miochinensis from the Miocene have also been reported for China. Cercis miochinensis was reported in the Caucasus paleoflora from the Upper Cretaceous, and Dilijan, Armenia and the Meotic of Abkhazia from the Oligocene (in Shakryl, 1992). Tertiary-

aged leaf impressions of C. komarovii from the Sarmatian of Armenia were also listed.

The collection of Tertiary flora of Abkhazia has impressions of parapinnate leaves with three to four pairs of leaflets that are reported to be Ceratonia emarginata (in Sharkyl,1992). Sharkyl also reports that fossils of this species occur in the pliocene flora of Switzerland and the Sarmation of Hungary. The Pontic Kodor flora is the richest Pliocene flora of Eurasia (Sharkyl, 1992). Ceratonia emarginata is one of the dominant species in this flora. The fossil record for Ceratonia is meager, especially when compared to that of Cassia. This is to be expected as the Ceratoniinae is a ditypic subgenus without known contemporary kinship to other groups within the family (Irwin and Barneby, 1981).

Fossil Miocene aged wood of Gleditsia has been described from Montana (Prakash et al., 1962) and Japan (Watri, 1952). Most fossil leaflets of Gleditsia reported from the Miocene of China need to be reevaluated (Guo and Zhou, 1992). A new species, G. parajaponica based upon leaflets that are similar to those of extant G. japonica was described from the Xiananshan Formation (Miocene), Zhejiang Province (Guo and Zhou, 1992). Fossil leaflets of G. allemanica were reported from the Miocene , Switzerland (in Sherkly, 1992). This species is also known from fossils from the Pontic Kodor flora (Abkhazia, Pliocene), the

Caucasus (Miocene), and the Kustanai (Miocene)(Sherkly, 1992).

Due to the problems associated with the discontinuity of fossil formation through time, the difficulty of obtaining those that are formed and the ambiguities that arise in classification, a reliable fossil record of the Fabaceae is relatively sparse. Despite its sparseness, it does confirm many of the taxonomic assumptions that are based upon independently derived taxonomic relationships between extant taxa.

The center of origin for the legumes appears to be Africa, based upon the relict flora of Madagascar and the relative diversity of the family on the continent (Polhill, et al., 1981). The fossil record supports this contention and also indicates that the Mimosoideae and the Papilionoideae were derived from the Caesalpinioideae and were established by the Paleocene-Eocene border. All of the major lineages except for the Cercideae are known from the Eocene of the Mississippi Embayment (Herendeen et al., 1992).

The fossils of reproductive structures suggest the evolution of reproductive characteristics that are adaptive to faithful pollinators: pollen grains shed in permanent compound units (Crepet and Dilcher 1977) and zygomorphic flowers with petal sculpturing (Crepet and Taylor 1985). In the case of the papilionoid type flowers, early pollinators

would probably have been bees (Arroyo 1981, Crepet 1979, 1984). The earliest record of fossil bees comes from the Baltic amber which dates from either the Eocene or the Oligocene (Crepet, 1985).

The fossil record for wood supports much of the history of the Fabaceae except for the lack of early fossil wood specimens in the basal genera, Gleditsia, Gymnocladus, Cercis, Ceratonia and Zenia (Wheeler and Baas, 1992). Gleditsia from the Miocene has the earliest record of fossil wood for this group (Prakash et al., 1962).

It is not surprising that early fossil wood of Cercis was not found. The group lacks vestured pits (Quirk and Miller, 1985) and is therefore hard to distinguish from other wood that would have been present in the fossil record at that time (Wheeler and Baas, 1992; Herendeen et al, 1992). Wunderlin, Larsen and Larsen (1987) propose that the Cercideae originated in Africa during the Cretaceous and began to diversify and spread from the source of origin to South America and southern Eurasia during the Paleogene. It would seem that collections from these sites would probably be a better place to look for early wood fossils of the Cercideae than from those used by Wheeler and Baas. Most of the Cretaceous wood fossils reported in the Wheeler and Baas (1992) paper come from North America and those of the Paleocene from India or Africa.

Based primarily upon the lack of fossil evidence,

Herendeen (1990) and Herendeen, Crepet and Dilcher (1992) propose a reevaluation of the archaic genera of the legumes. They argue that Gleditsia, Gymnocladus and Cercis are unknown from Eocene or older deposits despite the fact that today they grow in habitats and climates suitable for preservation in the fossil record from middle latitudes. These genera do not appear until the Oligocene which is later than the appearance of other legumes in the fossil record.

Considerably more evidence than the present fossil record would be needed to justify a reevaluation of the archaic genera of the legumes. The missing genera may not have been present in areas of collection during the Eocene. Sites of collection could have been recovering from some kind of climatic or volcanic disturbance. The genera represented could have been part of a flora in a different stage of succession that did not include the missing genera. It is also possible that the collection sites were not of suitable habitat for the missing plants. Lack of fossil evidence does not mean that plants were not present. Used alone, the fossil record can not confirm the lack of primitiveness of the missing genera. Other criteria must be taken into consideration.

The number of species in a genus and distribution patterns resulting from the major periods of evolutionary radiation of the legumes should be included in

considerations of phylogenetic relationships. For example, declining climatic conditions (warmer and drier or colder and wetter climates (Axelrod, 1992)) accelerated during the last major period of legume radiation. Abrupt diversification into specific regions and proliferation of species in the same genera occurred. Large genera such as Bauhinia, Cassia and Acacia evolved during this phase (Polhill et al., 1981). The oldest primarily woody taxa could not compete with aggressive new taxa, especially those which were herbaceous. The new taxa colonized the newly formed habitats during declining conditions and many extinctions occurred among the old. Small numbers of species would thus be expected for a relict genus. All of the basal genera have fewer than 15 species. Gymnocladus (Cowan, 1981) and Ceratonia (Irwin and Barneby, 1981) are ditypic genera.

Relict genera from the first period of radiation that have survived have scattered distributions primarily in north temperate and subtropical regions (Polhill,et al., 1981). Cercis is the only genus in the Cercideae that is dispersed throughout the warm temperate northern hemisphere (Wunderlin et al., 1981, 1987). Gymnocladus and Gleditsia have similar distributions (Polhill and Vidal, 1981).

Species within a relict genus also closely resemble each other. Species of Gleditsia from China and Argentina, which probably have been separated for more than 60 million

years, are morphologically more alike than species of Astragalus growing at the same site (Polhill, et al., 1981).

Floral development is another consideration in the determination of primitive genera. In the legumes, Tucker (1987, 1991) has argued that unidirectional initiation of floral organs is a highly specialized state while helical initiation is more primitive. Helical initiation of the sepals occurs in Cercis canadensis (Tucker, 1987) and all floral organs are helically initiated in six species of Gleditsia (Tucker, 1991) and in Ceratonia siliqua (Tucker, 1992).

Tucker (1991) also considers variability in floral characters to be primitive in legumes. Gleditsia flowers were found to be variable in merosity (the number of floral parts), position of the sepal, and carpel cleft position. Variability in the flowers of Ceratonia siliqua was first reported by Thompson (1944, 1945). Tucker (1992) found that the variability occurred in the sexuality of individual flowers, type of inflorescence, number of organs per whorl, and carpel cleft position. Both genera have flowers that are radially symmetric and are usually functionally unisexual (Tucker, 1992). Graham and Barker (1981) found that the pollen of Ceratonia is variable. Leaves of Gleditsia vary between pinnate and bipinnate and Ceratonia also has variable leaves (Polhill, et al., 1981). The developmental evidence found led Tucker (1992) to

hypothesize "a parallel low level of diversification for these genera in their separate tribes, Cassieae (or Ceratonieae) and Caesalpinieae.".

Although Cercis has more advanced zygomorphic flowers, it is the only diploid (2n=14) in the Fabaceae (Goldblatt, 1981; Polhill, et al., 1981; Wunderlin et al., 1981, 1987). The lack of vestured pits in the wood anatomy of Cercis (Quirk and Miller, 1985) is also considered to be primitive. It is significant because vestured pits are also lacking in the Connaraceae and the Sapindaceae considered to be putative outgroups of the Fabaceae (Herendeen and Dilcher, 1992). Ceratonia (Quirk and Miller, 1985) and Gleditsia (Prakash et al., 1962) are reported to have vestured pits.

The current fossil record for the legumes during the Cretaceous and Paleocene, when archaic genera were presumably evolving and probably more abundant, is almost non-existent. It is possible that in the future the fossil record will include more legumes from this period/epoch. This coupled with more advanced studies on extant taxa may support a reevaluation of what is primitive in the legumes. Until then, present evidence in my opinion indicates that Cercis, Gleditsia and Ceratonia represent the most primitive genera of the Fabaceae.

CHAPTER II

ARCHITECTURE of CAULIFLORY in the GENUS *Cercis* (Fabaceae: Caesalpinioideae)

Abstract

Cercis is a genus with a geographically disjunct distribution in North America, southern Europe and eastern Asia. The architecture of cauliflory (flowering from the lower branch and trunk areas of woody plants) was examined in ten taxa, including nine of the 11 recognized species in the genus *Cercis*. In each taxon, a linear series of first order buds (distinguished as 1) was formed in the axils of vegetative leaves before shoot elongation ceased. The first order bud developed into either a vegetative shoot or more frequently into an inflorescence. Inflorescences matured and then abscised. Second order and higher order buds were produced in the axils of the basal bud scales of abscised inflorescences. In addition, vegetative shoots that were from first or higher order buds produced "first order buds" (distinguished as 1') in their leaf axils. Buds from the axils of the basal-most leaves of these vegetative shoots, together with higher order buds from the parent shoot, perpetuated the cauliflorous condition in all taxa studied. Since cauliflory was present and since the architecture of cauliflory was similar in all taxa studied, regardless of geographic distribution, cauliflory probably arose only once

in Cercis, before the genus radiated from its site of origin.

Introduction

Cercis, commonly known as redbud, is a small genus of six (Wunderlin et al. 1981, 1987) to eleven (Huang & Yang, 1985) recognized species. The genus is geographically disjunct in the north temperate hemisphere with taxa in eastern and western North America, in southern Europe and in eastern Asia. Cauliflory, defined here as flowering on lower branches and trunks of woody plants, is a characteristic of the genus Cercis (Wunderlin et al. 1987). The development of cauliflory has been described for the southern European species, C. siliquastrum (Thompson 1946), and the eastern North American taxon, C. canadensis subsp. canadensis (Owens & Ewers 1991).

The presence of cauliflory and the geographically disjunct distribution of the genus Cercis presents three questions addressed in the present study: First, does cauliflory occur throughout the genus Cercis, especially in those taxa from Asia whose cauliflory has not been studied? Second, is the architecture of cauliflory similar throughout the genus? Third, what evolutionary implications can be drawn about the presence of cauliflory and its similar architecture in this genus?

Owens and Ewers (1991) determined that cauliflorous

development in C. c. subsp. canadensis was the result of two types of reproductive buds: first order buds that arose from the leaf axil, and higher order buds that formed in the axils of the lowermost bud scales of an inflorescence (raceme) below the abscission zone of the inflorescence axis (Fig. 1). A linear series of up to ten first order buds were basipetally formed in the axil of a foliage leaf before stem elongation was completed. The distal-most buds (those farthest away from the leaf scar) at each node were the first to mature into inflorescences. The first order buds could develop into either vegetative shoots or inflorescences. Axis formation of vegetative shoots was sympodial. The distal-most buds from the distal-most nodes produced vegetative shoots which replaced the abscised vegetative shoot apex of the previous year (Fig. 1). The other, more proximal buds, sequentially matured into first order inflorescences over a three to five year period. The inflorescences abscised after maturation, leaving the stump of the inflorescence attached to the stem. Buds in the axils of basal bud scales of the abscised inflorescence developed into second order inflorescences. Second order inflorescences gave rise to third order inflorescences, third order inflorescences to fourth order, etc. (Fig. 1). To simplify terminology, inflorescence buds above the second order are referred to as higher order buds. Some of the buds in the linear series developed into vegetative

branches. These branches also produced their own linear series of buds in the axils of leaves. The buds that formed in the axils of the basal-most leaves (closest to the parent branch) of these vegetative branches contributed to the cauliflorous condition.

Thompson (1946) described the development of cauliflory in C. siliquastrum but failed to provide diagrams or micrographs. The development was similar to what we found for C. c. subsp. canadensis in the following respects: A linear series of from five to seven buds were formed basipetally in the axil of a vegetative leaf. The buds sequentially matured after at least a one year delay. After the one year delay, all but the distal-most nodes, which produced vegetative branches, produced first order inflorescences from the distal-most buds in each linear series. In the following years, second order buds formed on the inflorescence stumps of the first order buds. These bud-bearing stumps were future sources of flowering (Thompson 1946).

Because of the relatively small size of the genus Cercis and because several of the species are cultivated as ornamentals, we were able to study the architecture of cauliflory in most of the named taxa. We have sampled every species in this genus except for C. chuniana Metc. from China and C. orbiculata Greene (See Ballenger 1992 = C. occidentalis sensu auct.) from the intermountain range of

Arizona, Utah and Nevada.

Materials and Methods

Sample collection: Only live material was collected for this study as herbarium specimens rarely include areas of the lower branches or trunk. Ten different taxa were examined (Table 1). The nomenclature used for the North American group was dealt with according to Ballenger (1992) and the Eastern Asian group according to Raulston (1990). Cercis californica (= C. occidentalis sensu auct. (see Ballenger, 1992)), samples were collected from the Rancho Santa Ana (RSA) Botanic Garden (August, 1991) and those of C. c. subsp. canadensis were from the Michigan State University (MSU) campus (1986-1993). Samples of C. racemosa were obtained from the National Arboretum (NA), Washington, D.C. (March, 1993). Due to its susceptibility to a canker disease, C. racemosa lower branch or trunk samples were not obtainable. The remainder of the Cercis samples were observed and sampled from the North Carolina State University Arboretum (NCSUA) in March of 1989, in July of 1991, and in June of 1992 and 1993.

First order bud tissue was obtained from current year shoots. In most cases, the leaf subtending the linear series of first order buds was pulled off rather than cut to avoid cutting into the first order buds that formed beneath the pulvinus. Areas containing all of the second order and

Table 1. Geographic distribution, scientific name, collection site and number of nodes sampled for the study of the architecture of cauliflory in the genus Cercis.

Distribution	Scientific name	Collection Site[a]	Number of Node
North America Eastern:	C. canadensis L. subsp. canadensis	MSU	100
	C. canadensis L. subsp. mexicana(Rose) Murray	NCSUA	26
Western:	C. californica Torr. ex Benth.	RSA	70
Southern Europe	C. siliquastrum L.	NCSUA	84
Eastern Asia	C. chinensis Bunge.	NCSUA	83
	C. chingii Chun	NCSUA	41
	C. gigantea Cheng & Keng	NCSUA	26
	C. glabra Pamp.	NCSUA	18
	C. racemosa Oliv.	NA	46[b]
	C. yunnanensis Hu & Cheng	NCSUA	32

[a] MSU, Michigan State University; NA, National Arboretum, Washington, D.C.; NCSUA, North Carolina State University Arboretum; RSA, Rosa Santa Ana Botanical Garden.

