

A MONOGRAPH:
MORPHOLOGY OF FLOWER PRIMORDIA
OF SELECTED WOODY PLANTS

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
Edwin David Carpenter, Jr.

1964

This is to certify that the

thesis entitled

A Monograph: Morphology of Flower Primordia
of Selected Woody Plants

presented by

Edwin D. Carpenter Jr.

has been accepted towards fulfillment
of the requirements for

Ph D degree in Horticulture

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Date 14 September 1964







ABSTRACT

A MONOGRAPH: MORPHOLOGY OF FLOWER PRIMORDIA OF SELECTED WOODY PLANTS

by Edwin David Carpenter, Jr.

An investigation was conducted to determine the time of flower bud initiation in selected woody ornamental species which were growing in an existing environment and normally flower in the spring, summer, autumn and late winter at East Lansing, Michigan.

Plants of Cornus mas L., Forsythia ovata Nakai., Spiraea thunbergi Sieb., Prunus glandulosa Thunb., Viburnum lentago L., Pyracantha coccinea Roem. lalandii Dipp., Rosa multiflora Thunb., Viburnum dentatum L., Hibiscus syriacus L., Indigofera potanini Craib., Clematis paniculata Thunb., Hamamelis virginiana L., and Hamamelis vernalis Sarg. were selected to represent 1 of 4 arbitrary seasons: spring (March to May); summer (June to August); autumn (September to November); and winter (December to February). All plants were located on the campus of Michigan State University (latitude 42° 47' N, longitude 84° 36' W) under similar environmental conditions.

Collections of both vegetative and floral buds were made bi-weekly from March 3 to October 27, 1962. In 1963, collection intervals were spaced 3 to 7 or 10 days apart throughout the growing season.

After collection, the buds were trimmed, processed in paraffin before median microscopic sections were cut and mounted for examination.

A MONOGRAPH: MECHANISM OF FLOW IN PRIMORDIAL
OF THE PRIMORDIAL FLOW

Field observations included flowering dates, date of leaf expansion, date of fruit maturation, and the beginning of vegetative growth. During 1962, 1963 and 1964 field observations were recorded 3 times per week throughout the growing season.

In those plants on which the flowers developed directly from initiation to anthesis, it was found that Clematis paniculata Thunb. initiated flower buds during the period of minimum vegetative growth and that Hamamelis virginiana L., Hibiscus syriacus L. and Rosa multiflora Thunb. initiated flower buds during the period of maximum vegetative growth.

In plants where flower development was interrupted by a rest period, all flowers were shown to be present at the time of dormancy except for Pyracantha coccinea Roem. alandii Dipp. and Viburnum dentatum L. Both of these plants showed inflorescence primordia at dormancy and individual flower initiation began the following spring. Cornus mas L., Forsythia ovata Nakai., Hamamelis vernalis Sarg., Prunus glandulosa Thunb., Spiraea thunbergi Sieb. and Viburnum lentago L. flowers were formed at the time of dormancy. Indigofera potanini Craib. initiated flowers throughout the growing season and miniature racemes could be found in various phases of development over-winter.

For the most part, floral structures initiated in acropetal succession. Hibiscus syriacus L. produced involucre bracts first, then sepals, staminal column and petals simultaneously or the petals somewhat later, and lastly the carpels. The order of appearance in the 12 other plants was found to be sepals, petals, stamens, and carpels.

The text is accompanied by 11 figures of camera lucida drawings and photomicrographs, and 16 tables.

These observations included the following: (1) the
date of last observation, and (2) the number of observations
1961, 1962 and 1963 field observations were recorded 3 times per year
throughout the winter season

A MONOGRAPH: MORPHOLOGY OF FLOWER PRIMORDIA
OF SELECTED WOODY PLANTS

By

Edwin David Carpenter, Jr.

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Horticulture

1964

9 33187
7-7-45

DEDICATED TO

Dorothy Lee Carpenter

ACKNOWLEDGEMENTS

To give the proper thanks for all assistance received in this work is more than words can express; for help and encouragement, other than financial, are often subtle and beyond definition.

To the chairman of the guidance committee, Dr. Donald P. Watson, who directed the work and the writing of this thesis, the author's most sincere appreciation. Thanks are expressed to the members of the committee, Drs. J. H. Beaman, L. W. Mericle and C. L. Hamner as well as to Dr. C. M. Harrison; and especially to Mr. C. E. Lewis for his help and suggestions.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
REVIEW OF LITERATURE	4
Tree Fruits	5
Nut Trees	8
Evergreen Fruits	9
Small Fruits	11
Woody Ornamentals	13
MATERIALS AND METHODS	19
RESULTS.	23
<u>Clematis paniculata</u> Thunb.	23
<u>Cornus mas</u> L.	27
<u>Forsythia ovata</u> Nakai.	31
<u>Hamamelis vernalis</u> Sarg.	36
<u>Hamamelis virginiana</u> L.	40
<u>Hibiscus syriacus</u> L.	41
<u>Indigofera potanini</u> Craib.	46
<u>Prunus glandulosa</u> Thunb.	51
<u>Pyracantha coccinea</u> Roem. <u>lalandii</u> Dipp.	55
<u>Rosa multiflora</u> Thunb.	59
<u>Spiraea thunbergi</u> Sieb.	64
<u>Viburnum dentatum</u> L.	68
<u>Viburnum lentago</u> L.	73
CONCLUSION	76
LITERATURE CITED	80

TABLE OF CONTENTS

Page

INTRODUCTION

CHAPTER I

CHAPTER II

LIST OF TABLES

TABLE	Page
1. Geographical Differences of Flower Bud Initiation, .	7
2. Literature Synopsis.	22
3. Growth Characteristic of <u>Clematis paniculata</u> Thunb.	24
4. Growth Characteristics of <u>Cornus mas</u> L.	28
5. Growth Characteristics of <u>Forsythia ovata</u> Nakai . .	32
6. Growth Characteristics of <u>Hamamelis vernalis</u> Sarg.	36
7. Growth Characteristics of <u>Hamamelis virginiana</u> L..	40
8. Growth Characteristics of <u>Hibiscus syriacus</u> L. . . .	42
9. Growth Characteristics of <u>Indigofera potanini</u> Craib.	47
10. Growth Characteristics of <u>Prunus glandulora</u> Thunb.	52
11. Growth Characteristics of <u>Pyracantha coccinea</u> Roem. <u>lalandii</u> Dipp.	56
12. Growth Characteristics of <u>Rosa multiflora</u> Thunb. .	60
13. Growth Characteristics of <u>Spiraea thunbergi</u> Sieb. .	64
14. Growth Characteristics of <u>Viburnum dentatum</u> L. . .	69
15. Growth Characteristics of <u>Viburnum lentago</u> L. . . .	73
16. Summary of vegetative growth, flower bud formation and flowering	77

1. *Table of contents* (see page 1)

2. *Table of contents* (see page 1)

LIST OF FIGURES

FIGURE		Page
1.	Stages in the development of flower buds of <u>Clematis paniculata</u> Thunb.	25
2.	Stages in the development of flower buds in <u>Cornus mas</u> L.	29
3.	Stages of development in flower buds of <u>Forsythia ovata</u> Nakai.	34
4.	Stages of development of the flower buds in <u>Hamamelis vernalis</u> and <u>H. virginiana</u> L.	38
5.	Phases of flower bud development in <u>Hibiscus syriacus</u> L.	44
6.	Flower bud development in <u>Indigofera potanini</u> Craib.	49
7.	Stages in the development of flower buds of <u>Prunus glandulosa</u> Thunb.	53
8.	The development of floral buds in <u>Pyracantha coccinea</u> Roem. <u>lalandii</u> Dipp.	57
9.	Development of flower buds in <u>Rosa multiflora</u> Thunb.	62
10.	Stages in the development of <u>Spiraea thunbergi</u> Sieb. flower buds	66
11.	Stages of flower development in <u>Viburnum dentatum</u> L. and <u>Viburnum lentago</u> L.	71

1. The first part of the table is a list of the names of the authors of the papers.

2.

3.

LIST OF FIGURES

FIGURE		Page
1.	Stages in the development of flower buds of <u>Clematis paniculata</u> Thunb.	25
2.	Stages in the development of flower buds in <u>Cornus mas</u> L.	29
3.	Stages of development in flower buds of <u>Forsythia ovata</u> Nakai.	34
4.	Stages of development of the flower buds in <u>Hamamelis vernalis</u> and <u>H. virginiana</u> L.	38
5.	Phases of flower bud development in <u>Hibiscus syriacus</u> L.	44
6.	Flower bud development in <u>Indigofera potanini</u> Craib.	49
7.	Stages in the development of flower buds of <u>Prunus glandulosa</u> Thunb.	53
8.	The development of floral buds in <u>Pyracantha coccinea</u> Roem. <u>lalandii</u> Dipp.	57
9.	Development of flower buds in <u>Rosa multiflora</u> Thunb.	62
10.	Stages in the development of <u>Spiraea thunbergi</u> Sieb. flower buds	66
11.	Stages of flower development in <u>Viburnum dentatum</u> L. and <u>Viburnum lentago</u> L.	71

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FIGURE

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INTRODUCTION

During the first half of the twentieth century Goff (1899, 1900, 1901), Drinkard (1909), Bradford (1915), Tufts and Morrow (1925), Ranker (1926), Rassmussen (1929), Aaron (1936), and Pickett (1942) produced a wealth of information concerning the time of flower bud initiation of apples, pears, peaches, cherries, plums, apricots and almonds. Their findings have been the basis of establishing times and methods of fertilizing, pruning, cultivating and reducing winter injury (Ruth, 1921; Harley, Masure and Magness, 1932; Crane and Dodge, 1935; Roberts, 1937; and Edgerton and Harris, 1950).

Very little information is available, however, concerning the time of flower bud initiation of woody plants that are not grown primarily for fruit production. It was generally agreed before 1900 that most trees in temperate climates which flowered early in the year produced flower buds at some time during the previous season.

Dr. Beale in 1656 stated that "before December by the bluntness of the bud, you may discover what branch will bear fruit the next season immediately following" (Davis, 1957). Thatcher in 1822 identified the time, and even the cause, more precisely when he said, "the blossom buds are formed by the first sap between April and June and are filled by the second sap between July and October" in the apple (Davis, 1957).

The flowering process is only a single response, is inherited, and involves the reaction of genes and their products to the environment (Salisbury, 1963). This is evident from the fact that a plant commonly flowering in one location may flower at a different time in another location even though the environmental requirement has not changed.

During the first half of the century, the population of the United States grew from 150 million to 200 million. The population of the United States in 1900 was 150 million. The population of the United States in 1950 was 200 million. The population of the United States in 1960 was 205 million. The population of the United States in 1970 was 215 million. The population of the United States in 1980 was 225 million. The population of the United States in 1990 was 235 million. The population of the United States in 2000 was 245 million. The population of the United States in 2010 was 255 million. The population of the United States in 2020 was 265 million. The population of the United States in 2030 was 275 million. The population of the United States in 2040 was 285 million. The population of the United States in 2050 was 295 million. The population of the United States in 2060 was 305 million. The population of the United States in 2070 was 315 million. The population of the United States in 2080 was 325 million. The population of the United States in 2090 was 335 million. The population of the United States in 2100 was 345 million.

The study of flowering in recent years has been conducted from the standpoint of controlled environments and the influence of chemicals (Gartner and McIntyre, 1957; Downs and Piringer, 1958; Boodley and Mastalerz, 1959; MacLean, 1962; Cannon and Gartner, 1963). Yet purely ecological studies of the flowering process have been few; the woody plants of the street, garden and forest having been studied the least.

The initiation of flowers is a change over from the indeterminate to the determinate type of growth. Thus, the initiation of floral organs exchanges the immortality potential for the possibility of combining germ plasm in order to produce a new individual or to perpetuate the original individual. The time of flower initiation depends somewhat on the rate of the preceding vegetative growth. The conditions which influence this rate of growth may, and do, cause differences in the time of flower formation without having affected initiation in any specific manner (Lang, 1952).

Grainger (1939), working in England, was perhaps the first to conduct detailed investigations on flower initiation in ornamentals, especially of English wild woody plants now used as ornamentals. Reports of flower initiation in Gaultheria species (Chou, 1952), Populus deltoides Marsh. and P. tremuloides Michx. (Nagaraj, 1952), Michelia fuscata Blume (Tucker, 1960), Cydonia oblonga Mill. (Zeller, 1960), Pyracantha coccinea Roem. lalandii Dipp. (Reisch, Chadwick and Hildreth, 1961) and Syringa species (Sijtesema, 1962) have since been published.

The present investigation was undertaken to determine the time of flower bud initiation in selected woody ornamental species growing in an existing environment. They were selected to represent species that flower in early spring, summer, autumn and winter. It was designed to obtain information useful for the augmentation and timing

cultural practices such as nutrition, pruning, and irrigation. It was hoped that knowledge about natural potentials possessed by such species might further extend the cultivation of these plants to localities outside their native habitats. It was also intended that plant breeders might find such information useful for selecting suitable parents and improving existing species and cultivars.

their native habitats. It is a very important global issue.

REVIEW OF LITERATURE

In the 19th century Hofmeister, Webb, Pfeffer and Goebel studying the order of succession of floral parts, observed that flowers of angiosperms developed in acropetal succession. Hofmeister (Coulter and Chamberlain, 1903) concluded for instance that carpel primordia of Rosa, Potentilla, and Rubus appeared before stamens reached their full number, and that sepal primordia of Hypericum calycinum L. appeared after the primordia of the stamens. Pfeffer (1872) showed that the petal primordia appeared after that of the stamens in Primulaceae and that each petal apparently formed from the dorsal surface of a young stamen. Goebel (1887) working with papilionaceous flowers of Leguminosae found that the anterior median sepal appeared first followed immediately by those to the right and left. Before the last two sepals were evident, the obliquely posterior petals were visible and these were followed by the 3 other petals in the same order as the corresponding sepals. Webb (1902) explained the order of succession in Astilbe to be sepals, inner stamens, carpels, outer stamens and petals. Thus, acropetal succession of certain cycles followed by basipetal succession of the remaining cycles became evident. Additional modifications of succession can be found in Compositae, Disacaceae, Valerianaceae, Rubiaceae (appearance of sepal primordia after that of the stamens and carpels), and Cruciferae Juss. (petal primordia last to appear).

By cutting buds of Sanguinaria canadensis L. Foersts (1891) found that all floral parts were clearly recognizable in mid-August, that the flower bud cluster of Cornus canadensis L. and the raceme of flower buds of Pyrola elliptica Nutt. were clearly distinguishable at this time.

Objective research regarding the time of flower bud initiation seemed to be lacking until Goff's work in Wisconsin in 1899. Goff stated as a purpose for his studies: "No systematic investigation seems to have been made that gives us any definite knowledge as to the time when the development of the flower actually begins, the rate at which it progresses or the period through which it continues in any of our fruit bearing plants. This information is important because it will enable us to make definite experiments on the effect of special practices upon the formation of flowers." In addition to presenting factual evidence relating to the time of floral initiation, Goff's researches emphasized a technique which has had wide application.

Tree Fruit

During the 1899 season, Goff found that floral growth started about the same time as vegetative growth ceased elongation. Flowers of apple (Malus sylvestris Mill.), plum (Prunus domestica L.) and pear (Pyrus communis L.) were observed to have started growth several weeks before fruit maturation. Flower growth of the cherry (Prunus avium L.), however, was observed to be almost simultaneous with fruit maturation. Goff (1899) observed flower primordia of the 'Hoadley' apple on June 30, 'Rollingstone' plum on July 8, 'Aitken' plum on August 9, 'Wilder Early' pear on July 21 and 'King's Amarelle' cherry on July 11 under natural environmental conditions at Madison, Wisconsin. Acropetal succession was established in all cases.

The apple and pear studies were continued in 1900. Since Goff had removed all of the 'Hoadley' apple flower buds the previous season (1899), these supposedly did not have any flower buds, but many swollen buds of flower bud size were visible in March of 1900. These dissected buds contained flowers. The first evidence of flower formation observed

Optimal control is a branch of applied mathematics
concerned with the design of systems that
achieve a purpose for the system. The optimal control
theory is a branch of applied mathematics.

to have been made that gives us any definite knowledge of the time
when the development of the law of the universe was first
discovered. It is the first time that the law of the universe

in the 'Hoadley' apple and 'Wilder Early' pear was in early September, 1900 but Goff apparently felt that the lateness of the season in 1900 compared to 1899, may have been caused by the removal of the plumpest buds for microscopic study. Goff also observed that flower formation in buds of the apple and pear continued until October during 1900. From these observations he proposed that flower formation may occur during two periods--early summer and mid-autumn until the beginning of cold weather. With the 'Bokara' peach (Prunus persica Batsch. cultivar) Goff observed that flower formation did not begin until late September with the advent of cool nights.

Perhaps stimulated by the findings of Goff the time of flower initiation and differentiation has been investigated in the last few years in a wide range of plant species and cultivars under many varied climatic and geographical conditions. In addition, dissection and classification techniques have been evolved with which comparisons of a quantitative nature can be made among responses under various conditions (Davis, 1957). Table 1 summarizes the findings of several of these workers.

Ranker (1926) did not find a second period of flower bud initiation in the 'Delicious' apple, except in isolated cases where buds developed on second-growth wood. Furthermore, Heinicke (1963) believed that apple flower buds initiated "relatively late in the season" were likely to be abnormal or partially developed. If these buds remained and formed fruit, the resultant fruits were usually small or misshapen.

In England similar results have been observed. Ball (1927) indicated that the 'Victoria' and 'Cambridge Gage' plums initiated flowers from mid-July to early August. Gibbs and Swarbrick (1930) found that apple (Malus sylvestris Mill.) flower buds were initiated at different times depending upon the location of the bud on the tree. Distinct flower primordia were found on July 2 in buds taken from 2-year and 3-year single spurs. Axillary buds on 1-year wood were not collected until the

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Table 1: Geographical Differences of Flower Bud Initiation

Fruit	Date	Area
'Oldenburg' apple	June 30	Virginia
'Kieffer' pear	July 22	Virginia
'Luster' peach	August 5	Virginia
'Whitaker' cherry	September 4	Virginia
'Louis Phillippe' cherry	September 10	Virginia
Plum--American group	September 4	Virginia
Japanese group	September 10	Virginia (Drinkard, 1909-1910)
"Yellow Newton" apple	July 5 to 10	Oregon (Bradford, 1915)
'Gravenstein' apple	June 11	California
'Bartlett' pear	June 21	California
'Elberta' peach	June 30	California
'Royal Ann' cherry	July 3	California
'Early Richmond' cherry	July 12	California
'French' plum	August 15	California
'Wickson' plum	August 15	California
'Royal' apricot	August 10	California (Tufts and
'Nonpareil' almond	September 9	California Morrow, 1925)
'Delicious' apple	June 19	Utah (Ranker, 1926)
'Baldwin' apple	July 15	New Hampshire
'McIntosh' apple	July 22	New Hampshire (Rasmussen, 1929)
'McIntosh' apple (spur buds only)	July 14	Pennsylvania (Aaron, 1936)
Peach - 'Mayflower'	September 13	Texas
'Early Rose Cling'	August 15	Texas
'Dr. Burton'	August 10	Texas
'Frank'	September 3	Texas
'Dee Lee Cling'	September 13	Texas
"late" unnamed	September 13	Texas
'Smith' (Honey)	September 13	Texas (Pickett, 1942)