[b] Nodes contained only first order buds

higher order buds from a node were cut from the branch or trunk areas with a razor blade. Before sampling, many nodes were observed on the intact plant using a hand lens. Representative samples of at least 18 nodes with either first order or higher order buds were collected for each taxon (Table 1). These samples were all observed with a dissecting microscope and subsampled for SEM observation. Voucher specimens were obtained and deposited in the MSU Beal-Darlington Herbarium (MSC) with continuous accession numbers 337645 to 337663.

Scanning electron microscopy (SEM): Samples studied were preserved in FAA or Allen-Bouin Type II Fixative (Berlyn & Miksche, 1976), dehydrated in graded series of ethanol, critical point dried using liquid CO_2 as the transitional fluid, mounted on aluminum stubs with adhesive tabs, sputter coated with gold and observed on a JEOL JSM-35CF SEM using an accelerating voltage of 10 keV. In some cases, large buds, axillary shoots and/or parts of the bud scales were removed to make the necessary observations.

Results

A linear series of first order buds was present in the axils of foliage leaves in all taxa of Cercis observed (Fig. 1). The distal-most buds (those farthest away from the leaf scar on the stem) in the series elongated during the year

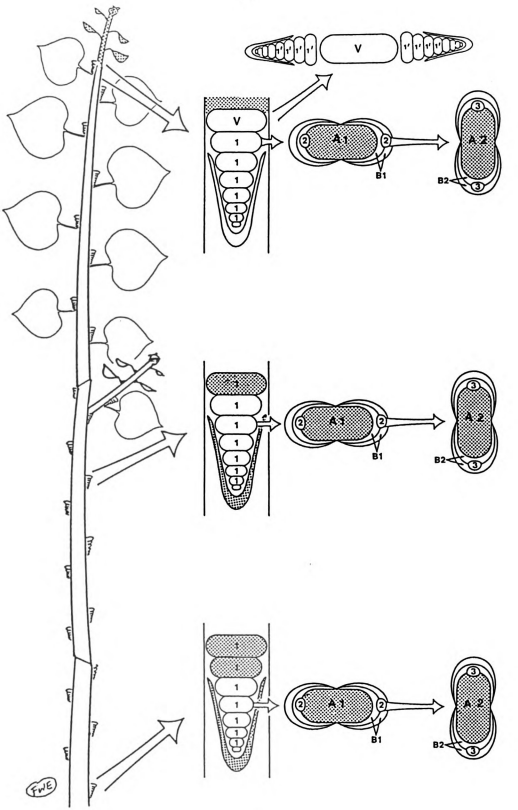
after they were produced, the remaining buds sequentially matured over several years. Although the first order buds can develop into either a vegetative or a reproductive shoot (Fig. 1), the majority became reproductive shoots.

Similarities in the linear series of first order buds from North American C. c. subsp. canadensis (Fig. 2), C. c. subsp. mexicana, (Fig. 3), and C. californica (Fig. 4) are shown. Comparable arrangements of first order buds are shown for C. siliquastrum (Fig. 5) which has a southern European distribution, and in the eastern Asian species, C. chinensis (Fig. 6), C. chingii (Fig. 7), C. gigantea (Fig. 8), C. glabra (Fig. 9), C. racemosa (Fig. 10), and C. yunnanensis (Fig. 11).

Similarities in the architecture of second and higher order axillary cauliflorous buds were observed in samples of all taxa (Figs. 12-29). In all taxa observed, first order inflorescences matured, abscised and formed second order buds in the axils of their basal bud scales (Fig. 1). Second order buds abscised and produced third order buds in the axils of their basal bud scales, fourth order buds arose from bud scales of abscised third order buds and so forth. Often times second order and higher order buds from the same node were at different stages of development (Figs. 13, 16, 17, 19, 21, 24, 25, 28).

Second and higher order buds are shown for representative Cercis samples from North American (Figs. 12-

Fig. 1. Schematic summary of a sympodial branch of Cercis canadensis subsp. canadensis in the summer showing current year (upper), previous year (middle) and two-year old stem segments (lower) and the architecture of the axillary buds present in representative nodes. The figure is not drawn to scale; many of the buds on the main axis would not be visible to the naked eye. The number of first order buds per node is variable. The two lines across the branch axis represent the pseudoterminal bud scale scars that divide the differently aged stem segments. Shaded areas represent organs that will abscise or have already abscised. First order buds (1) form in a linear series in the axils of foliage leaves and sequentially mature over a several year period. A partial sequence of maturing buds in representative nodes is represented by the three groups of illustrations found at the right hand side of the figure. The first order buds can follow either a vegetative or a reproductive pathway. The distal most buds on the distal most shoots are vegetative (V) and develop into vegetative shoots. These first order vegetative shoots have 'first order buds' (1') in the axils of their foliage leaves, including the basal-most leaves. Most of the remaining buds in the linear series (1) become reproductive buds that flower once and abscise (A1). In the axils of their 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 initiation of even higher order buds can continue indefinitely. Modified from Owens and Ewers (1991).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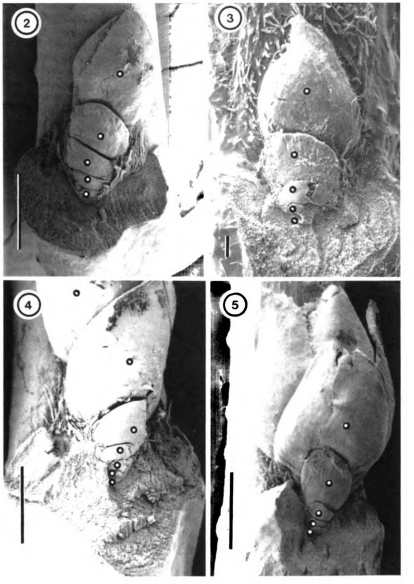
Abbreviations used for all Figures: A, abscised inflorescence scar; AF, abscised flower scar; * or B, bud scale; H, higher order bud; H', higher order bud present in the basal bud scales of an non-abscised higher order bud; LS, leaf scar; VS, vegetative shoot; . or 1, first order bud; 1', first order bud from a non distal-most vegetative shoot; 2, second order bud. Figures 2-28 are oriented such that the leaf scar would be at the bottom for each micrograph.

Figs. 2-5. First order buds (indicated by dots) in a linear series formed in the axil of a vegetative leaf in taxa of Cercis indigenous to North American, Mexico, southern Europe or the Middle East (SEM micrographs). Bar = 1000 μm unless otherwise indicated. The leaf was removed to reveal the first order buds beneath. The leaf scar is at the bottom of all the micrographs. Fig. 2. Five first order buds in C. c. subsp. canadensis. Fig. 3. Five first order buds in C. c. subsp. mexicana. The basal-most dot is positioned to the side of the bud. Bar = 100 μm. Fig. 4. Seven first order buds in C. californica. Fig. 5. Five first order buds in C. siliquastrum. The basal-most dot is positioned to the side of the bud.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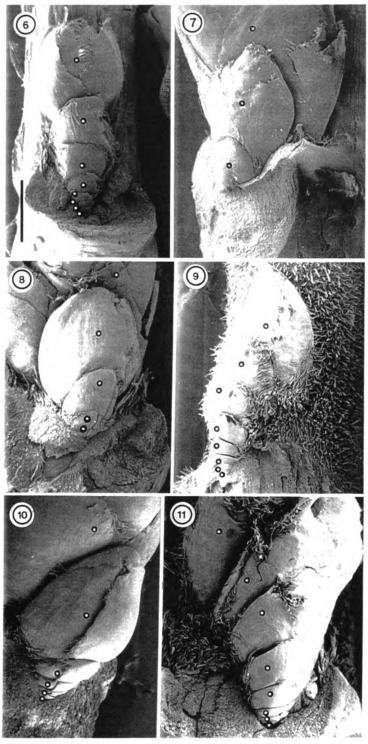
Figs. 6-11. First order buds (indicated by dots) in a linear series formed in the axil of a vegetative leaf in species of Cercis indigenous to China (SEM micrographs). Bar = 1000 μm for all Figs. Due to differences in bud size, only part of the distal-most first order bud is shown in Figs. 7, 8, 10 and 11. Fig. 6. Eight first order buds in C. chinensis. Dots indicating basal first order buds are positioned to the side of the bud. Fig. 7. Three first order buds in C. chingii. Fig. 8. Five first order buds in C. gigantea. Fig. 9. Eight first order buds in C. glabra. Fig. 10. Six first order buds in C. racemosa. Fig. 11. Eight first order buds in C. yunnanensis.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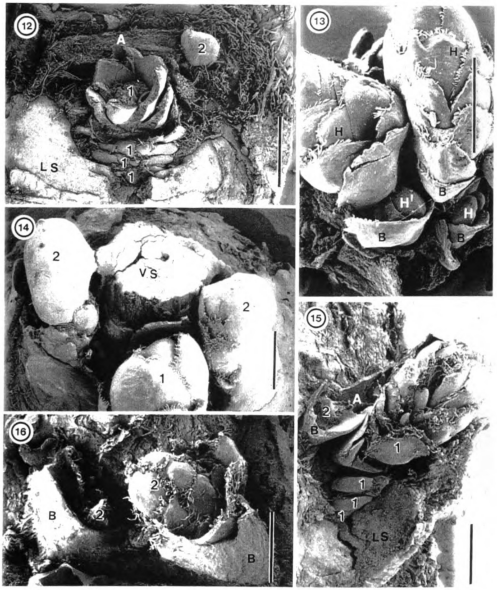
16). A second order bud in C. c. subsp. canadensis was observed in the axil of a basal bud scale of an abscised first order inflorescence (Fig. 12). An elongating first order bud was removed for this figure. In C. c. subsp. canadensis, two elongated higher order buds (H order) in a late stage of development and one (H order) in an early stage of development were produced in the axils of basal bud scales of three abscised higher order inflorescences (Fig. 13). One of the elongating higher order inflorescences has an even higher order bud (distinguished as H'order) present in its basal bud scale (Fig. 13). A linear series consisting of a first order bud, two second order buds and a vegetative shoot were observed in a sample from C. c. subsp. mexicana (Fig. 14). A linear series of first order buds from a sample of C. californica showed a second order bud in the axil of a bud scale of the abscised distal-most inflorescence (Fig. 15). Proximal to the abscised inflorescence was an elongated first order inflorescence bud above three resting first order buds. The leaf scar was dissected from one half of the sample to reveal the three buds. Two second order buds were present in the bud scale axils of an abscised first order inflorescence from a different sample of C. californica (Fig. 16).

The architecture of second order and higher order buds from representative Cercis samples from southern Europe (Figs. 17,18) and eastern Asia (Figs. 19-29) was similar in

Figs. 12-16. Second or higher order buds in samples of North American Cercis (SEM micrographs). Bar = 1000 μm for all Figs. Fig. 12. Second order buds of C. c. subsp. canadensis produced in the axils of bud scales of an abscised inflorescence. The distal-most of the remaining four first order buds was removed for this figure. Collected July, 1994. Fig. 13. Higher order buds were often in different stages of development. In C. c. subsp. canadensis, two higher order buds (H order) in late stages of development and one (H order) in an early stage were produced in the basal bud scales of three abscised inflorescences. One of the elongating higher order buds had a higher order bud (H′ order) forming in its basal bud scales. Collected August, 1989. Fig. 14. Second order buds in C. c. subsp. mexicana. Note the vegetative shoot and the proximal-most first order bud. Fig. 15. An entire linear series of buds in a sample of C. californica shows a second order bud and four first order buds. A second order bud was produced in the axil of a bud scale of the abscised distal-most inflorescence. The leaf scar was dissected longitudinally from half of the sample to reveal the three first order buds beneath. These three buds are beneath a first order bud that was elongating. Collected August, 1991. Fig 16. In a different sample of the same taxon, two second order buds were produced in the bud scales of an abscised first order inflorescence. To facilitate this observation, the leaf scar was positioned towards the top of the micrograph.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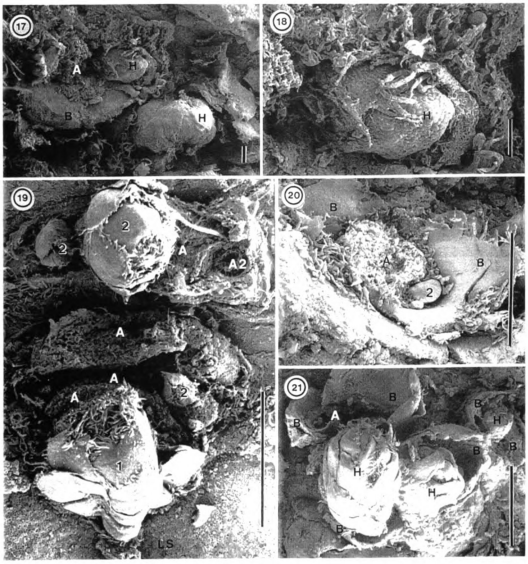
Figs. 17-21. Second order and higher order buds from samples of C. siliquastrum, indigenous to southern Europe and C. chinensis, indigenous to China (SEM micrographs). Bar = 1000 um unless otherwise indicated. Fig. 17. In C. siliquastrum, two higher order buds in the bud scales of an abscised inflorescence. Bar = 100 μm. Fig. 18. Higher magnification of the upper higher order bud shown in Fig 17. Bar = 100 μm. Fig. 19. In C. chinensis, three second order buds formed in the bud scales of four abscised inflorescences while the last first order bud was maturing. Note the abscised second order inflorescence scar (A2). Collected August, 1992. Fig. 20. A second order bud of the same species was produced in the axil of a bud scale of an abscised inflorescence. Collected July, 1992. Fig. 21. In the same species, two higher order buds formed in the basal bud scales of an abscised inflorescence. Another higher order bud was produced in the axil of another bud scale.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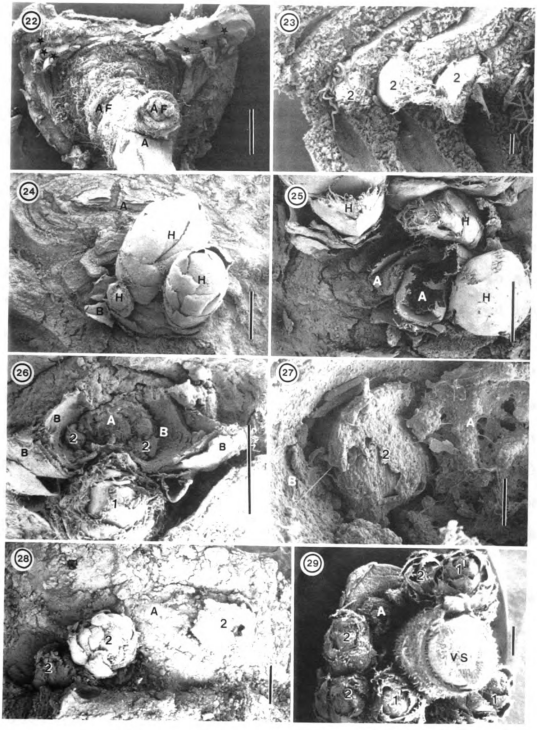
each case to that found in North American taxa. Higher order buds were observed in the axils of bud scales of abscised inflorescences in C. siliquastrum (Figs. 17, 18). A linear series of four abscised first order buds in a sample of C. chinensis was observed with three second order buds developing in the axils of basal bud scales of two of the abscised inflorescences (Fig. 19). The fifth first order bud in the series was still maturing and the second order buds are at different stages of development. In another sample from this taxon, a second order bud was observed in the axil of a basal bud scale of a dissected first order bud that was elongating (Fig. 20). Two higher order buds developed in the axils of a pair of bud scales from a single abscised inflorescence in a sample of C. chinensis (Fig. 21). In C. chingii, three second order buds have been produced on each side of an inflorescence axis that contained fruits were observed (Fig. 22, 23). Observations of samples of C. chingii showed higher order buds with different stages of development within the same node (Fig. 24, 25). Higher order buds were often flattened out due to crowding as illustrated in a sample of C. Chingii (Fig. 25). Two second order buds were present in the axils of basal scales of an abscised inflorescence of C. glabra (Fig. 26). A higher magnification of one of the second order buds from the same sample showed the position of the second order bud scales to be perpendicular to those of the