Table 1. Descriptive Statistics of Survey Data

Variable	Mean	Standard Deviation	Minimum	Maximum
Age	38.5	12.5	18	65
Gender	0.5	0.5	0	1
Education	12.5	1.5	9	16
Income	45,000	15,000	20,000	80,000
Home Value	150,000	40,000	80,000	250,000
Health Insurance	0.8	0.4	0	1
Life Insurance	0.6	0.5	0	1
Retirement Savings	0.7	0.4	0	1
Charitable Giving	0.2	0.3	0	1
Volunteering	0.3	0.5	0	1
Political Participation	0.4	0.5	0	1
Community Involvement	0.5	0.5	0	1
Religious Attendance	0.6	0.5	0	1
Marital Status	0.7	0.4	0	1
Number of Children	1.5	1.0	0	4
Home Ownership	0.8	0.4	0	1
Employment Status	0.9	0.3	0	1
Health Status	0.8	0.4	0	1
Life Satisfaction	0.7	0.4	0	1
Overall Well-being	0.7	0.4	0	1

first week of August but a few buds showed the presence of flower primordia. Thus, both Gibbs and Swarbrick (1930) and Magness (1916) agreed that the axillary buds did not initiate flowers until one month after the spur buds.

In Manchuria, flower bud initiation in the 'Jonathan' apple occurred during the first ten days of July (Watanabe and Yasaka, 1930). Thus, the period of flower bud initiation in Manchuria closely resembled the time of initiation of buds in Oregon (Bradford, 1915). Apple bud initiation in the Malatya district of Turkey occurred about June 20 according to Ulkumen (1940), followed by the pear and by July 30 for the apricot (Prunus armeniaca L.). Ushirozawa and Fukushima (1950) determined that apple buds formed in late June to late August in Japan and found the following: 'Yellow Transparent', 'Early McIntosh' and 'McIntosh Red' apples formed flower buds in the early part of the period; 'Golden Delicious' and 'Newton Pippin' formed flower buds during the middle part of the period; and the 'Delicious', 'Winesap' and 'Jonathan' formed flower buds during the latter part of the period.

Hirai, Nakagawa, Nanjo and Hirata (1961) observed in Japan that flower initiation in Prunus persica Batsch. 'Okubo' varied among 20 climatic regions despite differences of tree age and cultivation methods. Floral initiation was found to occur first on July 10 in the southern districts of Ehime, Kochi, Fukuoka and Miyazaki. Initiation occurred rather uniformly until the last evidence of initiation appeared on July 30 in the northern districts of Fukushima, Yamagata, Niigata, Ishikawa, and Nagano.

Nut Trees

Gardner, Bradford and Hooker (1952) state that Albert (1894, in Germany) found evidence of catkins in the filbert (Corylus avellana L.)

on June 10 before the embryonic leaves were laid down, but the female blossoms were not observed until early September. In the beech (Fagus L. species) Albert did not find flower buds until after leaf fall began but he indicated that initiation must have occurred much earlier since the pollen mother cells had already formed in the anthers.

Shuhart (1927) and Isbell (1928) observed that the pistillate flowers of the pecan (Carya illinoensis Marsh.) were initiated in late winter or early spring at the time when vegetative buds began to swell. These pistillate buds continued development until approximately 10 or more leaves had unfolded. At this time the pistillate flowers became visible. Staminate flowers were observed to initiate later in the season in the lateral buds. They do not complete their development or shed pollen, however, until the following year. Staminate flower initiation has been found to occur on secondary shoots rather late in the summer (Isbell, 1928).

Evergreen Fruits

In Citrus species, flower bud initiation was keyed more closely to periods of active growth and relative quiescence than to calendar dates (Abbott, 1935; Randhawa and Dinsa, 1947; Singh and Dhuria, 1960). Thus, flower initials were generally not seen until approximately the time at which the flower shoot emerged from the bud (Furr and Armstrong, 1956).

Smock (1937) stated that the flower development of the loquat (Eriobotrya japonica (Thunb.) Lindl.) was much like that of the apple flower development which was acropetally oriented. Falta Del Bosco (1961) in Sicily found that in most cultivars of loquat flower initiation began during the first 20 days of June and that in later flowering cultivars flower initiation began the latter part of July. In India, Bajpai and Shukla

no time to follow the instructions. In fact, the instructions were not followed at all. The instructions were not followed at all. The instructions were not followed at all.

But he indicated that instruction must be followed. The instructions must be followed. The instructions must be followed. The instructions must be followed.

The instructions must be followed. The instructions must be followed. The instructions must be followed. The instructions must be followed.

(1962) found two periods of flower initiation; the first being in July to mid-August and the second from the second week of October to the first week of December.

Floral initiation in the mango (Mangifera indica L.) in Florida occurred shortly before the end of October in the Haden, Cambodiana, Brooks and Turpentine cultivars (Mustard and Lynch, 1946). Dormancy has not been found to occur between the time of floral initiation and the time of inflorescence expansion. These data agreed fairly well with observations on the 'Langra' mango in India (Sen and Mallik, 1941).

As explained by Hartman (1951) Morettini first found evidence of olive (Olea europaea L.) flower primordia during the first half of March-- $2\frac{1}{2}$ months before flowering--in Italy. Savastano and Marcucci indicated that flower initiation started at the end of the winter--10 to 15 days before flowering, while in Portugal, De Almeida found that flower bud initiation occurred in the olive cultivars 'Galega' and 'Verdeal' during early February followed by the bloom in May (Hartman, 1951).

Further evidence of the similarity in time of olive flower bud initiation was found by Hartmann (1951) in California. He identified initiation in March--approximately 8 weeks before full bloom. He observed very little difference between the cultivars 'Mission', 'Manzanillo' and 'Swillana' or between the 5 locations in which they were growing. In addition, Hartmann observed no change in the buds from the time they first were recognizable in June until flower parts appeared the following March.

In the avocado (Persea americana Mill.) Reece (1942) found that floral initiation continued over a period of months during the part of the winter when leaf formation and growth were at a minimum.

Small Fruits

In 1900 Goff found flower initials in both the young runners and parent plants of the 'Clyde' strawberry (Fragaria chiloensis Duchesne.) on September 20, with the advent of cool nights.

The time of flower bud formation in the currant (Ribes L. species) varied with the cultivar--'Pomona', July 8; 'White-Grape', October 30; 'Black Victoria', August 3 (Goff, 1901). In the 'Downing' gooseberry (Ribes grossularia L.) and cranberry (Vaccinium macrocarpon Ait.) floral initiation was clearly visible in late August and early to mid-September, respectively. Goff's observations on plants whose flower buds were not readily distinguishable in the autumn (quince, raspberry and blackberry) showed "embryo" flowers to be present with the commencement of dormancy. The grape (Vitis L. species), red raspberry, blackberry (Rubus L. species) not only exhibited these same "embryo" flowers but in addition an "embryo" branch.

MacDaniels (1922) found Rubus L. and Ribes L. species to vary considerably in regard to flower bud initiation in New York. 'Cherry Red' currants were shown to initiate flowers in mid-August. A slight variation in the time of floral initiation in the 'Houghton' and 'Columbus' cultivars of gooseberry was found to be from mid-August to 10 to 14 days later, respectively. Flower initials were observed by MacDaniels in the 'Snyder' blackberry in mid-August just as found by Goff (1901). The red raspberry and 'Columbian' purple-cane raspberry showed only imperfect initiation in the autumn. Early October seemed to be the time of flower initiation in the 'Cumberland' black raspberry.

In Scotland, Mathers (1952) found that floral initiation in Rubus idaeus L. cultivars 'Lloyd George', 'Malling Promise' and 'Malling Landmark' began in mid-September and by the last week of September a definite inflorescence axis was terminated by the first formed flower.

Further development was observed to be basipetal in an irregular spiral with rapid development occurring during October.

Further investigation in Scotland on the genus Rubus L. (Robertson, 1957) showed that in the red raspberry, purple-cane hybrid raspberry and loganberry early flower initiation and considerable further development occurred in the autumn. Whereas, in the blackberry and black raspberry development of flower primordia occurred mainly in the spring.

Lacroix (1926) reported that the cranberry (Vaccinium macrocarpon Ait.) flower primordia were first visible during the middle of August in Massachusetts. The incipient flower started as a minute lateral "out-pushing", and developed acropetally. Cranberry flower buds passed the winter without stamens or carpels; stamens becoming evident in mid-April and carpels from early to mid-May.

Floret formation in the lowbush blueberry (Vaccinium angustifolium Ait.) was initiated during June (Bell and Burchill, 1955). During July, floral parts differentiated in acropetal succession. The miniature, epigynous floret was thus completely formed by the first of August. Active growth, including the initiation of meiosis did not generally start until April of the following year. Meiosis was completed in the anthers by the first week of May and in the carpel approximately 1 week late, but Eggert (1957) concluded that flower initiation apparently did not occur until after the death of the terminal growing point.

In Vitis labruscana Bailey 'Concord' cluster initiation occurred in the young buds and continued in newly formed buds throughout the growing season (Snyder, 1933). Snyder stated that "cluster primordia were initiated in newly forming buds" simultaneously with the "development of the early buds, so that by the end of the growing season all buds on the shoot contained approximately the same number of primordial clusters."

Further development was observed in the following in the following period
with rapid development occurring during 1950-51
Further investigation is required on the ground in 1951-52

It was shown that in 1951-52 the following was observed
and is reported in the following

The following is a summary of the results of the investigation

The first flower clusters have been shown to be evident in early June. Growth of this cluster was rather rapid until mid-July when both cluster and shoot growth slowed down. At this time the secondary clusters continued to branch so that numerous tertiary clusters were discernible at the end of the growing season. The differentiation of definite floral structures occurred in an acropetal order immediately following initiation of the flower clusters. The first evidence of flower formation occurred approximately in late April--at the time of bud swelling--appearing first and determinately in basal sub-clusters (Snyder, 1933).

Winkler and Shemsettin (1937) indicated that cluster primordia of Vitis vinifera L. 'Sultanina' began to initiate during the first week of June in California. This primordium appeared as a blunt, rather broad outgrowth of the bud apex. The formation of a bract was the first indication that division of the primordial cluster had occurred and took place a week to 10 days after the cluster was initiated. Lateral clusters were then initiated in the axils of these bracts. Thus, by the end of the growing season the lateral surface of the primordial cluster was a mass of bracts and branch primordia, the tendrils being initiated somewhat later in the season.

Zeller (1960) agreed with Goff (1901) that flower initiation in the quince (Cydonia oblonga Mill.) commenced in the autumn. In addition, Zeller found that flower initiation and development occurred throughout the winter.

Woody Ornamentals

In a study of greenhouse roses, Hubbell (1934) found that the first evidence of flower initiation was seen 8 days after an axillary bud had been made to assume the terminal position by removal of the terminal bud. The first actual differentiation was evident on the ninth day when sepal protuberances were observed. On the other hand, Laurie and

The first flower cluster to be seen was in the middle of the field. Growth of this cluster was very rapid and it was very large.

and some growth showed down. At first time the seedlings appeared continued to progress so that numerous plants of these were visible.

At the end of the first year the plants were very small and the growth was very slow.

During the second year the plants were very small and the growth was very slow.

During the third year the plants were very small and the growth was very slow.

Bobula (1938) found that the first evidence of initiation occurred 16 to 18 days after an axillary bud assumed the terminal position. Sepal primordia were observed to be present in buds which had been in the terminal position for 14 to 18 days. The order of succession was found to be acropetally oriented.

Grainger (1939) studying various wild plants in England arranged them by their type of flowering organization. In summary he found the following:

- I. Direct flowering plants where development from the first sign of flower initials to anthesis was uninterrupted.

- A. Direct flowering from the period of maximum vegetative growth; flowers were initiated when leaf growth was at a maximum (most common type).

<u>Calluna vulgaris</u> Hull.	initiated June 30 flowered August 20
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<u>Erica cinerea</u> L.	initiated July 26 flowered August 20
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<u>Rosa canina</u> L.	initiated April 24 flowered June 25
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- B. Direct flowering from the period of minimum vegetative growth; flowers were initiated in the late autumn or winter.

<u>Lonicera periclymenum</u> L.	initiated March 12 flowered August 10
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- II. Indirect flowering plants--a rest interval between flower formation and anthesis.

- A. Indirect flowering from the period of maximum vegetative growth; flowers were initiated toward the end of summer and the flower buds were usually complete; flowering occurred in the early months of the following year.

<u>Vaccinium myrtillus</u> L.	initiated July 17 flowered following May 6
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terminal position for 14 to 18 days. 1. A series of small, round, white to light

(to be a yellowish white)

to be a yellowish white

Salix caprea L.

initiated July 9
flowered following March 11

Ilex aquifolium

initiated August 15
flowered following June 17

B. Indirect flowering from the period of minimum vegetative growth; flowers were initiated after the leaves have withered and a period of dormancy follows after every organ was complete. Many bulbs of horticultural value.

III. Cumulative flowering--flower initials were produced in regular succession and all emerged together.

Plantago lanceolata L.

initiated February 17
flowered May 15

Taraxacum officinale Weber.

initiated November 9
flowered following April 30

IV. Climax flowering--a plant might be entirely vegetative for a number of years and then entirely floriferous for a year.

Some species of Agava L.

Chou (1952) investigated the flower morphology of Gaultheria procumbens L., G. ovatifolia Gray, and G. shallon Pursh, and found flower initiation to occur during June at Chicago, Illinois. After initiation, bud development proceeded rapidly with anthesis occurring in mid-July. All floral parts formed in acropetal succession.

Working with Populus deltoides Marsh. and P. tremuloides Michx., Nagaraj (1952) found that the pistillate catkins appeared near the end of the summer, whereas the staminate catkins arose toward the first part of the summer. Both catkins remained as buds during the winter and completed development early the following spring. The differentiation of the individual flowers was essentially acropetally and spirally oriented.

Flower buds of Prunus yedoensis Matsum. were initiated approximately August 8 in Japan (Kosugi, 1951-1952). Development continued in acropetal succession rather rapidly until approximately November 1

When early anthers, without primary sporogenous tissue were present. The differentiating sporogenous tissue was first observed on November 28 and pollen grains were completely developed by March 20. Carpel development followed the anther development except that it was observed to start about October 17.

Downs and Piringer (1958) in an experiment on the flowering response to photoperiod in various Viburnum species found that photoperiod did not seem to control flower initiation, although marked differences in the extent of flower bud formation were evident among the species. Viburnum burkwoodii Burkwood and V. chenaultii produced at least 1 flower bud per plant; only one-quarter of the plants of V. carlesii Hemal. formed flower buds; and V. juddii Rehd. and V. plicatum Thunb. tomentosum Miq. did not form visible buds by August 20 when the experiment was concluded. These authors indicated that those flower buds which did form appeared to be single terminal buds tightly subtended by bracts. However, upon microscopic study, each bract contained an entire inflorescence and in addition, in the axils of each bud an individual minute flower bud was produced. These minute flower buds remained compressed and inconspicuous throughout the entire experiment.

Downs and Piringer (1958) conducted a field experiment using the plants from the previous experiment with photoperiods. Five plants of each species (except V. plicatum Thunb. tomentosum Miq.) from each photoperiodic treatment were transplanted on August 20, September 17 and October 15. The small flower buds already visible were observed to expand and appeared as enlarged bud clusters on plants of each group 6 weeks after field planting. Certain buds of V. carlesii Hemal. (previously under 8 and 12 hours of light) developed until the corolla tubes expanded and colored; erratic anthesis often followed. By mid-December marked differences in total flower-bud formation were noted. V. carlesii Hemal. and V. juddii Rehd. were found to form no flower

buds after planting in the field. However, the flower buds of V. burkwoodii Burkwood and V. chenaultii nearly doubled in number. Some of these new flower buds may have formed in the greenhouse, but since plants on longer daylengths were forming leaves at that time, these new flower buds had more than likely been initiated in the field.

Flower initiation began in Syringa vulgaris L. 'Charles Joly' 29 to 35 days after anthesis of the first flowers in Ohio (Chadwick, Reisch and Traylor, 1959), in contrast to June 21 in the Netherlands (Sijtesema, 1962).

In Michelia fuscata Blume, growing in a conservatory in St. Paul, Minnesota, Tucker (1960) found that the vegetative apex was active the entire year and that periodicity was shown by the type of axillary bud produced. Axillary buds formed in the autumn and winter became vegetative whereas those axillary buds initiated in the spring and early summer became floriferous. In each axillary flower bud, initiation of bracts and perianth occurred in May and June; the stamens appeared from July through August and the carpels developed from July through September. Thus, there was evidence of acropetal succession of floral parts, but all flower buds were found to be in different stages of development at the same time.

Reisch, Chadwick and Hildreth (1961) found that the initiation of the inflorescence of Pyracantha coccinea Roem. lalandii Dipp. was first evident in late October with some inflorescent initiation occurring in late March the following year. It was also observed that the greatest development occurred during April with sepal primordia becoming evident in late April. This finding coincides with that of Girouard (1962) who stated that most floral part primordial stages were not complete until early May and that floral appendages differentiated over a period of 64 days in 1961 at Columbus, Ohio.

[illegible]

The results of Girouard's (1962) examinations showed that sepals were initiated on the flanks of the floral apex when the primordia averaged $100\ \mu$ in width. The 5 petal primordia arose simultaneously when the sepal primordia were $50\ \mu$ high and the concave apical meristem averaged $85\ \mu$ in width. In addition, the stamens apparently originated simultaneously with the petals or quickly in succession since few microscopic preparations showed petal primordia without stamen primordia. Carpel formation followed closely with the result that locules were present in the carpels at the time primary sporogenous tissue was evident in the stamens. Microsporogenesis and megasporogenesis were observed to be limited to the last 3 weeks preceding anthesis.

... 100 ft in width. The 2nd bed is ...
when the ... were 50 ft ...
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MATERIALS AND METHODS

All plant materials were selected to represent 1 of the following 4 arbitrarily defined seasons: spring (March to May); summer (June to August); autumn (September to November); and winter (December to February). In addition, the following plants were chosen for a succession of flowers during each of the 4 seasons but with a limited amount of overlapping of the flowering periods.

Spring	early	<u>Cornus mas</u> L. and <u>Forsythia ovata</u> Nakai.
	mid	<u>Spiraea thunbergi</u> Sieb. and <u>Prunus glandulosa</u> Thunb.
	late	<u>Viburnum lentago</u> L.
Summer	early to mid	<u>Pyracantha coccinae</u> Roem. <u>lalandii</u> Dipp. <u>Rosa multiplora</u> Thunb. <u>Viburnum dentatum</u> L.
	mid to late	<u>Hibiscus syriacus</u> L.
	all season	<u>Indigofera potanini</u> Craib.
Autumn	early to mid	<u>Clematis paniculata</u> Thunb.
	mid autumn to early winter	<u>Hamamelis virginiana</u> L.
Winter	late winter to early spring	<u>Hamamelis vernalis</u> Sarg.