Figs. 22-29. Second order and higher order buds in four species of Cercis indigenous to China (SEM micrographs). Bar = 1000 μm unless otherwise indicated. Fig. 22. In this sample from C. chingii, three second order buds in the axils of basal bud scales (indicated by *) were observed on each side of an inflorescence axis that had produced a fruit. Fig. 23. Three of these buds at a higher magnification showing their position in relation to the basal bud scales of the inflorescence. Bar = 100 μm. Fig. 24. Higher order buds were produced in the axils of bud scales in this sample of C. chingii. There were two different stages of bud elongation in this grouping. Fig. 25. Another sample of the same species shows three higher order buds. The middle higher order bud was flattened due to crowding. Fig. 26. Two second order buds were found in the axils of the basal bud scales of an abscised C. glabra inflorescence while the last first order bud in the linear series was elongating. Fig. 27. A higher magnification of one of the second order buds showed the position of the bud scales to be perpendicular to those of the first order bud. Bar = 100 μm. Fig. 28. Three second order buds were produced in the basal bud scales of two abscised C. gigantea inflorescences. Fig. 29. Two second order buds formed in the axils of a pair of basal bud scales of an abscised inflorescence of C. yunnanensis. Another second order bud, a first order bud and a vegetative shoot were also formed at this node. Notice the first order buds (1′) produced on the vegetative shoot.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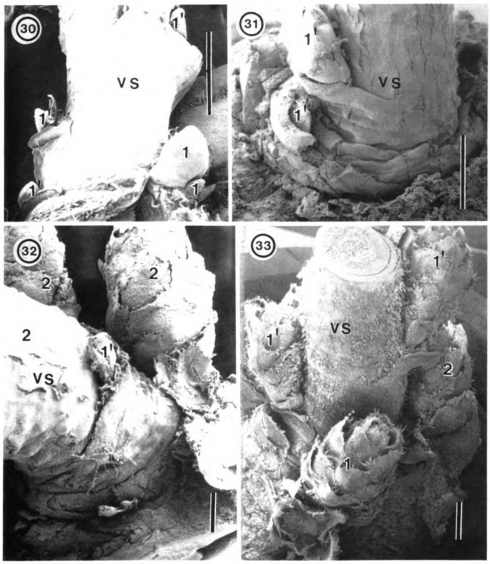
first order bud (Fig. 27). Three second order buds were observed in the region of two abscised inflorescences of C. gigantea (Fig. 28). A sample of C. yunnanensis showed two second order buds each in the axil of a basal bud scale of an abscised inflorescence (Fig. 29). Another second order bud adjacent to a vegetative shoot can also be seen.

In all taxa observed, branching of vegetative shoots was sympodial, with the terminal shoot apex abscising every year and the distal-most axillary buds of the distal-most nodes becoming vegetative shoots (Fig. 1). Also, in all taxa observed, some of the non-distal buds developed into vegetative shoots (Fig. 14, 29-33). First order buds (distinguished as 1′ order) from these vegetative shoots formed in the axils of the basal leaves, close to the parent branch, as well as in the axils of all other leaves on the shoot. The 1′ order buds normally developed into floral buds which had the potential to produce second and higher order buds, and could thus contribute to the cauliflorous condition.

The basal-most 1′ order axillary buds on vegetative shoots contributed to the cauliflorous condition in all taxa studied. A few examples from representative taxon are shown in Figures 29-33. Part of a linear series from C. c. subsp. canadensis showed a small vegetative shoot with two of its basal-most first order buds (1′order) and the remaining two

Figs. 30-33. The basal-most first order buds that formed in the axils of leaves on vegetative shoots of representative taxa of Cercis (SEM micrographs). Bar = 1000 μm for all Figs. Fig. 30. A small vegetative shoot with two basal axillary first order buds (1′) in C. c. subsp. canadensis. The two subtending first order buds (1) were from the same linear series as the vegetative shoot. Fig. 31. Two first order buds formed, each in the axil of a leaf, at the base of a C. chingii vegetative shoot. Fig. 32. A first order axillary bud formed at the base of a vegetative shoot on C. gigantea. Fig. 33. On C. yunnanensis, a vegetative shoot produced by a first order bud also produced first order buds (1′) in the axils of its leaves. The bud at the base of the micrograph was a first order bud from the parent shoot. One of the two second order buds observed elongating behind the vegetative shoot in Fig 29 was also visible. Figures 29 and 33 were from the same node observed from different positions.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first order buds (1 order) of the parent shoot (Fig. 30). Similarly, first order buds (1'0 were observed at the basal nodes of C. chingii (Fig. 31), C. gigantea (Fig. 32), and C. yunnanensis (Figs. 29, 33).

Discussion

Observations indicate that cauliflory is present and its architecture is similar in all Cercis taxa studied. Our study of cauliflory in C. siliquastrum also supports the observations made by Thompson for that species (1946). In all of the taxa we examined, a characteristic linear series of first order buds formed basipetally in the axil of a foliage leaf. Although not addressed in this study, the number and size of the buds appeared to vary between taxa. Each first order reproductive bud flowered only once, but second or higher order buds were produced, each in the axil of a basal bud scale of the inflorescence, located beneath the abscission zone of the inflorescence axis. Cauliflorous buds thus formed in the axillary position in all cases. Cauliflory was also perpetuated by first order buds (1') produced in the leaf axils at the base of vegetative shoots. These shoots often abscise but the abscission zone is above the basal-most nodes og the vegetative branch.

In the genus Cercis, all of the cauliflorous buds, first order, second order and higher order, arise in the axils of leaves or bracts. Axillary buds thus follow the normal phyllotaxy of the plant. Other descriptions of

axillary cauliflory have been published for the Fabaceae family, C. siliquastrum (Thompson 1946) and Swartzia pinnata (Thompson 1951); the Apocynaceae family, Pleiocarpa mutica (thompson 1949); and the Sterculiaceae family, Theobroma cacao (Lent 1966).

In some genera, cauliflorous buds can also arise from adventitious positions. These are buds that arise 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). Adventitious cauliflory has been described for the Fabaceae family, S. shomburgkii (Papilionoideae) (Fink 1983); the Moraceae family Ficus glomerata, F. pomifera (Pundir 1972, 1975), and Artocarpus integrifolia (Fink 1983); and the Lecythidaceae family, Couroupita guianensis (Thompson 1952; Fink 1983)

In some taxa, the mode of origin of cauliflorous buds can differ either with the age of the tree or with the age of the parent branch within a tree. In young trees of F. glomerata, inflorescences develop in the axillary position, but as the tree matures, inflorescences are reportedly produced adventitiously (Pundir 1972). Inflorescences of Ceratonia siliqua (Fabaceae) (Thompson 1944) and S. shomburgkii (Fink 1983) are produced in an axillary position on young shoots but in an adventitious position on older branches and trunks of the same tree. We did not find occurrences of adventitious cauliflory in the genus Cercis.

occurrences of adventitious cauliflory in the genus Cercis.

Although cauliflorous buds in Cercis can mature at different times on the same node, those that actually flower the following spring do so synchronously. In contrast, inflorescences of T. cacao flower first on the trunk and sequentially flower, node by node, in an acropetal manner up to the one-year-old stems (Lent, 1966). For a detailed account of types of cauliflory in the Angiosperms and a survey of West African plants exhibiting this characteristic see Mildbraed (1922).

Multiple first order axillary buds were produced in all taxa of Cercis studied. Multiple buds are not unusual for cauliflorous plants. They can form a linear (vertical) series when buds form directly below the preceding bud (Thompson 1946, 1949, 1951) or in a collateral (horizontal) series when buds form lateral to a principle bud (Thompson 1944; Lent 1966). Of the cauliflorous legumes studied, species of Cercis, Ceratonia and Swartzia all produce a linear series of first order buds in the axils of leaves (Owens & Ewers 1991; Thompson 1946, 1949, 1951). This arrangement also occurs in P. mutica, a member of the Apocynaceae family (Thompson, 1949). Axillary collateral buds have been described for T. cacao (Lent 1966). Multiple buds probably occur in many non-cauliflorous plants but the presence of multiple buds are rarely included in plants descriptions.

A recent revision of the North American species of Cercis, divided taxa into an eastern complex, consisting of one species and two subspecies, and a western complex, consisting of two species and one subspecies (see Ballenger 1992). Cercis c. subsp. canadensis is distributed throughout the eastern United States and southward into the mesic regions of Mexico. The two subspecies in the eastern complex are found in arid regions of Texas, Oklahoma or Mexico. Taxa of the western complex are located in specific regions of the Laguna and Sierra Nevada Mountains in California or the intermountain regions of Arizona, Nevada and Utah (Ballenger, 1992).

Cercis siliquastrum is distributed throughout southern and central Europe, Turkey, western Syria, Lebanon, Palestine and western Iran. Two subspecies, C. s. subsp. siliquastrum and C. s. subsp. hebecarpa, have sometimes been recognized (in Chamberlain & Yaltirik 1970).

Classification of Asian species of Cercis is controversial. Li (1944) recognized five species of Cercis from Eastern Asia; C. racemosa, C. chuiana, C. chinensis, C. chingii and C. pauciflora. Huang & Yang (1985) recognized the five species above as well as C. yunnanensis and C. gigantea. Only C. chinensis occurs (usually in cultivation) throughout the temperate regions of China. The other eastern Asian taxa are more restricted in their distribution (Li 1944; Huang & Yang 1985). Since most of our samples of

Asian species came from the North Carolina State University Arboretum, classification follows the treatment given to them by Raulston (1990) as indicated in Table 1.

Cercis is the only genus in the Fabaceae which has retained the basic chromosome number (x = 7) and is believed to be one of the basal groups of the legume family (Polhill et al. 1981). Cercis probably originated in the Mediterranean region during the Paleogene and then spread to Asia and North America (Wunderlin et al. 1987). Evidence from the fossil record indicates that by the middle Oligocene species of Cercis were scattered between western North America (MacGinitie 1953; Manchester & Meyer 1987; in Axelrod 1992), Armenia (in Shakryl 1992) and eastern Asia (in Guo & Zhou 1992).

Since all taxa of Cercis studied, regardless of geographic distribution, exhibited cauliflory and since the architecture of cauliflory was similar for each taxon, cauliflory probably evolved only once in this genus, and that once must have been before the Oligocene, that is, before the geographic radiation of the genus from its site of origin.

Cercis is a member of the Cercideae tribe and its success in temperate regions is the exception within this primarily tropical group. Features of the leaves and seeds suggest that the Cercideae was "an early offshoot" of Caesalpinioideae (Wunderlin et al. 1981, 1987). Within the

for Adenolobus, a south-west African genus with two species (Wunderlin et al. 1987). A study of the cauliflorous architecture in this genus would contribute to our understanding of the evolution of cauliflory in this lineage.

Within the Caesalpinioideae, there are three reported groups of archaic woody genera; Cercis, Gleditsia-Gymnocladus, and Ceratonia-Zenia (Polhill et al. 1981; Dickison 1981; Cowan 1981). Due to extinctions, there are no known living links between these three groups. Interestingly, some type of cauliflory has been reported for Cercis (Thompson 1946; Owens & Ewers 1991), Gleditsia (Paclt 1984) and Ceratonia (Thompson 1944). Whether cauliflory evolved independently in these basal groups of the Caesalpinioideae, or just once, awaits further studies.

CHAPTER III

EXPERIMENTALLY INDUCED CHANGES IN BUD FATES IN *Cercis canadensis* (Fabaceae)

Abstract

Stems of *Cercis canadensis* were pruned to three differently aged segments at three different times during the summer of 1992 to determine the effects of treatment on bud fates (vegetative or reproductive). In addition, the development of vegetative and reproductive buds was microscopically examined on untreated stems. In *Cercis*, multiple axillary buds are produced in a linear series at each node. The distal most buds on the distal most nodes become vegetative and the remaining buds sequentially mature into reproductive buds over a 1 to 5 year period. Microscopic buds elongate and become macroscopic in the summer prior to maturing the next spring. The number of inflorescences that elongated in 1992 was not affected by the pruning treatment but of those, the number of inflorescences that aborted in 1993 increased with the number of nodes pruned. Deeper pruning thus reduced the number of mature inflorescences per node. Some buds that would have normally developed into reproductive shoots became vegetative shoots after stems were pruned. Microscopic observations of buds from non-treated stems indicated that in all of the buds, initial leaf primordia had an orthodistichous phyllotaxy but in those buds that

become inflorescences, the phyllotaxy changed to helical during floral initiation. Although a reversal in eventual bud fate occurred in pruned stems, phyllotaxy suggested that the buds are initiated in the vegetative state and therefore a reversion from the floral to the vegetative state did not occur. Intermediate shoots produced on some experimental stems developed four foliage leaves instead of four bracteose leaves but the flowers on the inflorescence appeared normal.

Introduction

Once the flowering process begins, it is usually irreversible, but in some plants, reversions, in which vegetative growth interrupts the flowering process, can occur. Reversion of flowering can be a flower reversion where the flower meristem resumes the production of foliage leaves or an inflorescence reversion where the inflorescence meristem changes from initiating flowers in the axils of floral bracts to initiating vegetative branches in the axils of leaves (Battey and Lyndon, 1990). Reproductive meristems become more fixed as the flowering process proceeds and reversions to the vegetative state generally occur in meristems that are in early stages of transition (Steeves and Sussex, 1989).

Most of the reported reversions in the literature were brought about by the reversal of environmental conditions,

such as day length and temperature, from conditions favorable to flowering to conditions that are unfavorable to flowering (see Battey and Lyndon, 1990 for a review). Herbaceous plants were generally studied since reversions are rare in woody plants, where the flowering process is in many cases complicated by dormancy requirements and where manipulations of environmental conditions that induce reversions are more difficult to control.

Preliminary observations indicated that if a shoot of an adult eastern redbud tree, Cercis canadensis (Fabaceae), was damaged or pruned, axillary buds that would have normally become inflorescences became vegetative shoots. An inflorescence reversion was therefore expected in Cercis for some of the reproductive buds after release from the influences of the shoot apex. To determine whether an inflorescence reversion occurred in this taxon, factors such as the morphological state of the multiple buds at initiation (are they initiated as vegetative, reproductive or undifferentiated meristematic tissue?) and differences between vegetative and reproductive buds were examined.

At each node in Cercis, there are up to ten axillary first order buds in a linear series that begin to sequentially mature over a one-to-five year period (Owens and Ewers, 1990). Microscopic buds elongate to become macroscopic in the summer prior to their maturation the next spring. When the first order buds in the linear series

mature, they produce second order buds (not examined in the present study) in the axils of their bracteose leaves. Following terminology used for Cercis siliquastrum (Weberling, 1989), bracteose leaves will be used for the scale leaf structures initiated after the prophylls on the lower part of the inflorescence axis. The first order buds at each node mature in a basipetal manner (toward the leaf scar). Cercis is unusual in that each linear series (after the first year) produces at least one maturing bud a year and the majority of these buds develop over time into raceme inflorescences (Owens and Ewers, 1990).

Floral evocation is distinguished by several universal morphological events, one of which is a change in phyllotaxy (Bernier et al., 1981). Prior to floral initiation the reproductive meristems in C. canadensis reportedly do not differ in size, shape or organization from vegetative meristems, but when floral initiation begins, the reproductive apex becomes flatter and wider (Worthington, 1961). The inflorescence of Cercis is reported to have a helical phyllotaxy (Worthington, 1961; Tucker, 1987) and the vegetative bud, an orthodistichous phyllotaxy (Owens and Ewers, 1990).

Lateral bud outgrowth is thought to be regulated by dominance and by competition from leaves and stems for hormones and nutrients (Leakey and Longman, 1986; Bangerth, 1989; Cline, 1991). The degree of inhibition of lateral buds

in some plants is relative to the position of the bud on the stem (Brown et al., 1967; Zamski et al., 1985; Suzuki et al., 1988; Harmer, 1991). Current shoot growth in which the apical meristem is active and the axillary buds below are inhibited is known as apical dominance or correlative inhibition of buds (Wareing and Phillips, 1970). The inhibition is a type of physiological dormancy which originates within the plant but not within the dormant organ itself (Romberger, 1963).

Correlative inhibition is more complex in woody plants than in herbaceous plants. In woody plants, in addition to the shoot apex and young leaves, adjacent stems (Suzuki, 1990a), mature leaves (Reece, et al, 1946; Romberger, 1963; Mullins, 1967; Tinklin and Schwabe, 1969; Leakey and Longman, 1986; Suzuki, 1990a), and bud scales (Tinklin and Schwabe, 1969) have been reported to inhibit the outgrowth of lateral buds. Apical control, which allows outgrowth but inhibits the relative rates of elongation of previous year branches by younger, more apical shoots, applies strictly to woody plants (Brown et al., 1967; Zimmerman and Brown, 1971).

The growth of an axillary bud on a current year stem in a perennial plant can be either sylleptic, which is an axillary bud that grows simultaneously with the bud that produced it, or proleptic which is an axillary bud that requires a period of dormancy before it grows (Tomlinson,

1978; Leakey and Longman, 1986). Proleptic buds are associated with strong apical dominance (Brown et al., 1967). Strong apical dominance is expected in Cercis since all of the axillary buds are proleptic and wait at least one year after their initiation to mature. If strong apical dominance is associated with proleptic buds, release from apical dominance could result in buds maturing on current year stem segments (sylleptic buds) in Cercis.

Floral initiation is also reported to be regulated by correlative influences, such as dominance and competition, with other plant organs for growth regulators and nutrients (Reece, et al, 1946; Bernier et al., 1981; Zamski et al., 1985). Bud fates are often determined by the position of a bud along the stem (Goldschmidt and Monselise, 1972; Zamski et al., 1985: McDaniel et al., 1987). The fate of a first order bud in Cercis is to become either a vegetative shoot or an inflorescence. In normal stems, vegetative branches can arise only from the first to fourth distal-most nodes of the current year's growth and only from the first and second distal-most buds in the linear series at these nodes (Owens and Ewers 1990; Owens et al., 1995).

In the present study, Cercis stems were pruned back to three differently aged segments and buds were then counted to quantify the influence of decapitation on bud fates of current year, previous year and two-year-old stem segments in this taxon. Microscopic observations on non-treated

shoots were used in conjunction with experimental data to address the following questions; does a phyllotactic change occur prior to floral evocation in this woody plant or are reproductive buds initiated with a helical phyllotaxy 2) can buds that would normally differentiate into reproductive buds become vegetative and if so, 3) does a reversal from a reproductive to a vegetative shoot occur, 4) is there a period of time during the growing season (June, July and August) when the commitment to a reproductive structure is irreversible and 5) do the changes in bud fate vary with their distance from the main apex and leaves?

Materials and Methods

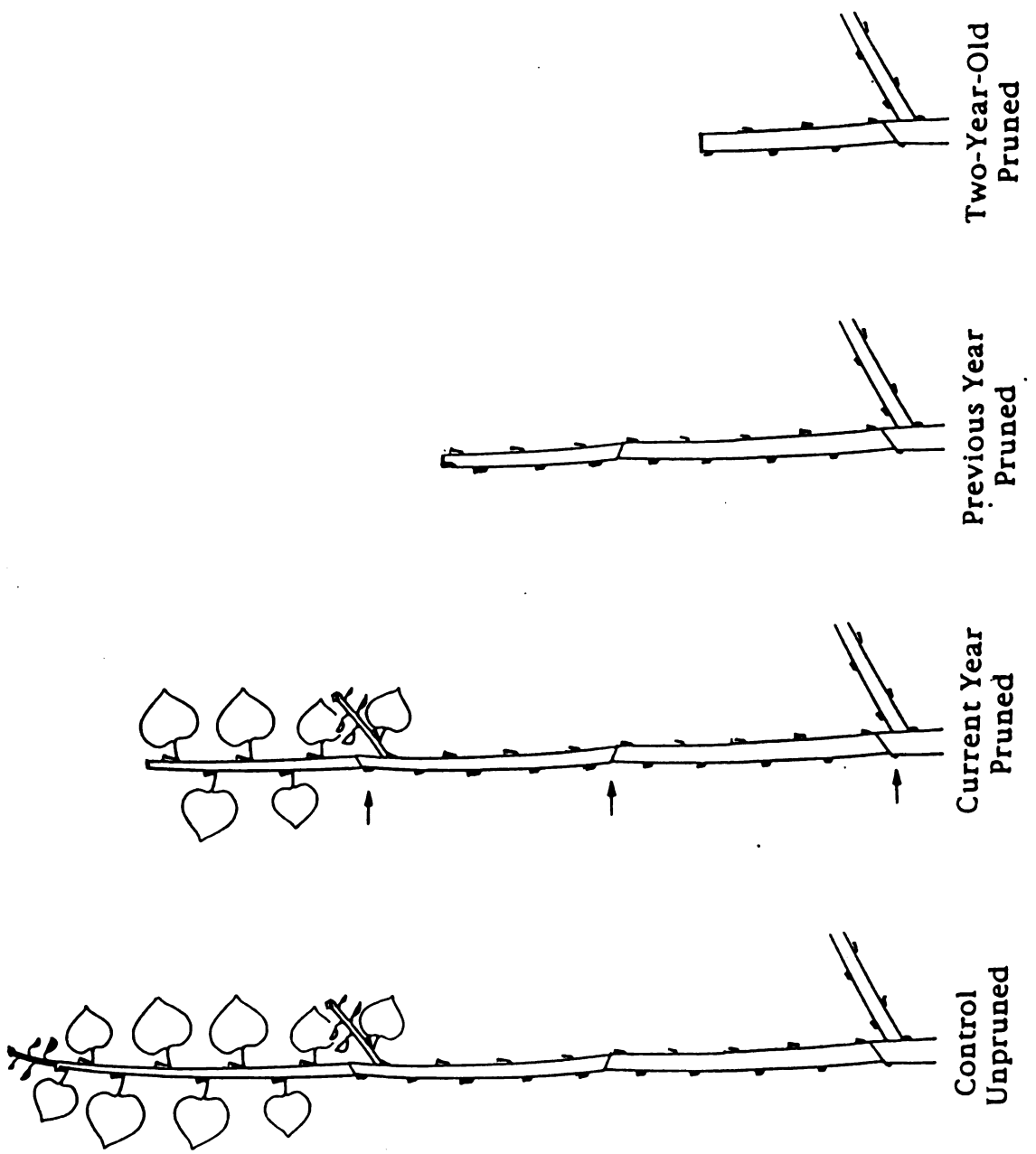
Light Microscopy: Samples of first order buds of C.canadensis were collected from trees located on the Michigan State University (MSU) campus from 1989-1995 and fixed in FAA (formalin-aceto-alcohol), dehydrated in a graduated TBA (t-butyl alcohol) series, embedded in paraffin and sectioned at 8 or 15 μm. The serial sections were stained with safranin O and fast green (Johansen 1940). Brightfield images were obtained on a Zeiss 10 Laser Scanning Confocal Microscope using a monochromatic (633 nm) laser.

SEM: Samples of first order buds of C.canadensis were collected from trees located on the Michigan State

University (MSU) campus from 1992-1995, fixed in either FAA (formalin-aceto-alcohol) or 4% glutaraldehyde in a 0.1 M sodium phosphate buffer (Ph = 7.0).dehydrated in graduated concentrations of ethanol, critical point dried in CO_2, sputter coated with gold and imaged using either a JEOL JSM-35CF or a JEOL JSM-6400V SEM (10 kV of accelerating voltage).

Statistical design: In June, 1992, five C. c. subsp. canadensis trees (individuals), each about 7 m in height and 7 m in crown width, growing on the Michigan State University campus, were arbitrarily selected. For each tree, two limbs (replications), each with four similar branches, were then selected for treatment. To avoid bias, the four different treatments were assigned using a random number table (Brower et al, 1990). Treatments consisted of 1) not pruning the branch, 2) pruning off half of the current year segment (determined by the number of nodes) and pruning off the entire stem segment distal to the first 4 nodes of 3) a previous year segment and 4) a two-year-old segment (Fig 34). The pruning treatment on previous year and two-year-old stem segments often resulted in the removal of axillary branches formed in previous seasons, since the distal and not proximal nodes in a segment produced all of the vegetative branches in undamaged stems. Stems were labeled (treatments and date of treatment) to allow for monitoring.

Fig. 34. Schematic illustration of the method of pruning done to four of the stems on each experimental branch of Cercis canadensis during the summer of 1992. Treatments consisted of not pruning the branch, pruning off half of the current year segment and pruning off the entire stem segment distal to the fourth node of both a previous year segment and two-year-old segment. The stippled shoot tip in the control normally abscised in this sympodial shoot system. Arrows indicate pseudoterminal bud scale scars. The linear series of first order buds are axillary, in fact, much smaller than shown, with most being microscopic in scale.


Control
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Two-Year-Old
Pruned

The treatments described above were repeated on different branches of the same tree at three different times during the growing season: June 9, July 14, and August 25, 1992. Thus a total of 24 stem segments per tree were monitored. Macroscopic buds were counted every month during the summer and fall of 1992 and again on the same branches in spring and summer of 1993. All buds and shoots that formed on the stem segment between the pruned cut and the psedoterminal bud scale scar located below were counted (Fig. 34).

Since the number of nodes per stem segment varied, inflorescence data was transformed to inflorescences per node. Inflorescences were not produced at the distal-most nodes of unpruned current year stem segments. Therefore, nodes with only macroscopic vegetative buds and lacking macroscopic inflorescences were omitted from the inflorescence per node transformations. Treatment, time of treatment and tree were the fixed independent variables. Dependent variables were the number of vegetative structures present in 1992 and 1993, inflorescences per node in 1992, and the number of inflorescences per node that matured in 1993.

Results

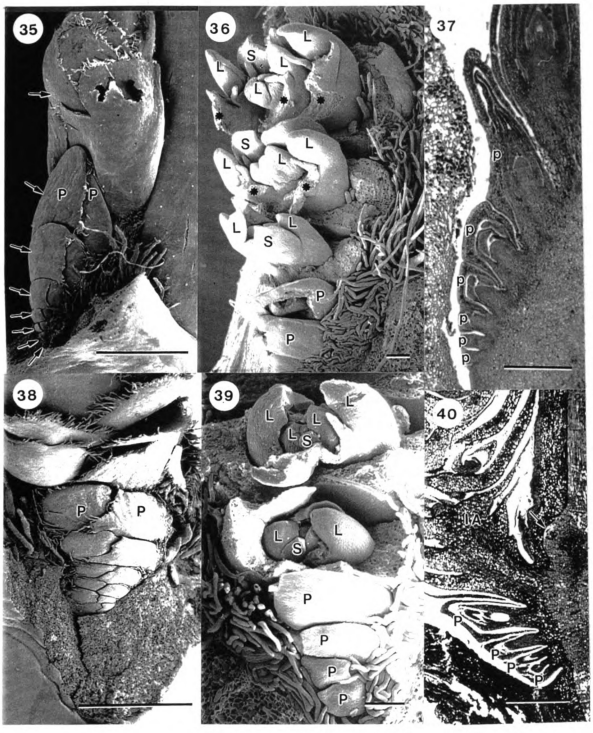
Microscopic observations: A linear series of microscopic first order buds formed in the axils of foliage leaves on

elongating vegetative shoots (Fig. 35). Morphological comparison of the series of buds (with and without prophylls) together with longitudinal serial sections of these buds at the nodes of current year stem segments showed a basipetal (towards the leaf scar) decrease in the size and degree of differentiation in buds (Figs. 36, 37). The distal-most remaining buds mature within a series during the following spring. A comparison of the linear series of buds from the nodes of current year (Figs. 35-37), previous year (Figs. 38-40) and 2 year-old (Figs. 41-43) stem segments indicated that resting buds changed very little from the developmental state in which they were initiated until the summer before they matured.