Specimen plants were selected at various permanent locations on the campus of Michigan State University (latitude $42^{\circ}47' N$, longitude $84^{\circ}36' W$) to supply sufficient samples over a 2 year period. Since mature plants of large size or a large group of less mature plants in 1 location were required to supply a sufficiently large number of collections some variations in the environmental conditions of shade, exposure, soil, and irrigation were necessary.

STATE AND COUNTY

At the time of the first census, the population of the State of New York was 1,100,000. The population of the State of New York in 1900 was 4,500,000. The population of the State of New York in 1910 was 5,500,000. The population of the State of New York in 1920 was 6,500,000. The population of the State of New York in 1930 was 7,500,000. The population of the State of New York in 1940 was 8,500,000. The population of the State of New York in 1950 was 9,500,000. The population of the State of New York in 1960 was 10,500,000. The population of the State of New York in 1970 was 11,500,000. The population of the State of New York in 1980 was 12,500,000. The population of the State of New York in 1990 was 13,500,000. The population of the State of New York in 2000 was 14,500,000. The population of the State of New York in 2010 was 15,500,000. The population of the State of New York in 2020 was 16,500,000.

Collections of both vegetative and reproductive buds were made at frequent intervals. During 1962, collections of buds were made at approximately the same time of day every 14 days starting on March 3 and ending October 27.

During 1963 collections of buds were taken more frequently. Samples from the winter, spring and summer groups were collected every other day from March 1 until the flower buds were visible and fully swollen. The autumn flowering specimens were collected every 7 to 10 days until growth was rapid at which time samples were taken every other day until late summer. From the time the flower buds were visible and clearly identifiable, samples were collected less frequently--5 to 7 days apart.

From early November, 1963 until early April 1964 collections were made at 3 to 4 week intervals. Collections were terminated at the end of April, 1964.

For the purposes of this investigation, the time of flower initiation was considered to be that time at which the meristem was observed to be somewhat elongated and showed a definite broadening and flattening of the buttress. Differentiation was considered to start when the first protuberances were noticed emerging from the buttress surface. When the flower was completely formed in the bud, differentiation was considered to be ended.

After collection each bud specimen was trimmed of excess parts, placed in a 2 ounce bottle containing formalin-acetic acid--70 percent alcohol (FAA) solution and evacuated in an aspirator for at least 12 hours, and stored in FAA.

During 1962 the alcohol-chloroform (with Eosin B added to the 70 percent alcohol solution) dehydration series was used exclusively. During 1963 and 1964 the tertiary butyl alcohol (TBA) dehydration series was substituted to save time with the larger number of samples needed.

Eosin B was added to the 70 percent TBA solution to aid in ease of placement of the specimens in the paraffin blocks, and a 35 percent and 70 percent TBA-paraffin oil solution were substituted for the 50 percent paraffin oil solution. Embedding was accomplished in $56^{\circ}\text{C.} (\pm 1^{\circ}\text{C.})$ "Tissuemat" paraffin.

In order to facilitate sectioning, buds were placed in a softening solution (2:1 70 percent alcohol-glycerin solution) for about $1\frac{1}{2}$ weeks. Since dormant buds of Hamamelis vernalis Sarg. and Hamamelis virginiana L. were still too hard for cutting another softening solution containing 75 parts absolute alcohol, 15 parts glycerin and 20 parts glacial acetic acid was employed for buds of these species. After this treatment for 2 weeks these buds were sufficiently soft to be sectioned without difficulty.

Microscopic sections were made on a rotary microtome 12 to 15 micra in thickness. Median sections were mounted on microscopic slides and stained with Heidenhain's hematoxylin using ferric ammonium sulfate (purple crystal) as the mordant. More than 7000 slides were prepared and observed.

The following field observations of seasonal traits were recorded for all plants: flowering dates, date of leaf expansion, date of fruit maturation, fruit type and color, and the time vegetative growth began. The first flowering date was considered to be the time the plant first produced flowers. The final date was considered to be the date at which 90 percent or more of the flowers had faded. The date of fruit maturation was recorded when 90 percent of the fruit showed mature color (Table 2). The date of leaf expansion was considered to be that date on which the average length of 10 leaves--in centimeters--fell within the limits designated in Table 2. The date of vegetative growth commencement was considered to be that date on which vegetative parts could be seen with the naked eye pushing through the bud.

Field observations during 1962, 1963 and 1964 were recorded 3 times per week throughout the growing season.

Table 2: Literature Synopsis

Plant	Flowering Time	Fruit Maturation	Fruit Color	Fruit Type	Flowers or Wood of	Family
<u>Clematis paniculate</u> Thunb.	Sept. -Oct.	Fall	Silvery	Achene	Current year	<u>Ranunculaceae</u>
<u>Cornus mas</u> L.	March-April	Early fall	Scarlet	Berry	Previous year	<u>Cornaceae</u>
<u>Forsythia ovata</u> Nakai.	April-May	Fall	Brown	Capsule	Previous year	<u>Oleaceae</u>
<u>Hamamelis vernalis</u> Sarg.	Dec. -March	Fall	Brown	Capsule	Previous year	<u>Hamamelidaceae</u>
<u>Hamamelis virginiana</u> L.	Sept. -Oct.	Fall of next season	Brown	Capsule	Current year	<u>Hamamelidaceae</u>
<u>Hibiscus syriacus</u> L.	Aug. -Sept.	Fall	Brown	Capsule	Current year	<u>Malvaceae</u>
<u>Indigofera potanini</u> Craib.	June-July	Fall	Reddish-brown	Legume	Current year	<u>Leguminosae</u>
<u>Prunus glandulosa</u> Thunb.	May	Mid-summer	Scarlet	Berry	Previous year	<u>Rosaceae</u>
<u>Pyracantha coccinea</u> Roem. lalandii Dipp.	May-June	Fall	Red-orange	Pome	Current year	<u>Rosaceae</u>
<u>Rosa multiflora</u> Thunb.	June-July	Fall	Orange-red	Hip	Current year	<u>Rosaceae</u>
<u>Spiraea thunbergi</u> Sieb.	April-May	Early summer	Brown	Follicle	Previous year	<u>Rosaceae</u>
<u>Viburnum dentatum</u> L.	May-June	Early fall	Blue-black	Berry	Current year	<u>Caprifoliaceae</u>
<u>Viburnum lentago</u> L.	May-June	Fall	Blue-black	Berry	Previous year	<u>Caprifoliaceae</u>

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RESULTS

Clematis paniculata Thunb. (Ranunculaceae Juss.)

Gross Morphology: The period of vegetative growth began from mid-April to early May from axillary buds near the crown of the plant. Much of the previous season's growth of this vine died back without harm to the plant. Vegetative growth continued at a rapid rate until the end of June. At this time, a reduction in growth resulted from the decrease in the length of the nodes accompanied by an increase in size of the axillary buds. The normal vegetative growing point became a long, slender tube with the nodes spaced further apart (Figure 1-A). Vegetative growth stopped entirely when the first flower buds became visible in mid-July.

Flower formation began at the same time vegetative growth began to decrease. Flower initiation became evident from mid to late July with anthesis occurring between mid-August and early September. The "king" flower of the panicle was the first to be initiated with the others following in succession. The "king" flower was also the first to open with others following rapidly. Flowering occurred acropetally on current season's growth.

Fruits matured a week to a week and a half after flowering. While the fruit was maturing on some flower receptacles other flowers were developing to anthesis. Normally a small amount of flower development occurred during the period of anthesis.

Table 3: Growth Characteristics of Clematis paniculata Thunb.

Year	Vegetative Growth Began	<u>Flowering</u>		Flower Bud First Visible to Naked Eye	Date of Initi- ation	Days from Initiation to Flowering
		Began	Ended			
1962	5/5	8/15	10/19	7/10	6/26	40
1963	3/29	8/15	9/18	7/14	7/16	30
1064	4/16	8/27		7/17		

Vegetative Apex: Before vegetative growth commenced in the spring, the vegetative apex was a low, compressed primordial mass with a rather shallow buttress (Figure 1-B). As growth started the growing point soon was high and dome-like (Figure 1-C). Several pairs of opposite primordial leaves were visible in the last half inch of the growing point until floral appendages started to appear. The high domed buttress presented a high degree of cell disorganization during growth. An organized 2-celled tunica layer was visible, however.

Floral Apex: Floral primordia became evident about 30 days before anthesis (Figure 1-D). At this time, the petaloid sepals were strongly visible enclosing a rather high primordial dome. The dome at this time had begun to widen somewhat at the base. Approximately 5 days later protuberances were formed on this enlarged basal area (Figure 1-E). The high dome was still present as stamen primordia were being laid down. Several cycles of stamens were initiated and began growth. At the end of July the anthers began to expand and carpels were initiated (Figure 1-F), and the high dome became non-existent. The dome became the receptacle on which the achenes rested. Some 10 days later, locules in the carpels could be identified as well as ovule development (Figure 1-G). By this stage the stamens had surmounted the carpels. By late August the carpels and stamens were well developed



Figure 1: Stages in the development of flower buds in Clematis paniculata Thunb.

- A. Left --vegetative bud.
Right--flower buds a few days before anthesis.
- B. Vegetative apex during dormancy (approx. 35x).
- C. Vegetative apex after growth resumed (approx. 35x).
- D. First indication of flower bud formation (approx. 45x).
- E. Stamen primordia laid down (approx. 45x).
- F. Carpel initiation (approx. 25x).
- G. Flower a few days before anthesis (approx. 10x).
- H. Ovule development (approx. 18x).