During early development, the phyllotaxy of the vegetative and reproductive buds appeared to be identical. All buds were covered with a pair of orthodistichous prophylls. In vegetative buds, each foliage leaf primordium was also initiated 180° from its predecessor (orthodistichous phyllotaxy) (Figs. 44, 45). Four folded foliage leaves in early stages of development were observed in the buds collected before bud break in the spring. Similarly in a reproductive bud, the four bracteose leaves were initiated in an orthodistichous arrangement (Fig. 46).

Abbreviations for all Figures: B; bracteole, FS; floral bud scale, F; floral bud primordia, IA; inflorescence axis, L; leaf primordium, FL; foliage leaf, BL; bracteose leaf, P; prophyll, S; stipule, V; vegetative bud primordia. In all Figures, the buds are positioned so that the leaf scar would be the towards the bottom of the micrograph.

Figs. 35-40. SEM (Figs. 35, 36, 38, 39) and light micrographs (Figs. 37, 40) of the developmental state of C. canadensis buds on current year, previous year and two-year-old stem segments nodes. Although samples used for the SEM images in Figs. 35-43 were collected in April, before the elongating buds matured, stem segment age corresponds to the age of the stem during bud elongation. This corresponds with the quantitative data. Fig. 35-37. Linear series of buds on the nodes current year stem segment showing that varying degrees of differentiation correspond to the order in which the buds in the series were initiated with distal nodes further developed. Fig. 35. Outer morphology of eight buds (arrows) with prophylls. The distal most bud was initiated first and is a macroscopic inflorescence bud. Bar = 1 mm. Fig. 36. Buds with prophylls removed, showing that the number of leaf primordia in each bud decreases basipetally from the distal most to those closer to the leaf scar. The two distal-most buds have differentiated into vegetative buds in this sample. Bar = 100 μm. Fig. 37. A longitudinal section through the linear series of buds, showing the basipetal decrease in differentiation and in number of leaf primordia per bud. Bar = 50 μm. Figs. 38-40. Micrographs of the linear series of buds on nodes of previous year stem segments. The distal-most buds in each sample had matured and abscised. Fig. 38. Outer morphology of buds with bud prophylls. The bud partially visible at the top of the micrograph had elongated but the remaining buds were comparable to similar buds in Fig 35. Bar = 1 mm. Fig. 39. Prophylls removed showing the morphology of the leaf primordia of the first two buds directly beneath the buds that have elongated in this linear series of buds. Bar = 100 μm. Fig. 40. Longitudinal section of an inflorescence abscision area (arrow) beneath periderm, the inflorescence axis of an elongating inflorescence and four resting buds at various stages of differentiation. Bar = 50 μm.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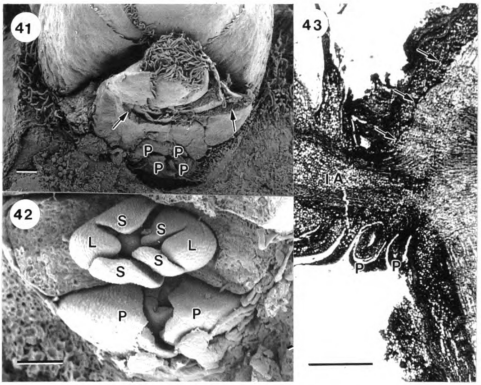
Figs. 41-43. Sem and light micrographs of the linear series of C. canadensis buds on nodes of two-year-old stem segments. Several of the distal most buds had matured and abscised in each sample. Fig. 41. Outer morphology of buds with prophylls in April. The bud partially visible at the top of the micrograph had elongated. The bud directly beneath was too poorly developed for maturing in June. The two remaining buds with prophylls labeled were comparable to similar buds in Fig. 42. Bar = 100 μm. Fig. 42. Prophylls removed showing the morphology of the leaf primordia of the last two (most proximal) buds in a linear series in April. Leaf primordia are shown in the top bud (prophylls have been removed) and the lower bud is partially covered by prophylls. Bar = 100 μm. Fig. 43. Longitudinal section through a linear series showing the abscission zones of previously abscised inflorescences (arrows), the inflorescence axis of an elongating inflorescence and two resting buds at different stages of differentiation in December. Note internodal elongation of the inflorescence axis. Bar = 50 μm.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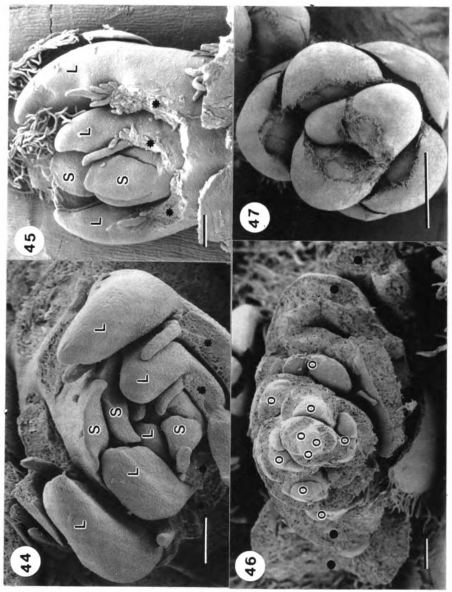
Figs. 44-47. Sem micrographs comparing the phyllotaxy of vegetative and reproductive shoots in C. canadensis. Prophylls, bracteose leaves (●), floral bud scales (★) or stipules (✱) have been removed for all images. Samples were collected in March, 1995, except for those in Figs. 44, 46, which were collected in July, 1995 and June, 1994 respectively. Bars = 100 μm. Fig. 44. Polar view of a vegetative bud showing the orthodistichous phyllotaxy with each leaf primordium initiated 180° from its predecessor. Fig. 45. Lateral view of a vegetative bud. Note the folded developing leaf blade (arrow). Fig. 46. Polar view of early development of an inflorescence. Four bracteose leaves are initiated with an orthodistichous phyllotaxy, which changes to a 2:3 Fibonacci spiral when floral bud primordia are initiated in the florescence. Fig. 47. Polar view showing the helical phyllotaxy of the floral buds prior to bud burst.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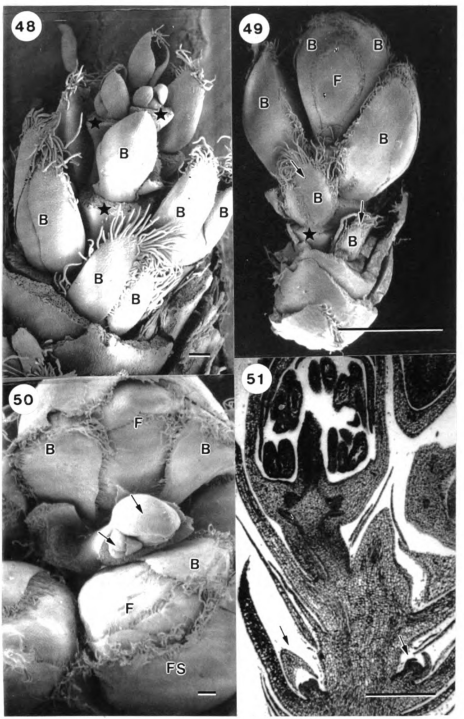
Figs. 48-51. SEM and light micrographs illustrating the fate of floral buds in an inflorescence of C. canadensis. All floral bud scales were removed from samples imaged in Figs. 48, 49. Fig. 48. SEM micrograph of the lateral view of an elongating inflorescence sampled in July. Each floral bud is subtended by a floral bud scale and consists of a pair of bracteoles and the primordium for one flower. Note the helical phyllotaxy, and the larger size and greater differentiation of the first formed lower buds. Bar = 100 μm. Fig. 49. SEM micrograph of the lateral view of a mature inflorescence sampled in March showing two lower floral buds in an arrested state of development (arrow). A third such bud is hidden from view. Compare to Fig. 48. Bar = 1 mm. Fig. 50. A longitudinal section through a pair of lower buds from a different inflorescence showing the arrested state of the meristematic region (arrows) as compared to the normally developed floral bud above. Bar = 50 μm. Fig. 51. SEM micrograph of the developmental state of the distal most floral buds (arrows) of elongated inflorescence. Collected in late March. Bar = 100 μm.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In contrast, in the reproductive bud, during the elongation phase that preceded its maturation the following spring, the phyllotaxy along the floral axis changed from orthodistichous to a 2:3 Fibonacci spiral (Figs. 46, 47). A floral bract, a pair of valvate bracteoles and a flower primordium were then initiated at each node (Fig. 48). Internodes along the inflorescence axis elongated during summer development (Figs. 37, 49, 43). At this time, reproductive buds and vegetative buds could be distinguished macroscopically by differences in their size (reproductive buds are larger) and color (reproductive buds are red).

Prior to their maturation the next spring, floral buds within the inflorescence were initiated in an acropetal manner but the two or three basal-most and the distal-most floral meristems ceased to develop soon after bracteole initiation (Figs. 49, 50). Some of the floral bud primordia withered and the inflorescence failed to mature (Fig. 51).

Variation between Individual Trees: Significant differences were found between the means of all of the dependent variables and the independent variable Individual Tree (Table 1). Individual tree number five had the lowest number of macroscopic inflorescence buds per node and fewer of those buds actually reached maturity (Table 2). The mean number of elongated vegetative shoots per stem segment in

1993 was also lower in individual tree number five than for the other individuals in the study.

Table 2. ANOVA for the dependent variables; number of vegetative structures (macroscopic buds/shoots) per stem segment in 1992 and in 1993, inflorescences per node 1992 and inflorescences that matured spring 1993, with independent variables; treatment, time of treatment and individual tree.

Source	df	Prob>F 1992	Prob>F 1993
Vegetative /stem segment			
Treatment	3	0.000	0.000
Time of Treatment	2	0.002	0.815
Individual Tree	4	0.000	0.000
Inflorescences per node			
Treatment	3	0.136	0.067
Time of Treatment	2	0.191	0.028
Individual Tree	4	0.000	0.000

Variation between Treatments: There were significant differences between the means of vegetative structures present in 1992 and 1993 when using treatment as the independent variable (Table 2). Vegetative structures (macroscopic vegetative buds and elongated vegetative shoots) per stem segment produced in 1992 were lower for pruned (x = 0.27, 0.10 and 0.43 per stem segment) than for the unpruned stem segments (x = 2.40 per stem segment) (Table 4). By the summer of 1993, the mean number of

Table 3. Mean number of vegetative structures per stem segment[a] produced in 1992 (macroscopic buds) and 1993 (elongated shoots); inflorescences per node that elongated in 1992 (macroscopic buds) and 1993 (matured inflorescences) by individual tree.

Individual Tree	Veg 92 ±SE	Veg 93 ±SE	Inf 92/node ±SE	Inf 93/node ±SE
1	0.542 ± 0.180 (N=24)	1.363 ± 0.268 (N=22)	1.282 ± 0.109 (N=24)	0.762 ± 0.146 (N=22)
2	0.542 ± 0.190 (N=24)	1.333 ± 0.287 (N=21)	1.258 ± 0.102 (N=24)	1.076 ± 0.095 (N=21)
3	0.833 ± 0.274 (N=24)	2.050 ± 0.344 (N=20)	1.390 ± 0.177 (N=24)	1.201 ± 0.165 (N=20)
4	0.708 ± 0.244 (N=24)	2.083 ± 0.366 (N=24)	1.775 ± 0.160 (N=24)	1.222 ± 0.143 (N=24)
5	1.375 ± 0.334 (N=24)	0.250 ± 0.171 (N=16)	0.627 ± 0.114 (N=24)	0.215 ± 0.089 (N=16)

[a]Stem segment=stem segment between the distal most node to the first psedoterminal bud scale scar below.

Table 4. Mean number of vegetative structures per stem segment[a] produced in 1992 (macroscopic buds) and 1993 (elongated shoots); inflorescences per node that elongated in 1992 (macroscopic buds) and 1993 (matured inflorescences) by treatment.

Treatment	Veg 92 ± SE	Veg 93 ± SE	Inf 92/node ±SE	Inf 93/node ± SE
Current Year (control)	2.400 ± 0.201 (N=30)	2.650 ± 0.333 (N=26)	1.246 ± 0.059 (N=30)	1.107 ± 0.110 (N=26)
Current year (pruned)	0.270 ± 0.135 (N=30)	1.200 ± 0.208 (N=25)	1.106± 0.09 (N=30)	0.942± 0.129 (N=25)
Previous year (pruned)	0.100 ± 0.056 (N=30)	0.960 ± 0.261 (N=26)	1.494 ± 0.120 (N=30)	0.965 ± 0.175 (N=26)
Two-tear old (pruned)	0.430 ± 0.177 (N=30)	1.120 ± 0.268 (N=26)	1.219 ± 0.149 (N=30)	0.720 ± 0.125 (N=26)

[a]Stem segment=stem segment between the distal most node to the first psedoterminal bud scale scar below.

Table 5. Mean number of vegetative structures per stem segment[a] produced in 1992 (macroscopic buds) and 1993 (elongated shoots); inflorescences per node that elongated in 1992 (macroscopic buds) and 1993 (matured inflorescences) by time of treatment.

Time of treatment	Veg 92 ± SE	Veg 93 ± SE	Inf 92/node ± SE	Inf 93/node ± SE
June 1992	1.075 ± 0.190 (N=40)	1.620 ± 0.259 (N=39)	1.154 ± 0.121 (N=40)	0.709 ± 0.107 (N=39)
July 1992	0.550 ± 0.152 (N=40)	1.552 ± 0.0.283 (N=29)	1.241 ± 0.094 (N=40)	0.951 ± 0.0116 (N=29)
August 1992	0.775 ± 0.236 (N=40)	1.40 ± 0.240 (N=35)	1.404 ± 0.137 (N=40)	1.169 ± 0.124 (N=35)

[a]Stem segment=stem segment between the distal most node to the first psedoterminal bud scale scar below.

vegetative structures per pruned stem segment increased to at least one vegetative structure per stem segment regardless of treatment (Table 4).

The mean number of macroscopic inflorescence buds per node that elongated in 1992 were not significantly different regardless of the pruning treatment (Tables 2, 4). The percentage of inflorescences that elongated in 1992 but then aborted in 1993 were similar for the current year unpruned versus pruned stem (11.2 to 11.8%), but the percentages of aborted inflorescences increased for previous year (35.4%) and two-year-old (40.9%) pruned stem segments (Table 4).

Variation between Time of Treatment: There were significant differences between the mean number of vegetative structures per stem segment present in 1992 and 1993 when using time of treatment as the independent variable (Table 2). Stem segments pruned in July of 1992 produced fewer macroscopic vegetative buds by the end of the 1992 growing season ($\bar{x}$ = 0.55 per stem segment) than those pruned either in June ($\bar{x}$ = 1.075 per stem segment) or in August ($\bar{x}$ = 0.775 per stem segment) of 1992 (Table 5). By the summer of 1993, the mean number of vegetative structures per pruned stem segment increased to at least one vegetative structure per stem segment regardless of time of treatment (Table 5).