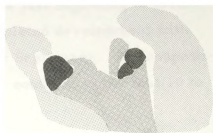
A



B



C



D



E



F



G



H

and microsporogenesis and megasporogenesis were almost completed (Figure 1-H). Four to five days later anthesis occurred, first in the "king" flower and progressed successively to each of the other flowerd in the panicle.

Flower initiation occurred during mid-summer after approximately 60 days of vegetative growth. A high domed buttress enclosed by petaloid sepals was apparent at first. By the end of July the stamens were developing rapidly and the carpels were just beginning to form. During August the carpels and stamens completed development with anthesis occurring from late August to early September. Microsporogenesis and megasporogenesis seemed to be confined to the last 10 to 14 days of flower development.

Cornus mas L. (Cornaceae Lk., Section macrocarpum Spach.)

Gross Morphology: Vegetative growth commenced in April after flower anthesis and continued rapidly until the end of May. At this time growth began to slow down as buds began to develop, but the flower and vegetative buds were not distinguishable. Growth ceased altogether during mid-June when flower buds became visible. Both types of buds were observed to enlarge through the summer. The flower buds at the time of dormancy were approximately one-quarter inch in diameter and the vegetative buds about one-eighth inch in diameter in mid-October. Buds passed the dormant season in this condition (Figure 2-A).

Floral growth became evident during late May or early June and progressed rapidly until the end of August. At this time the floral parts were complete but microsporogenesis and megasporogenesis had not begun. The flower over-wintered in this stage, completing development with the commencement of growth the following spring. Anthesis occurred in early April, 4 to 5 days before vegetative growth appeared.

The fruit matured in mid-August, developing and reaching maturity with the flower buds.

Table 4: Growth Characteristics of Cornus mas L.

Year	Vegetative Growth Began	Flowering		Flower Bud First Visible to Naked Eye	Date of Initi- ation	Days from Inflorescent Initiation to Flowering
		Began	Ended			
1962	4/26	4/22	5/3	6/12	5/28	
1963	4/6	4/2	4/24	6/12	5/27	309
1964	4/18	4/13	4/23	5/28		321

Vegetative Apex: The vegetative apex presented a shallow concave surface with leaf primordia cut off in an opposite arrangement (Figure 2-B). The buttress consisted of a tunica at least 2 cells deep. The corpus appeared to have cells stacked in a modified tier arrangement. As vegetative growth progressed and new leaf primordia were cut off, the buttress appeared to flatten out slightly (Figure 2-C). Although this feature was observed frequently it could not be associated only with floral growth.

Floral Apex: The first indication of flower formation was a broad and flattened buttressed surface (Figure 2-C) in late May. The floral apex at this time was observed to be somewhat wider than in a vegetative apex which showed a flattened apex. Four to five days later the apex surface presented a series of ridges which eventually developed into florets (Figure 2-D). Each ridge-like primordial mass represented a floret of the umbel. By mid-June the primordial mass developed into a cup-shaped receptacle with sepal primordia present and a slight convex-shaped surface (Figure 2-E). At the same time, or 2 or 3 days later,

The first method is not suitable for the present purpose.

with the lower body.

Table 1. Summary of the results of the present study.

Table 1. Summary of the results of the present study.



Figure 2. Stages in the development of flower buds in Cornus mas L.

- A. Vegetative bud, left.
Flower bud, right.
- B. Vegetative apex (approx. 45x).
- C. First indication of inflorescence formation (approx. 45x).
- D. Floret initiation (approx. 35x).
- E. Sepal formation (approx. 35x).
- F. Petal primordia (approx. 30x).
- G. Stamen initiation (approx. 35x).
- H. Carpel and disk formation (approx. 30x).
- I. Antropous ovule and microsporogenesis (approx. 25x).
- J. Flower bud with the onset of dormancy (approx. 10x).



petal primordia had emerged (Figure 2-F). By late June the stamen primordia could be ascertained (Figure 2-G). Sepal elongation had ceased, a carpel with a locule became visible, and a very small disk was beginning to form (Figure 2-H) during the last 2 or 3 days in June; the petals had lengthened, encircling the floret. Floral development during July appeared to have decreased after rapid development during June. Ovule development and microsporogenesis appeared to begin at approximately the same time in mid to late July. By late July the anatropous ovule was evident as was microsporogenesis (Figure 2-I). The flower bud continued to expand until the time of dormancy, with microsporogenesis being completed and the ovule developed to at least the point of megasporogenesis (Figure 2-J). In early spring megasporogenesis apparently began at least 2 weeks before and was completed several days before flowering. Some evidence was found, but could not be substantiated, that megasporogenesis began in the late fall.

The inflorescence was initiated in late May with floret primordia appearing 4 to 5 days later. Floret development occurred in acropetal succession rather rapidly until early July. Carpels were evident in early July, however, ovule development did not begin until mid to late July. Ovule development and microsporogenesis appeared to begin at approximately the same time. When dormancy set in, microsporogenesis had been completed. Megasporogenesis appeared to take place in early spring, starting at least 2 weeks before anthesis. Anthesis occurred in early to mid-April.

Forsythia ovata Nakai. (Oleaceae Lindl.)

Gross Morphology: Vegetative growth began during April and continued rather rapidly until the first of June, when growth began to decrease until it completely stopped at the end of June. Buds became

partial retrogression has not occurred (Figure 10). The basal part of the section

formation could be not considered (Figure 10). The basal part of the section

formed, a sample with a fairly low degree of metamorphism, and a very small area

was beginning to form (Figure 10). During the time of the formation of the

the petals had a fairly low degree of metamorphism, and a very small area

during the time of the formation of the petals had a fairly low degree of

metamorphism, and a very small area

of

evident toward the end of May but were not distinguishable except by position. Vegetative buds were produced in the axils of leaves and at the apex of the new shoot (Figure 3-A). In many cases vegetative buds were not observed in axils of the 2 most proximal leaves.

Flower buds became clearly evident by the end of June toward the base of the current season's growth. Flower buds were often situated in the axils of the 2 most proximal leaves. Development of flower buds continued through the summer and by the end of October these buds were approximately twice as large as the vegetative buds. The flower buds were commonly in a multiple collateral arrangement (Figure 3-A).

Fruit development started soon after flowering and was evident through the summer. The tear-drop shaped fruit matured in late September to early October.

Table 5: Growth Characteristics of Forsythia ovata Nakai.

Year	Vegetative Growth Began	<u>Flowering</u>		Flower Buds First Visible to Naked Eye	Date of Initi- ation	Days from Initiation to Flowering
		Began	Ended			
1962	4/26	4/21	4/30	5/12	6/10	
1963	4/3	4/2	4/25	5/11	5/20	296
1964	4/17	4/12	4/25	5/14		328

Vegetative Apex: The vegetative apex appeared as a rather high concave buttress with leaf primordia cut off in an opposite arrangement (Figure 3-B). The tunica consisted of 2 highly organized cell layers and 1 cell layer not as highly organized. The corpus was about 5 to 7 cells deep with the upper cells apparently part of the third cell layer of the tunica.

evidence showed the soil of the ... and there was ...
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Floral Apex: The first indication of flower formation became apparent in mid-June when the surface was flat across the top of a raised buttress (Figure 3-C). Sepal primordia appeared a few days later surrounding a concave buttress which was shallow (Figure 3-D). By the end of June the buttress surface was much lower in outline (Figure 3-E) with petal primordia evident in early July (Figure 3-F). Stamen primordia were evident by mid-July and by the end of July (or occasionally August), the carpel and a locule were present (Figure 3-G). Ovule formation was observed in mid-August (Figure 3-H) at the time of microsporogenesis, when the carpel had elongated considerably displaying the 2-lobed stigma of the style. The flower bud continued to expand until mid-September when the anatropous ovule was distinct and microsporogenesis appeared to have been completed (Figure 3-I). At this time the microstyle was evident with a short 2-lobed stigma and 2-loculed ovary. The flower bud was approximately three-quarters of an inch in length and quite plump. The bud overwintered in this stage and completed development the following spring when megasporogenesis commenced approximately 2 weeks before anthesis.

The floral apex was slightly concave until the petal primordia were formed. Floral parts initiated in an acropetal succession beginning during mid-June. Ovule formation and microsporogenesis were evident during mid-August and were completed by the end of September. Megasporogenesis was not observed until approximately 2 weeks before anthesis. Anthesis took place from early to mid-April.

1. The first part of the report is a general introduction to the subject of the study. It discusses the importance of the study and the objectives of the research.

2. The second part of the report is a detailed description of the methodology used in the study. It includes information about the sample size, the data collection methods, and the statistical analysis techniques.

3. The third part of the report is a discussion of the results of the study. It presents the findings of the research and discusses their implications for the field of study.

4. The fourth part of the report is a conclusion and a summary of the main findings of the study. It also includes recommendations for further research.

5. The fifth part of the report is a list of references. It includes all the sources of information used in the study.

6. The sixth part of the report is an appendix. It contains additional information that is not included in the main body of the report.

7. The seventh part of the report is a glossary. It defines the key terms and concepts used in the study.

8. The eighth part of the report is a list of figures and tables. It includes all the visual aids used in the study.

9. The ninth part of the report is a list of abbreviations. It defines the abbreviations used in the study.

10. The tenth part of the report is a list of symbols. It defines the symbols used in the study.

11. The eleventh part of the report is a list of acronyms. It defines the acronyms used in the study.

12. The twelfth part of the report is a list of footnotes. It includes all the footnotes used in the study.



Figure 3: Stages of development in flower buds of Forsythia ovata Nakai.

- A. Vegetative (left) and flower buds (right).
- B. Vegetative apex (approx. 45x).
- C. First appearance of flora structures (approx. 45x).
- D. Sepal primordia (approx. 45x).
- E. Stage just before petal initiation (approx. 45x).
- F. Petal formation (approx. 40x).
- G. Stamen primordia, carpel and locule (approx. 30x).
- H. Ovule formation (approx. 30x).
- I. Flower bud as it over-wintered (approx. 10x).





Hamamelis vernalis Sarg. (Hamamelidaceae Lindl.)

Gross Morphology: Vegetative growth began in mid-April 1 to 3 days after flowering had occurred. Shoot and leaf growth continued rapidly until mid to late June at which time flower buds were distinguishable. Stem growth was observed to average approximately 6 to 8 inches during the period of greatest activity. Vegetative growth began to decrease in length during mid-June and had ceased completely by mid-July.

Floral bud clusters became evident from mid to late June. They appeared as a small rounded mass of tissue surmounting a peduncle about one-quarter inch long. As the season progressed, the size of the cluster mass continued to increase until the individual flowers could clearly be distinguished by mid to late July (Figure 4-A). The flower clusters were observed to contain 1, 2, or 3 flowers and very rarely 4 flowers. The individual flowers continued to develop and swell until dormancy at which time they were approximately one-eighth inch in diameter. The buds remained in this condition over-winter and anthesis took place in mid-March the following year. All flowers were produced on the previous season's wood.

Fruit development started soon after the flowers wilted and continued throughout the summer. The woody capsule matured in early to mid-October of the same year of anthesis.

Table 6: Growth Characteristics of Hamamelis vernalis Sarg.

Year	Vegetative Growth Began	Flowering		Flower Buds First Visible to Naked Eye	Date of Initi- ation	Days from Initiation to Flowering
		Began	Ended			
1962	4/14	3/17	4/14	6/19	6/10	
1963	4/18	3/18	4/18	6/12	6/3	281
1964	4/18	3/2	4/14	5/28		273

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Vegetative Apex: The vegetative apex was observed to consist of a rather high concave, evenly rounded surface with leaf primordia cut off alternately (Figure 4-B). A 1-celled tunica was present with a highly disorganized 10 cell deep corpus beneath the tunica. Vegetative apices, in general, were axillary with the exception of the terminal point for approximately 4 inches proximal to the terminal.

Floral Apex: Flower initiation began in late May to mid-June. At this time the floral apex showed a central pyramidal column of tissue, sloping gradually to the bracts which surrounded the apex (Figure 4-C). The tissue between the bracts and column was highly meristematic and by late May had flattened out considerably (Figure 4-D). The surface of the flattened area also showed a slight protuberance which later developed into a flower. The outer bracts at this time had elongated some and covered the flower cluster. In early June the bracts of the individual flowers became visible (Figure 4-C). Also visible at this time was a slight concave surface on the concave buttress surface with the first evidence of the sepals (Figure 4-F). The petals became evident from early to mid-July (Figure 4-G). The stamens arose simultaneously or soon after the petals. At the same time very small carpel primordia were present. In early August, the carpel was well-developed including the presence of a locule (Figure 4-H). Ovule formation and microsporogenesis were not observed. Ovules, however, were formed from late August to early September (Figure 4-I). Microsporogenesis had begun at this time also. Pollen grains were completely formed at the time of dormancy (Figure 4-J). Most ovules remained undifferentiated throughout the winter with megasporogenesis starting 5 or 6 days before anthesis. Anthesis occurred in mid to late March.

Flower initiation began in early June approximately 45 days after vegetative growth began. The individual flowers in the cluster became visible in early June. The sepals, petals, stamens and staminoids, and

[illegible]

Figure 1. Stages of development of the Great Salt Lake in
western Utah, and its extension to the west.

Figure 4: Stages of development of the flower buds in Hamamelis vernalis Sarg. and H. virginiana L.

- A. Vegetative bud, right
Flower bud, left.
- B. Vegetative apex (approx. 35x).
- C. Floral apex (approx. 35x).
- D. Primordia of inflorescence (approx. 35x).
- E. Bracts of flowers and flattened buttress (approx. 30x).
- F. Appearance of sepal primordia (approx. 40x).
- G. Petal primordia (approx. 40x).
- H. Carpel with locule (approx. 40x).
- I. Ovule formation (approx. 20x).
- J. Flower at the onset of dormancy or before anthesis (approx. 10x).



A



B



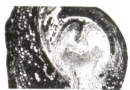
C



D



E



F



G



H



I



J

carpels arose in acropetal succession throughout the summer. Ovule formation became evident during early September at the time microsporogenesis began. Microsporogenesis was completed by the time dormancy began. Ovule development and megasporogenesis were completed the following March. Megasporogenesis was observed to start in early March and complete development a few days before anthesis in mid to late March.

Hamamelis virginiana L. (Hamamelidaceae Lindl.)

Gross Morphology: Vegetative growth commenced 2 to 10 days later than in Hamamelis vernalis Sarg. By mid-June growth had caught up to the same stage as in H. vernalis Sarg. and continued to show similar stages throughout the remainder of the season (Figure 4-A). In general, vegetative growth was less rapid or achieved less length growth than H. vernalis Sarg.

Floral bud clusters became evident during mid-June and continued development as in H. vernalis Sarg. Flowers buds were approximately one-half the size of those in H. vernalis Sarg. (Figure 4-A). Individual flower buds were about one-sixteenth inch in diameter when anthesis occurred in early to mid-October.

Fruit development did not start until growth resumed the next spring and proceeded until maturity the same autumn. The woody capsule matured in early to mid-October.

Table 7: Growth Characteristics of Hamamelis virginiana L.

Year	Vegetative Growth Began	Flowering		Flower Buds First Visible to Naked Eye	Date of Initi- tion	Days from Initiation to Flowering
		Began	Ended			
1962	4/28	10/16	12/9	6/14	5/25	144
1963	4/20	10/20	12/7	6/12	5/30	143
1964	4/28			6/4		

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...the ... of ...
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Vegetative Apex: Similar to Hamamelis vernalis Sarg. (Figure 4-B).

Floral Apex: Although similar to Hamamelis vernalis Sarg. (Figure 4-C, D, E, F, G, H, I, and J), flower initiation commenced 4 to 15 days earlier. Individual floral parts appeared in acropetal succession and within a few days of those in buds of Hamamelis vernalis Sarg. Microsporogenesis and megasporogenesis started at least 1 month later, toward the end of September, and were completed a day or 2 before anthesis in mid-October.

Flower initiation began in late May or very early June. Flower part formation and development were observed to be similar to Hamamelis vernalis Sarg. Microsporogenesis and megasporogenesis began toward the end of September and were completed a day or 2 before anthesis. Anthesis occurred in mid-October and continued until the flowers were killed by freezing in early December.

Hibiscus syriacus L. (Malvaceae Zeck.)

Gross Morphology: Vegetative growth commenced from buds embedded beneath leaf scars (Figure 5-A) in mid-spring and continued until approximately mid-August. Approximately 30 days after vegetative growth began the first small flower bud could be seen in a leaf axil 2 or 3 inches up the shoot. Stem and leaf growth continued until all flower buds were formed and the 2 or 3 most proximal buds had bloomed. At this point vegetative growth had stopped completely.

Flower buds were formed in acropetal succession starting in early to mid-June. Flowering, also in acropetal succession, commenced during July or early August. The buds at this time were about one-half inch in diameter and 1 inch long. Flower bud formation was observed to proceed while anthesis was taking place further down the stem.

Executive Order: 12812 - Environmental Protection

4-81

Final Order: Although similar to Executive Order 12812

Executive Order 12812, it is not identical to it.

to 15 days before the date of the meeting.

Executive Order 12812, it is not identical to it.

Executive Order 12812, it is not identical to it.

Conversely, fruit development was proceeding while the upper flower buds were open or developing to anthesis.

Fruit development rapidly followed anthesis with the first capsules dehiscent during early October. All fruit had dehisced by mid-November. The capsule persisted into the fall of the year following. Seed was dispersed throughout the winter.

Table 8: Growth Characteristics of Hibiscus syriacus L.

Year	Vegetative Growth Began	Flowering		Flower Buds First Visible to Naked Eye	Date of Initi- ation	Days from Initiation to Flowering
		Began	Ended			
1962	5/1	8/6	9/6	6/19	6/1	66
1963	4/18	7/20	9/14	6/3	5/22	59
1964	4/23	7/6	9/2	5/26		

Vegetative Apex: The vegetative growing point presented a shallow concave surface with leaf primordia cut off in an alternate arrangement (Figure 5-B). The tunica consisted of a single highly organized cell layer and perhaps a second layer which was not as highly organized. Beneath the tunica layer was a central corpus of disorganized cells 5 to 6 cells in depth.

Floral Apex: The first indication of floral initiation was a flattened apex of an axillary bud (Figure 5-C) in early to mid-May. Several bracts of the involucre which surround the flower bud were also visible at this time. Toward the end of May the peduncle of the flower bud had elongated to about 3 mm in length and sepals were evident (Figure 5-D). At this time, the buttressed apex had assumed a shallow concave surface and became flattened. The floral apex presented a surface much like that of

Consequently, their development was characterized by the fact that
 both were open to developing in different
 ways. Development rapidly followed and with the first signs
 of development during early October. At this time the animals were well-developed.

The capsule passed into the 2nd stage of development
 period from 1st to 2nd.