The mean number of inflorescence buds per node that elongated in 1992 were not significantly different

regardless of time of pruning (Tables 2, 5). However, fewer inflorescences per node matured on stem segments that had been pruned in June ($\bar{x}$ = 0.709 per node) than those pruned in July ($\bar{x}$ = 0.951 per node) or August ($\bar{x}$ = 1.169 per node) (Table 5).

Variation by node position: Paired t-tests showed significant mean differences between the number of vegetative structures produced at nodes 4 and 5 (distal-most remaining nodes of the pruned stem segments) of pruned and unpruned current year and pruned and unpruned previous year stem segments (Table 6). Unpruned stem segments rarely produced vegetative structures at these nodes. Most of the vegetative shoots (1993) were produced on the remaining distal-most nodes (nodes 4 and 5) of the pruned current year (85 %) and previous year (56%) stem segments, but not on the pruned two-year-old (21%) stem segments. Vegetative structures were generally not found on the basal-most nodes of the stem segments regardless of treatment (Table 6).

Paired t-tests indicate that the inflorescences per node that elongated (1992) at nodes 4 and 5 on pruned versus unpruned current year and previous year stem segments did not have significant mean differences (Table 7). The inflorescences from the basal nodes of unpruned ($\bar{x}$ = 1.067 inflorescences per node) and pruned ($\bar{x}$ = 0.833 inflorescences per node) current year stem segments did have

significant mean differences. However, mean differences between inflorescences that elongated in 1992 and then matured in 1993 at the distal-most nodes (4 and 5) were significant for all of the pruned stem segments studied. The basal-most nodes of the previous year and two-year-old stem segments had the lowest percentage of aborted inflorescences (15.6 and 14.4%). The percentage of aborted inflorescences at nodes 4 and 5 increased with the degree of pruning of the stem segment (Fig. 52).

It should be noted that buds that elongated and matured on experimental stem segments did so in the same order within the node as they did on unpruned stems. That is, the order of elongation corresponded with the basipetal order of bud initiation at each node, with the distal buds maturing first.

Table 6. Paired t-test comparisons of the mean number of vegetative structures 1993 (elongated shoots) at three different nodes of unpruned and pruned stem segments by age of the stem segement.

Stem Age[a]	Node[b]	Mean unpruned	Mean pruned	Mean difference ±SE
Current year	4*	0.167	0.750	-0.583 ± 0.119
	5*	0.000	0.542	-0.542 ± 0.104
	Basal	0.000	0.125	-0.125 ± 0.069
Previous year	4	0.120	0.360	-0.240 ± 0.145
	5*	0.000	0.160	-0.160 ± 0.075
	Basal*	0.000	0.160	-0.160 ± 0.075

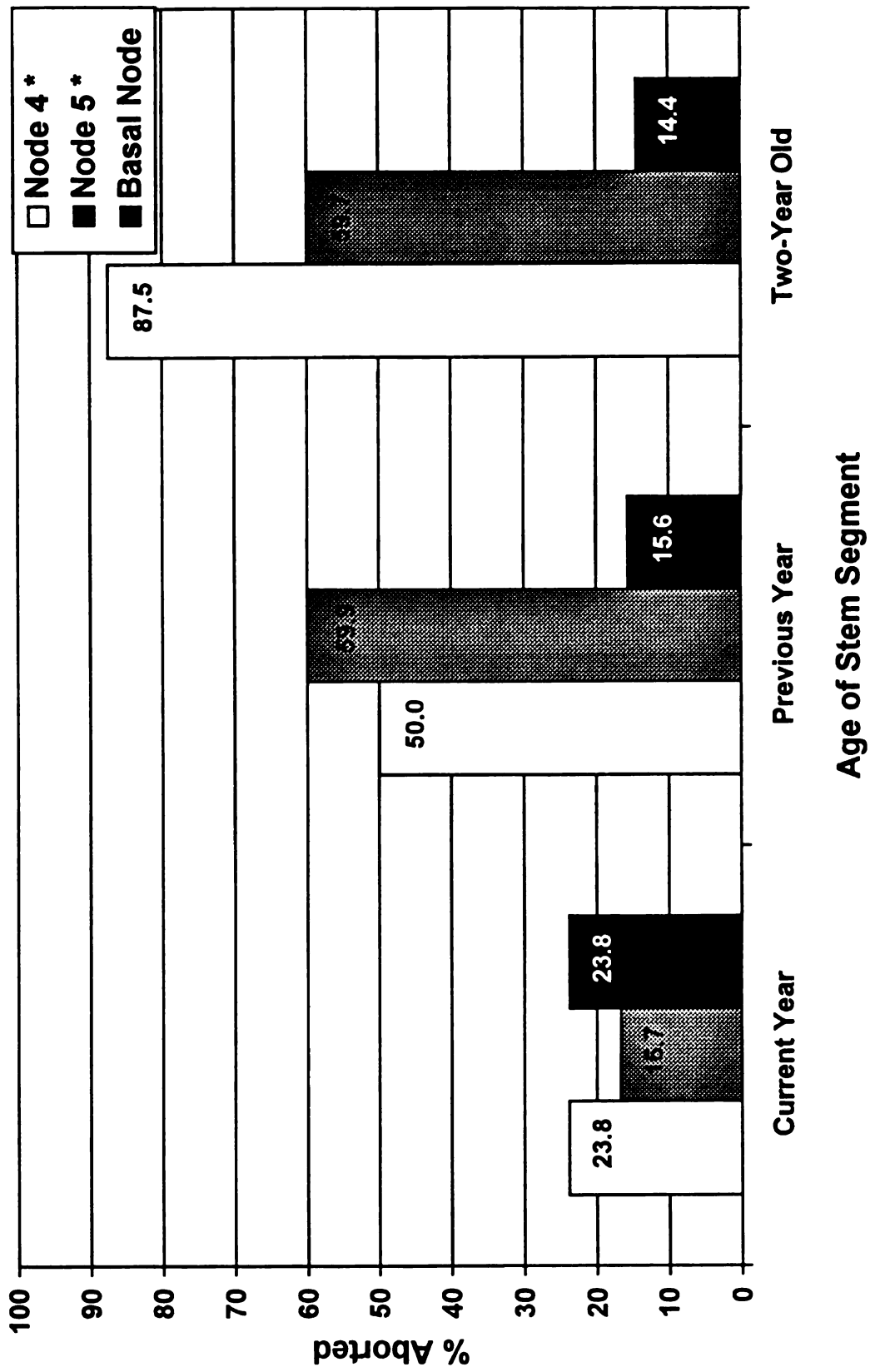
[a] Stem age at the time of treatment.
[b] node number for previous year stem segments were counted from the distal psedoterminal bud scale scar.
* Mean difference with Prob ≤ 0.05

Table 7. Paired t-test comparisons of the mean number of inflorescences (1992) at different nodes for unpruned and pruned stem segments by stem age.

Stem Age[a]	Node[b]	Mean unpruned	Mean pruned	Mean difference ±SE
Current year (N=30)	4	1.133	1.267	-0.133 ± 0.157
	5	1.233	1.300	-0.067 ± 0.166
	Basal*	1.067	0.833	0.233 ± 0.092
Previous year (N=28)	4	1.714	1.750	-0.036 ± 0.202
	5	1.643	1.679	-0.036 ± 0.289
	Basal	1.321	1.143	0.179 ± 0.272

[a] Stem age at the time of treatment.
[b] node number for previous year stem segments were counted from the distal psedoterminal bud scale scar.
* Mean difference with Prob < 0.05

Fig. 52. Percentage of macroscopic inflorescence buds at specific nodes that elongated in 1992 and aborted in 1993 by pruning treatment. * = differences in the means with Prob < 0.05 at these nodes for all pruned stem segments.


Node 4 *
Node 5 *
Basal Node
% Aborted
100
90
80
70
60
50
40
30
20
10
0
87.5
14.4
63.7
15.6
63.3
50.0
23.8
16.7
23.8
Current Year
Previous Year
Two-Year Old
Age of Stem Segment

Intermediates: Most of the inflorescences produced four bracteose leaves beneath the floral buds during the summer of elongation. Floral buds matured during the following spring with the basal bracteose leaves remaining small upon anthesis (Fig. 53). Exceptions were the twenty-two 'intermediate' shoots in which foliage leaves developed in place of the bracteose leaves beneath the flowers which were morphologically normal (Fig. 54). The lowermost (first initiated) floral buds, like those in the normal inflorescence, failed to develop. The flowers from the intermediate shoots matured in the fall of 1992 instead of the spring of 1993. Every tree produced at least one of the intermediate shoots. Thirteen of the intermediate shoots were produced on stems pruned in June, seven on stems pruned in July and two on stems pruned in August. Three intermediate shoots developed on previous year segments of stems that were unpruned and two on pruned current year stems while nine developed on the pruned previous year and eight on two-year-old stem. Only one of the intermediates was produced on a current year stem segment.

Ten of the 923 macroscopic inflorescence buds observed in 1992 also matured in the fall of 1992. rather than in the spring of 1993. Only one of the early maturing inflorescences was found on a pruned current year stem segment. The rest were from previous year and two-year-old pruned stem segments. Abnormal flowers were not observed on

Figs. 53-54. SEM micrographs comparing a normal inflorescence of C. canadensis (Fig. 53) with an intermediate shoot (Fig. 54). Bars = 1 mm. Fig. 53. Prophylls and four bracteose leaves from a mature inflorescence collected June, 1995. Flowers were removed from the inflorescence for critical point drying but the floral bud scales, bracteoles and peduncles can be seen. Fig. 54. Prophylls and four foliage leaves at the base of an intermediate shoot collected in October of 1992. Although the flowers matured out of season, their morphology appeared normal. The folded lamina of the largest leaf is perpendicular to the aluminum stub in this Fig. (arrow).

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any of the inflorescences that matured during this study. Macroscopic vegetative buds that formed on current year pruned stem segments matured in 1993, the same as those on unpruned stems. Eleven of the stem segments from two of the trees died (treated in either June or August).

Discussion

Results from the quantitative data in this study indicate that pruning of Cercis stems induced vegetative shoot formation in buds that would normally have become inflorescences. However, the microscopic observations do not support the hypothesis that an inflorescence reversion occurred. Macroscopic observations of buds in the linear series (non-treated) indicated that in all of the buds, initial leaf primordia had an orthodistichous phyllotaxy but in those buds that become inflorescences, the phyllotaxy changed to helical during floral initiation. Intermediate shoots produced on some experimental stems developed four foliage leaves instead of four bracteose leaves at the base of an otherwise normal inflorescence.

Intermediate shoots do not normally develop in Cercis but they are similar to the mixed shoots which commonly occur in Citrus (Shamouti orange and Eureka lemon) trees. Mixed Citrus shoots produce foliage leaves and a terminal inflorescence. The trees also produce strictly leaf bearing and strictly flower bearing shoots. The application of

small amounts of GA reduces flowering and increases the number of mixed and vegetative shoots in Citrus trees (Goldschmidt and Monselise, 1972).

In another study on Citrus, resting lateral buds were reverted from a reproductive fate to vegetative growth by the applications of GA, but terminal flowers eventually formed on all of these shoots (Lord and Eckard, 1987). The intermediate shoots of Cercis could also be interpreted in this manner except that the foliage leaves differentiated from bracteose primordia that were already present. The reverted shoots of Citrus also had a variable number of foliage leaves while intermediates of Cercis always had four leaves in the basal most position on the inflorescence axis, the same number as for bracteose leaves in a normal inflorescence. In Cercis, basal leaf primordia were initiated (in many cases several years) before buds were determined. The same primordia could differentiate into foliage leaves or bracteose leaves depending on the fate of the bud.

Lateral buds in an adult Citrus tree are thought to be determined to flower from their inception but dormancy and the influence of GA may inhibit them from doing so (Goldschmidt and Monselise, 1972; Lord and Eckard, 1987). Microscopic observations of the phyllotaxy suggest that unlike Citrus, the buds in Cercis are initiated in a vegetative state. Early in their differentiation, the

meristems of all first order buds in the linear series initiate prophylls and leaf primordia in an orthodistichous pattern. Vegetative buds retain the orthodistichous phyllotaxy but reproductive shoots undergo a phyllotactic change to a 2:3 Fibonacci spiral system prior to floral bud initiation. In many plants, phyllotactic changes have been reported to occur prior to or at the time of inflorescence or flower initiation (Bernier et al., 1981; King, 1983; Kinet et al., 1985). In addition, although not addressed in this study, second order buds are formed in the axils of the orthodistichous bracteose leaves at the base of the reproductive shoots (Owens and Ewers, 1990; Owens et al., 1995), suggestive of a sympodial mode of development as occurs in vegetative shoots.

Strong apical dominance was expected in Cercis since all of the axillary buds are proleptic, waiting at least one year after their initiation to mature. Strictly proleptic pre-formed lower buds of roses sprout and differentiate into a floral apex when pruning releases them from inhibition (Zamski et al., 1985). Pruning in Cercis did not release the buds on current year stems from dormancy, since most of the 398 reproductive buds and the 80 vegetative buds remained dormant until the following spring. One normal inflorescence and one intermediate shoot did elongate and mature during the same season in which they were initiated (on current year stem segments) and might be considered as

arising from sylleptic buds.

Statistical differences between individual trees in the mean number of vegetative structures per stem and inflorescences per node might indicate genetic differences between individual trees or differences in environmental conditions but this study can not distinguish between these possibilities.

The timing of pruning (June, July or August) had little impact on flower production. Since. the total number of inflorescences in Cercis exceeded the number of initiated vegetative shoots in both pruned and unpruned stems, most of the inflorescences must have been committed to the floral state by the time of the first pruning (June 9). Since there were no significant differences between the mean number of macroscopic inflorescence buds per node produced on pruned and unpruned stem segments, perhaps the induced vegetative buds came from buds that would have normally elongated during another year.

Knowledge of the effects of pruning position on inflorescence abortion could be useful to horticulture since Cercis is an important landscape tree noted for its spring flowers. The present study suggests that pruning position had little affect on the number of macroscopic inflorescences buds produced per node in 1992. Similarly, when Triplochiton scleroxylon trees were pruned at four different positions along the stem, the number of sprouting

floral buds per node were similar on all stems regardless of where they were pruned (Leakey and Longman, 1986). Although the position of pruning was not significant for the number of Cercis inflorescences that elongated in 1992, more of these buds aborted on the stems pruned back to two-year-old positions than at nodes on stems with less of the shoot removed. Therefore, horticulturalists should be aware that while the timing of pruning (June, July or August) may have little impact on the production of inflorescences, pruning down to one or two-year-old growth will result in fewer inflorescences maturing the year following pruning.

The number of macroscopic vegetative buds produced in 1992 was influenced by the position of the pruning cut. However, whatever inhibited the outgrowth of vegetative buds in 1992 was removed by the summer of 1993 when the number of vegetative structures on pruned stem segments was similar regardless of the position of pruning.

Removal of the shoot apex from coppice shoots of Morus alba was experimentally shown to be effective in breaking inhibition for only a short distance (a few buds below it) and removal of the sprouting upper buds also had only a slight effect on the buds beneath (Suzuki, 1990b). Similar results were obtained for the current year pruned stem segments of Cercis where vegetative structures were produced primarily on the two nodes directly beneath the pruned cut. Vegetative structures were rarely produced at these nodes in

the unpruned stems. Although previous year pruned stems also produced vegetative structures at nodes directly beneath the cut, the vegetative structures were less confined to these nodes and even less for two-year-old pruned stem segments.

Perhaps the above indicates less apical dominance at work in the older stem segments. Alternately, enhanced competition from adjacent branches could have inhibited vegetative structures from forming on the distal-most nodes of the two-year-old pruned stems segments in our study. Similar results were found in one-year-old M. alba shoots (grown on 12-year-old coppice stumps). The upper lateral buds become dominant and develop into long shoots while those beneath ceased growth in the early spring and become short shoots (Suzuki and Kitano, 1989b). When pruned in the spring, high pruned and middle pruned shoots also produced dominant long shoots at the distal-most remaining nodes but elongation of the upper lateral shoots was inhibited in low pruned shoots. This inhibition was removed in M. alba when all of the stems were pruned to a low position, indicating competition between adjacent branches inhibits the elongation of some lateral buds (Suzuki, 1990b).

In studies of lateral bud inhibition, it is generally difficult to separate the influence of dominance from that of competition between plant structures for limited assimilates (Bangerth, 1989). In the present study, the

combined influence of these factors on the fate of multiple buds was presumably in effect since pruning removed not only the stem apex but also leaves, stem segments and other buds. Apical dominance by definition generally refers to current year stems and our pruning experiments were done on current year, previous year and two-year-old stem segments. Stems were pruned beneath previous vegetative shoots to eliminate the dominant influence of vegetative short shoots released from apical control. Vegetative shoots on the older segments beneath the segments studied were in many cases elongated but these were not removed.

Mature leaves have been found to inhibit lateral bud outgrowth in some woody plants. The number of upper lateral buds that elongated on decapitated shoots of M. alba increased when plants were also defoliated (Suzuki et al., 1988). In cuttings of Vitis vinifera, inflorescences usually aborted soon after bud burst unless the leaves were removed from the elongating shoots. In the same study, decapitation coupled with defoliation stimulated inflorescence elongation in grape cuttings but decapitation alone was ineffective (Mullins, 1967). Studies also indicate that removal of young leaves promoted inflorescence development in Bougainvillea 'San Diego Red' where newly developing leaves act as a sink for assimilates and probably produce an inhibitor to inflorescence development (Tse et al., 1974; Ramina et al., 1979).

In addition to the production of photosynthates, leaves are thought to be associated with the production of the flowering stimulus (King 1983). The development of inflorescences in Bougainvillea 'San Diego Red' is a function of leaf area (Ramina et al., 1979). Floral bud abscission in the 'Enchantment' lily increased dramatically after 50% or more of the leaves are removed. After 75% of the leaves were removed, 69% of the floral buds aborted (Meetere, 1981). Similarly, in Cercis in the present study, the percentage of inflorescence that aborted increased for the previous year pruned and two-year-old pruned stem segments, where greater leaf areas were removed by the pruning treatment. The percentage of aborted inflorescences were similarly low for unpruned versus current year pruned segments. Perhaps, as in lily above, removing only about one-half the leaf area in Cercis (current year pruned) had minimal effect on inflorescence abortion, whereas removing more leaf area greatly increased abortion rates.
Larger, more developed buds have been reported to inhibit the other buds in a group of multiple buds at the same node. Up to four buds form at a node in Pisum sativum, a large bud and several adjacent buds. The largest bud inhibits the adjacent buds (Gould et al., 1985). Morus alba produces three proleptic buds, one main bud that matures the year after it is produced, and two accessory buds that can also elongate but only if the stem is pruned just prior to or

during bud break (Suzuki, 1990a).

Dominance of the larger buds within each linear series in Cercis is plausible. The present study has shown that the buds sequentially develop and mature in the order of their initiation even when released from the inhibiting influences of the stem apex. In addition, each node, regardless of where it is located along the stem, produces some buds that mature each year. Regulation of the outgrowth of these buds appears to be more from dominance relationships between buds within the same node rather than from their position within the stem. This would be consistent with the 'primigenic dominance' hypothesis in which the degree of dominance or inhibition is based upon the sequential development of structures in relation to each other rather than on their morphological position within the stem. This has been demonstrated for fruits, with the dominance of earlier developed fruits over those that develop later (Bangerth, 1989).

Within the Cercis inflorescence, undeveloped floral buds were present at the basal nodes and also at the apex. Similar aborted buds in the inflorescence of this taxon were reported by Worthington (1968). Future studies on these aborted floral buds could increase our understanding of the complex dominance relationships in Cercis.

CHAPTER IV

DEGRADATION OF THE UPPER PULVINUS IN LEAVES OF *Cercis canadensis* L. (FABACEAE)

Abstract

Identification of fossil leaves to *Cercis* has been questioned based upon the presence or absence of a pulvinus at the base of the lamina (upper pulvinus). The present study of the leaves of *Cercis canadensis* L. before and after leaf abscission concerns the degrading processes that may have occurred in leaf structures prior to fossilization. Results indicate that 1) the pulvinus consists largely of tissues with non-lignified cells (a wide cortex, phloem and ground tissue in the vascular core) that degrade rapidly after leaf abscission, 2) the lignified xylem tissue that remains in the pulvinus after degradation is in brittle strands, 3) the pulvinus degrades at a faster rate than the lamina or the petiole proper and 4) the pulvinus and petiole proper are often folded back over the lamina after abscission. Thus the lack of an upper pulvinus in a fossil leaf that is otherwise similar to *Cercis* should not constitute a reason for reclassification. Rather than the upper pulvinus, the distinctive pattern left by the degraded cushion of pulvinus tissue or the presence of separated vascular strands at the base of the lamina can be used as positive indicators for *Cercis*. These should be used in

conjunction with other identifying features that tend to be preserved during fossilization.

Introduction

Leaves with differentiated motor organs (pulvini) are often found in plants of the Fabaceae (Satter and Morse, 1990) but fossilization of pulvini has been little explored. In the Fabaceae, the pulvinus consists of a thick cylinder of many layers of cortical parenchyma cells surrounding a relatively slender vascular core (Fleurat-Lessard, 1990). The cortical tissue characteristically has intercellular spaces between cells and the cells themselves have flexible non-lignified walls and large vacuoles (Fleurat-Lessard, 1990). The vascular tissue is usually surrounded by a cylinder of perivascular non-lignified collenchyma. Differences in the turgor pressure (correlated with the movement of ions) between regions of cortical cells cause the bending and straightening of the pulvinus that are responsible for leaf movement in legumes (Fleurat-Lessard, 1990; Fromm and Eschrich, 1990; Lee, 1990; Satter and Morse, 1990). Pulvini allow the leaves to move in response to external stimuli such as light. Some of the features that allow for leaf movement, such as non-lignified cells, might fossilize poorly.

Leaf impressions, along with fruit impressions, provide us with the most reliable fossils for the genus Cercis L.

(Caesalpinioideae; Fabaceae). Wood fossils are unreliable since unlike most legumes Cercis lacks vestured pits (Quirk and Miller, 1985) and is therefore hard to distinguish from other wood present in the fossil record (Wheeler and Baas, 1992). Leaf impression for fossil species include Oligocene-aged impressions of C. komarovii Palibin from the Sarmatian of Armenia (in Shakryl, 1992), three Oligocene-aged impressions of C. parvifolia Lesquereux from the Florissant Beds, Colorado (MacGinitie, 1953) and six Miocene-aged impressions of C. miochinensis Hu et Chaney from Shantung Province, China (Hu and Chaney, 1940; Institute of Botany, 1978).

Cercis has a simple palmately veined leaf with a lower pulvinus at the base of the petiole proper and a large upper pulvinus at the base of lamina (Pijl, 1951). Questions have arisen concerning fossil leaves from the Florrissant Formation in Colorado described as Cercis parvifolia by Knowlton (1916) and MacGinitie (1953) because there is no clear evidence of a upper pulvinus at the base of the lamina (Herendeen et al., 1992).

The degree of preservation in a plant fossil depends on the amount of tissue decay that occurred prior to fossilization. Thin walled parenchyma cells that are typically found in pith, cortex, and phloem tend to break down before fossilization while xylem, fibers, and leaf cuticles tend to be resistant to degradation (Stewart,

1983). The upper pulvinus, consisting of a large volume of cortical tissue relative to the vascular tissue, might not be preserved in a fossil leaf impression. In contrast, the lamina might be more resist to degradation. Under natural conditions, how does the rate of decay in the upper pulvinus compare to that of the lamina and petiole proper? Should the lack of an upper pulvinus in a fossil leaf discredit its classification as Cercis? To answer these questions, studies were made of the leaves of Cercis canadensis before leaf abscission and periodically thereafter following natural weathering until the cortical tissue of the pulvinus was degraded.

Materials and Methods

Abscised decomposing Cercis leaves were collected from the ground at Michigan State University (MSU) during the late winter and early spring of 1994 and the late Fall of 1995 for observation. Intact leaves were also collected from Cercis trees during the summer and fall of 1995.

Fresh material was freehand sectioned with a double edged razor blade for observations with a light microscope. Brightfield and fluorescent images were obtained on a Zeiss 10 Laser Scanning Confocal Microscope. For fluorescence images, a monochromatic argon ion laser (488nm) with a 520 nm long pass filter was used. The fluorescence of cell walls was used as a test for lignin. Material preserved in

FAA was also stained with phloroglucinol with a drop of HCl as a second test for lignin (Peacock, 1966).

Some of the pulvini and attached structures were dissected from abscised leaves, air dried and mounted on aluminum stubs. In addition, upper pulvini were dissected from the leaf, fixed in 0.4% glutaraldehyde in a 0.1 M sodium phosphate buffer (Ph = 7.0), dehydrated in graduated concentrations of ethanol, critical point dried in CO_2, mounted on aluminum stubs, sputter coated with gold and imaged using either a JEOL JSM-35CF or a JEOL JSM-6400V SEM (10 kV of accelerating voltage).

Results

The upper pulvinus is easily distinguished from the petiole proper in an intact leaf of Cercis (Fig. 55). The petiole proper consisted of an epidermis, 3-4 layers of cortex, a sheath of fibers and one or two cylinders (depending on position) of vascular tissue surrounding pith (Fig. 56, 57). The sheath surrounding the vascular core fluoresced and also stained reddish purple (positive for lignin) when phloroglucinol/HCl was applied to the sections. Shortly after leaf abscision, the cortex and phloem became crushed but the epidermis, xylem and pith remained intact (Figs. 58, 59).

The upper pulvinus consisted of a cortex with many (14-20, depending on the area) layers of parenchyma cells, a

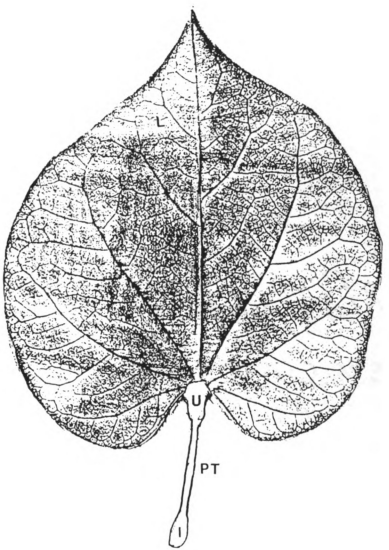
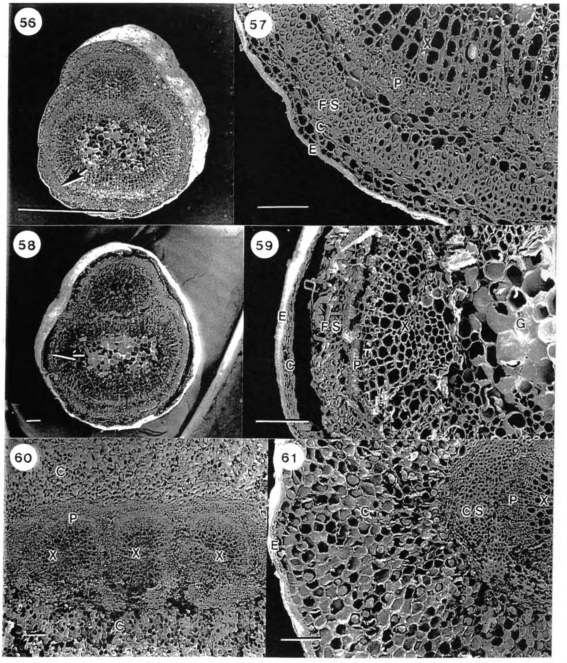


Fig. 55. Schematic representation of a simple leaf of Cercis canadensis redrawn from a leaf rubbing. Lower pulvinus, l; petiole proper, PT; upper pulvinus. u; lamina, L.

Tissue abbreviations for all Figures: cortex, C; collenchyma sheath, CS; epidermis, E; fiber sheath, FS; phloem, P; pith, G; xylem, X.

Figures 56-61. SEM images of transverse sections through the middle of a petiole proper before (Figs. 56, 57) and after (Figs. 58, 59) leaf abscission. SEM images of the upper pulvinus before leaf abscission (Figs. 60, 61). The adaxial side of the structure is towards the top in all figures. Bars = 100 μm unless otherwise indicated. Fig. 56. Petiole proper with a large and small vascular cylinder each surrounding a pith, and small cortex (arrow). Collected August 1995. Bar = 1mm. Fig. 57. Higher magnification of the area indicated by arrow (Fig. 56) showing the epidermis, the cortex consisting of 4-5 layers of parenchyma cells, the sheath of perivascular fibers surrounding the vascular tissue. Fig. 58. The degraded cortical tissue separating the intact epidermis from the sheath of perivascular fibers and the vascular cylinders. Collected in December 15, 1995. Fig. 59. Higher magnification of the area indicated by arrow (Fig. 58) with crushed cortex and phloem. The epidermis, sheath of fibers, xylem and pith remain intact. Fig. 60. The cortex consists of many layers of parenchyma cells, a sheath of collenchyma, and a bilateral vascular core. The epidermis and some of the cortex are not visible in this image. Collected August, 1995. Bar = 100 μm. Fig. 61. Higher magnification and extension of the area indicated by arrow (Fig. 60) showing the epidermis, the cortex with 12-16 layers of parenchyma cells, a collenchyma sheath, phloem and xylem. Compare to the petiole proper in Fig. 57. Bar = 100 μm.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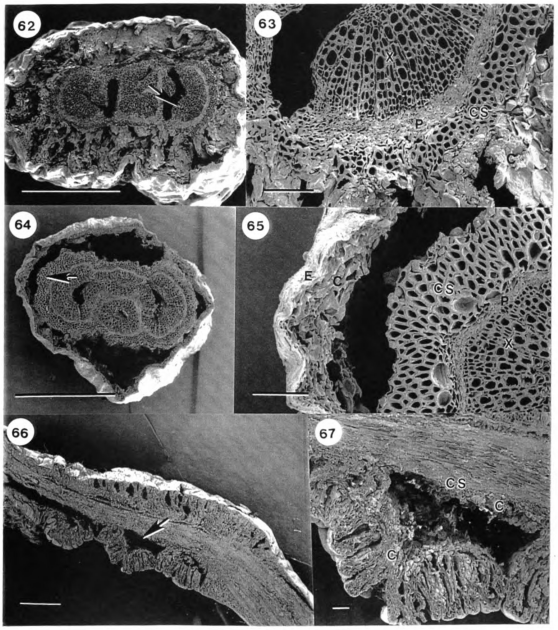
Figures 62-67. SEM images of transverse (Figs. 62-65) and longitudinal (Figs. 66, 67) sections through the middle of the upper pulvinus are representative of the degrading tissue observed in these structures by December 15, 1995 which was approximately six weeks after leaf abscission. The adaxial side is towards the top in all Figures. Fig. 62. Early stage of degradation of the pulvinus with numerous breaks in the cortical tissue and two breaks in the vascular core. The epidermis and the collenchyma sheath surrounding the vascular tissue are intact. Bar = 1 mm. Fig. 63. Higher magnification of the area indicated by arrow (Fig. 62) showing degrading parenchyma cells in the cortex, the still intact collenchyma sheath, the crushed phloem and a break in the ground tissue between sections of xylem. Bar = 100 μm. Fig. 64. Late stage of degradation of the cortical tissue of the pulvinus. There are two breaks in the ground tissue between the xylem of the vascular core but the epidermis and collenchyma sheath are still intact. Compare with Fig. 62 which is at the same at the same magnification. Bar = 1 mm. Fig. 65. Higher magnification of the area indicated by arrow (Fig. 64) with the intact epidermis, collenchyma sheath, the parenchyma cells in the cortex degraded and the phloem crushed. Bar = 100 μm. Fig. 66. Separation of the cortical tissue from the collenchyma sheath and the vascular core of the pulvinus. Differences in the degree of degradation of the cortical tissue on the adaxial (above the vascular core in the image) and abaxial side (below the vascular core in the image) of the pulvinus are shown. Compare the degradation of the petiole area on the right with that of the upper pulvinus. Note the continuity between the perivascular fibers in the petiole proper and collenchyma sheath of the pulvinus. Bar = 1 mm. Fig. 67. Higher magnification of the area indicated by arrow (Fig. 66). The parenchyma cells first crushed together and then broke away from the collenchyma sheath. Bar = 100 μm.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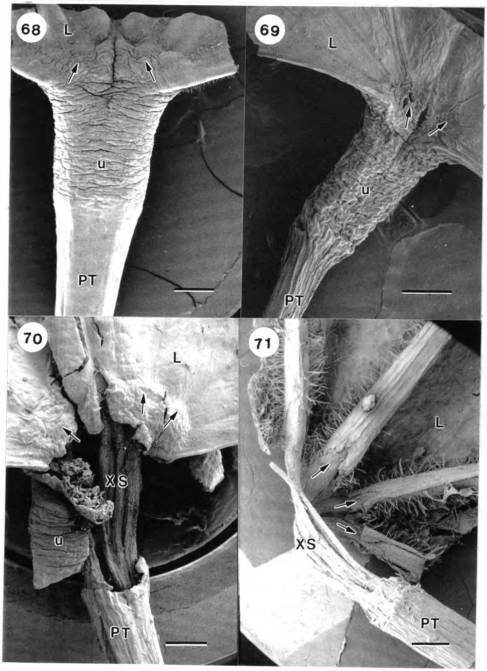
sheath of collenchyma cells and an oblong vascular core (Figs. 60, 61). The collenchyma sheath was not fluorescent and it also failed to stain red with phloroglucinol; thus the lignin tests were negative. The xylem was in three-to-four cylinders surrounded by bands of phloem.

The cortex of the upper pulvinus began degrading shortly after abscission (Figs. 62, 63) and eventually broke away from the collenchyma sheath surrounding the vascular core (Figs. 64-67). At the same time breaks appeared in the ground tissue that is dispersed within the vascular core and the phloem became crushed. Longitudinal sections through the upper pulvinus and part of the petiole showed that the cortical parenchyma cells crushed together, forming gaps, the cortex then broke away from the collenchyma sheath (Figs. 66, 67). The perivascular fibers of the petiole were continuous with the collenchyma of the upper pulvinus (Fig. 66).

The lamina did not abscise from the upper pulvinus (Figs. 68-71). The leaf abscised at the base of the lower pulvinus and the petiole, upper pulvinus and lamina were shed as a single unit. Comparison of the upper pulvinus before abscission (Fig. 68) and after the abscised leaves had remained on the ground over the winter (Figs. 69-71) showed that the cortical tissue became degraded, the epidermal sheath sloughed off and the vascular core broke into several separate strands. The petiole and lamina

Figures 68-71. SEM images of the leaf petiole, upper pulvinus and sections of the lamina comparing degradation of the upper pulvinus over time. The laminas were partially removed for imaging. Notice that the lamina and petiole are comparatively less degraded than the upper pulvinus in all Figures. Arrows indicate the edges of the cushions of pulvinus tissue that extend into the lamina. The adaxial surface of the leaf is shown except in Fig. 71, where the leaf is twisted showing the abaxial surface of the lamina. Bars = 1 mm in all Figs. Fig. 68. Upper pulvinus on a leaf before leaf abscission. Collected in October, 1995. Fig. 69. Upper pulvinus on a leaf after leaf abscission. Collected in March 1994. Fig. 70. The cortical tissue of the pulvinus had shrunk and broken away from the strands of the vascular core. Collected March 1994. Fig. 71. All of outer tissues of the pulvinus have sloughed off except for the strands of the vascular core. The strands, which serve as connectors between the lamina and petiole proper. Collected April, 1994.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remained intact, connected by the vascular strands. In many cases, the abaxial side of the leaf blade folded back onto the petiole (Fig. 71).

Discussion

The cortical tissue in the upper pulvinus of C. canadensis leaves did not preserve as well as the lamina and petiole proper. Degradation of the pulvinus began shortly after leaf abscission. Soft tissue such as the cortex, phloem and ground tissue within the vascular core degraded, leaving lignified parts of the core in strands. The petiole, with lignified perivascular fibers and a narrow cortex, was less degraded. The lamina, excluding the cushion of pulvinus tissue at its base, also degraded far less than the upper pulvinus during the periods of observation. The upper pulvinus often bent the petiole back over the abaxial side of the lamina, presenting additional difficulties in its detection.

The perivascular sheath surrounding the vascular core in the pulvinus is described in the literature as thick walled collenchyma (Fleurat-Lessard, 1990; Satter and Morse, 1990). As might be expected for thick walled cells, this sheath degraded slower than the pulvinus cortex but faster than the perivascular fibers of the petiole proper. The cells lack the characteristic variability in thickness that identifies collenchyma (Essau, 1960) but fluorescence

microscopy and phloroglucinol tests indicated that the cell walls were, indeed, not lignified. In contrast, the thick walled cells of the perivascular fibers in the petiole proper were continuous with the collenchyma in the pulvinus, but unlike the pulvinus collenchyma, the petiole perivascular fibers tested positive for lignin.

Poor preservation of the upper pulvinus has also been reported in herbarium specimens of Cercis and Bauhinia (Pijl, 1951). During leaf movement, the volume of the cortical cells in a pulvinus swell or shrink during osmotic water uptake or loss (Satter, 1990; Lee, 1990). Eventually, all of the cortical cells in the pulvinus will shrink once the leaf is severed from its source of water. Our study showed the shrinkage and eventual collapsing of the cortical cells occurs shortly after leaf abscission.

The terminology, lower pulvinus and upper pulvinus were chosen here for Cercis due, simply, to the position of a pulvinus in relation to the petiole proper. It is uncertain whether the simple palmately veined leaves of Cercis evolved from the fusion of leaflets of an imparipinnate (pinnately compound leaf with an unpaired central leaflet) or palmately compound leaf or from the reduction of one of these compound leaves to a single leaflet (Pijl, 1951 and references therein). Pijl uses the terminology primary pulvinus (for the lower pulvinus) and secondary/apical pulvinus (for the upper pulvinus) which implies the fusion of leaflets from a

compound leaf.

Fossilization of organic material in sedimentary rock requires an anaerobic aquatic environment and a source of sediment (Stewart, 1983). Simulation of any of these conditions was not attempted in this study. Focus instead was on the degrading processes that might have occurred before leaf fossilization in Cercis. The study showed that 1) the upper pulvinus consists of cells that degrade rapidly once they are shed from the tree, 2) the lignified tissues of xylem that remain in the pulvinus after degradation are in brittle strands, 3) the upper pulvinus degrades at a faster rate than the lamina or the petiole and 4) the petiole is often folded back over the lamina after abscission. During the fossilization process, the petiole and the brittle strands of xylem of the pulvinus could be lost or folded back over the lamina where they might appear to be one of the palmate leaf veins.

The lack of clear evidence of a pulvinus at the base of the lamina of a fossil leaf that is otherwise similar to Cercis would not constitute a reason for reclassification. Perhaps the distinctive pattern left by the degraded cushion of pulvinus tissue or the presence of separated vascular strands at the laminar base can be used as a positive indicators for Cercis. Of course, these should be used in conjunction with other identifying leaf features that tend to be preserved during fossilization. Several of the leaf

impressions described as C. miochinensis from China appear to have this distinctive pattern (Plate 25, Fig. 5, Hu and Chaney, 1940; Plate 89, Fig. 4, Plate 91, Fig. 1, Plate 93, Fig. 1, Institute of Botany, 1978).

Interestingly, the earliest known fossil record for Cercis in North America is from the Oligocene aged Florissant Lake Beds in Colorado (Knowlton, 1916; MacGinitie, 1953). Cercis leaf impressions from these beds are the ones whose classification has been questioned because they lack a pulvinus at the base of the leaf lamina. Perhaps our study shows that a pulvinus may not have fossilized as well as lamina. The fossils should be reexamined and if they are otherwise similar to Cercis, perhaps the radiation of the genus into North America should be reexamined.

CHAPTER V

GENERAL DISCUSSION and RECOMMENDATIONS

Chapters II, III, and IV although very different in approaches, have in common the advancement of the knowledge of the evolution of the cauliflorous genus, Cercis. Chapter II deals with how many times cauliflory evolved in the genus Cercis. Chapter III concerns the mechanisms of cauliflory in this genus. This gives weight to the dominance factors that must have been involved in the evolution of this trait. Chapter IV focuses on interpretation of leaf impressions found in the fossil record of Cercis. This may be useful in determining when and from where Cercis radiated into North America. A general discussion of the implications of the research and some recommendations for future research are contained in the following paragraphs.

A comparison of the architecture of cauliflory among most of the species in the genus, Cercis was done for this dissertation and has been published in the Canadian Journal of Botany (Owens et al., 1995). The similar architecture of cauliflory in this small relict genus, with a disjunct geographical distribution, would suggest that cauliflory may be a plesiomorphic characteristic in this group.

Cauliflory may also be a primitive characteristic for the subfamily Caesalpinioideae as it has been reported for taxa in all three groups of primitive Caesalpinioideae

legumes (Cercis, Gleditsia and Ceratonia) (Thompson, 1944, 1946; Paclt,1984; Owens and Ewers, 1991; Owens et al., 1995). If cauliflory occurs in all three groups and they are basal genera for the legume family, it could be a plesiomorphic characteristic for the family. Similar architecture of cauliflory in all three groups could support this.

Cauliflorous architecture could be a useful characteristic for comparing the legumes to other plant families. This characteristic might also be useful in determining affinities within the family, at tribal levels.

Complex dominance relationships were shown to exist between the vegetative and the reproductive buds in Cercis. The complexity in dominance is amplified by second order and even higher order reproductive buds that were not even considered for the experimental study. Results from developmental data and the effects of experimental pruning experiments showed that changes in bud fates were not inflorescence reversions in this taxon.

Relationships between the floral buds in an inflorescence warrant future studies. There are several interesting questions concerning dominance of the buds within each node and inhibition of the lowermost and uppermost floral buds in an inflorescence that remain unanswered for Cercis. Developmentally, the lower-most floral buds may be cleistogamous.

Literature on the fossil record for the Fabaceae prompted the study on the degradation of structures, such as the upper pulvinus in Cercis. The anatomical structure of such organs, cell degrading enzymes and the presence of microorganisms that rapidly decompose non-lignified tissue make them unlikely candidates for fossilization. Perhaps, Heerenden should reevaluate the Eocene fossils from SE North America if the upper pulvinus was used as the major classification characteristic.

The current fossil record for the legumes during the Cretaceous and Paleocene, when archaic genera were presumably evolving and probably more abundant, is almost non-existent. It is possible that in the future the fossil record will include more legumes from this period/epoch. This coupled with more advanced studies on extant taxa may support a reevaluation of what is primitive in the legumes. Until then, present evidence in my opinion indicates that Cercis, Gleditsia and Ceratonia represent the most primitive genera of the Fabaceae.

Interestingly, the earliest known fossil record for Cercis in North America is from the Florissant Lake Beds in Colorado (Knowlton, 1917; MacGinitie, 1953). Perhaps the genus could have entered North America from Eurasia.

The adaptive relevance in of cauliflory in Cercis probably involves genetic variability between reproductive buds on the same plant. Cauliflorous conditions such as

reproductive modules produced on differently aged sections of the same or other branches or trunks would increase the probability of mutations that lead to mosaics. Some of these mosaics will produce progeny through sexual reproduction.

An important and often overlooked characteristic of breeding system/pollination analysis is the number of flowers of a species that open at the same time (Cruden, 1977) and a decrease in plant density (Levin, 1986; Lloyd, 1980). These factors increase the probability of the movement of pollinators among flowers on the same plant (geitonogamy) (Frankie, 1975, Arroyo, 1976, Hessing, 1988). The adaptive relevance of mass flowering according to the genetic mosaic hypothesis would be an increase in the number of ways to acquire genetic recombination; through xenogamy and geitonogamy (Gill, 1986).

In preliminary studies, Cercis appeared to be pollinated by bees that visited many flowers on single trees (unpublished study). Geitonogamous pollination certainly occurs, due in part to the multitude of synchronously maturing cauliflorous buds.

Testing the genetic mosiac hypothesis is difficult. Determining the sexual system of the plant, the choice of modules for geitonogamous pollination, testing for viable pollen and receptive stigmas and anther removal to eliminate the probability of self fertilization are just a few of the

difficulties. After pollination experiments, tests for seed viability and heritable mutations would take many years to complete.

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