10/10/50

the vegetative apex. Within 1 or 2 days this apex showed 2 primordial masses rising to either side with the flattened central surface remaining flat (Figure 5-E). On the outer portion of these larger primordial masses was a single smaller vesture which developed into juvenile petals; the larger masses in the vesture became the young staminal column. During early June protuberances of the staminal column continued to develop at a faster rate than the petal primordia (Figure 5-F) and the central part of the buttress remained flattened. By mid-June, however, the staminal column enclosed a cavity which contained several carpels with locules (Figure 5-G). The petals were now almost as long as the staminal column and stamen primordia could be distinguished. The styles of the carpels were observed to be separate and just starting to elongate. Flower buds continued to develop rapidly until the staminal column filled the bud (Figure 5-H) toward the end of June. The bud at this time was approximately one-quarter inch long. The petals had surmounted the staminal column, recurved to a certain extent, with the style branches almost grown through it. Ovule development and microsporogenesis commenced from mid to late June (Figure 5-I). The style branches had grown completely through the staminal column by early to mid-July (Figure 5-J). Microsporogenesis had been completed and megasporogenesis had just begun. Within 4 or 5 days the buds began to open.

As the buds opened, the petals were observed to be convolute and to remain tight until they extended to a length of approximately 4 inches. During this time the staminal column also elongated to approximately the same length and the style branches had elongated to 1 inch above the stamens. Megasporogenesis continued and was completed when the petals opened. From the time that the petals emerged until petal anthesis occurred 4 to 8 days had passed. Anthesis normally occurred from early July to early August.

the vegetation zone. Within 1 mile of the river, the vegetation
changes along to grass with the dominant species being
in the (Figure 2-3). On the other hand, in the upper reaches
of the river, the vegetation is mostly grass and shrubs.

Within the 1 mile of the river, the vegetation

changes along to grass with the dominant species being

in the (Figure 2-3).

On the other hand,



Figure 5: Phases of flower bud development in Hibiscus syriacus L.

- A. Leaf scar and stem.
- B. Vegetative apex (approx. 30x).
- C. Flower initiation showing involucre bracts (approx. 40x).
- D. Elongated flower bud with sepal primordia (approx. 40x).
- E. Staminal column and small petal primordia (approx. 30x).
- F. Growth of petal and staminal column primordia (approx. 30x).
- G. Carpel primordia with locules (approx. 15x).
- H. Petal and staminal column elongation (approx. 15x).
- I. Ovule and microsporogenesis initiation (approx. 15x).
- J. Flower 3 or 4 days before anthesis (approx. 4x).



A



B



C



D



E



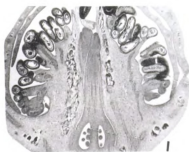
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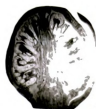
G



H



I



J

Flower bud development was a modified acropetal succession. Involucre bracts and sepals were formed from the middle to the end of May. In early June a primordial mass arose, containing both staminal column and slightly later the petals. Undifferentiated stamen primordia and carpel primordia appeared to arise simultaneously during mid-June. Locules were evident a few days later. Ovule development and microsporogenesis occurred toward the end of June. Megasporogenesis began approximately 3 to 4 days before petal emergence. The petals, staminal column, style and megasporogenesis completed development from early to mid-June with anthesis following. Flower buds formed acropetally.

Indigofera potanini Craib. (Leguminosae B. Juss.,
Subfamily Lotoideae)

Gross Morphology: Vegetative growth and flower bud development both began in mid-spring and continued until mid-August. As growth ceased, buds ceased pushing out primordial leaves and began to produce bracts. In the axil of each bract "embryo" racemes formed and over-wintered. By the end of October buds were one-quarter inch in length, about one-eighth inch in width, and contained miniature racemes, leaf and other vegetative structures (Figure 6-A).

Flower inflorescence initiation and development resumed when vegetative growth commenced in the spring. The first raceme became evident to the naked eye approximately 16 days before anthesis. Racemes continued to be initiated through the summer and up to the time of dormancy. During the winter some of these highly undifferentiated meristematic racemes were killed by low temperatures but others survived to develop to anthesis the next spring. The flowering period extended through the entire summer and into mid or late September. Racemes and flowers developed in acropetal succession with anthesis

There is a development and a significant increase in the
number of people who are able to read and write in the
state. In early 1960, the literacy rate was 10%.
In 1965, it had risen to 15%.

1965-1966

1966-1967

1967-1968

occurring in the proximal flowers while the distal flowers were still developing (Figure 6-A). Flower parts appeared to be formed in acropetal succession.

Small fruits were first evident toward the last of July and maturity was reached in early to mid-October. The fruit often persisted until early March.

Table 9: Growth Characteristics of Indigofera potanini Craib.

Year	Vegetative Growth Began	<u>Flowering</u>		Flower Raceme First Visible to Naked Eye	Date of Initi- ation	Days from Initiation to Flowering
		Began	Ended			
1962	5/1	5/22	9/30	5/10	Continuous	Continuous
1963	4/18	6/3	9/16	5/19	from growth	from growth
1964	4/28	5/19		5/3	resumption to dormancy	resumption to dormancy

Vegetative Apex: The vegetative apex presented a rather shallow domed apex with leaf primordia cut off alternately (Figure 6-B). The tunica contained 3 layers of organized cells and a corpus 3 or 4 cells deep. The corpus appeared to be somewhat organized.

Floral Apex: The first indication of floral initiation was evident from the development of an apex similar to the vegetative apex with primordia in axils just below the apex (Figure 6-C). The floral apex at this time was flattened on the shoulder and raised in the center. Within 10 days the inflorescence had expanded exposing many more flowers in the raceme (Figure 6-D). Sepals appeared to have been initiated in the proximal flowers in the inflorescence. The raceme continued to expand in length cutting off bracts and flower primordia as it elongated (Figure 6-E) with the small raceme still enclosed by a bract

and invisible to the naked eye. The above 3 stages were observed in over-wintering multiple buds.

The first actual differentiation was not observed until approximately 7 days after vegetative growth had started when several stages of development could be observed. The proximal flowers of the raceme appeared to have all floral parts present (Figure 6-F). Approximately 10 days after the raceme became visible in early to mid-May, anthesis started and proceeded over a period of 3 to 4 months.

As vegetative growth began individual flower formation resumed growth. The flower primordia at first presented a rather high domed primordial mass, always axillary until the terminal primordia differentiated (Figure 6-F). The buttress appeared to flatten across the top and at the same time primordial masses were cut off on the side (Figure 6-G). Petal primordia were cut off to the sides of the domed primordial mass just inside the sepals. Stamens apparently formed simultaneously or slightly later than the petals. As the raceme began to emerge and become visible, ovule development and microsporogenesis became evident (Figure 6-H). By this time the racemes were one-half inch long, the ovules in the lower-most flowers were well formed and microsporogenesis was approximately half completed (Figure 6-I). From the first appearance of the racemes to anthesis required approximately 10 to 15 days during which microsporogenesis was completed; megasporogenesis began and finished during the same period. Anthesis took place between late May and early June and continued into mid-September or late September. The greatest amount of flowering occurred in the first 4 to 5 weeks. The rest of the season flowering gradually decreased until the end of September.

Flower racemes were shown to over-winter in a highly undifferentiated state; in some cases, sepals and petals were barely visible. While the acropetal order of succession appeared to be usual the petals,





Figure 6: Flower bud development in Indigofera potanini Craib.

- A. Dormant mixed buds (arrow).
- B. Vegetative apex (approx. 40x).
- C. Raceme primordia mostly undifferentiated (approx. 40x)
- D. Raceme with some flower differentiated in the proximal flowers (approx. 40x).
- E. Raceme elongating with some flower differentiation (approx. 40x).
- F. Floral parts; sepals (approx. 20x).
- G. Sepals, petals, stamens (approx. 20x).
- H. Ovule and microsporogenesis initiation (approx. 10x).
- I. Flowers several days before anthesis (approx. 55x).



A



B



C



D



E



F



G



H



I

stamens and carpel often seemed to initiate and develop at the same time. Ovule and microsporogenesis were initiated as the raceme first became visible to the naked eye. The ovules were well formed at the time the raceme was one-half inch long. In the 10 to 15 days before anthesis, microsporogenesis was completed and megasporogenesis was initiated and completed development. Anthesis first occurred in mid-May to early June and continued until mid-September. Vegetative growth, floral initiation and development, and fruit development were shown to proceed simultaneously throughout the summer.

Prunus glandulosa Thunb. (Rosaceae Juss.,
Subfamily Prunoideae Focke.)

Gross Morphology: In mid-spring vegetative growth started and continued until the end of July. In mid-July buds were observed in leaf axils but were not distinguishable between flower and vegetative buds. During the remainder of the summer the buds increased in size and by mid-September the collateral bud arrangement became visible (Figure 7-A).

Flower buds were present by mid-September and continued to enlarge until dormancy. At the time of dormancy the collateral bud arrangement was clearly visible with the vegetative bud surrounded by floral buds.

Flower development began during late August or early September. By the last of October all flower parts were almost fully developed. With the commencement of growth the following spring the stamens and carpels completed development and microsporogenesis and megasporogenesis started approximately 10 days before anthesis. Anthesis occurred in late April or early May.

Fruits developed to maturity during the first half of the summer reaching maturity from mid to late July.

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Fruits developed to maturity during the first half of the summer reaching maturity from mid to late July.

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Table 10: Growth Characteristics of Prunus glandulosa Thunb.

Year	Vegetative Growth Began	Flowering		Flower Bud First Visible to Naked Eye	Date of Initi- ation	Days from Initiation to Flowering
		Began	Ended			
1962	4/24	5/1	5/16	9/30	8/18	
1963	4/20	4/28	5/13	9/18	8/21	252
1964	4/19	5/1	5/9			253

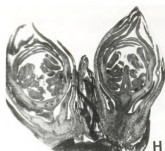
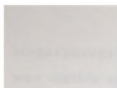
Vegetative Apex: The vegetative apex presented a concave, high domed buttress with leaf primordia cut off alternately (Figure 7-B). The tunica was at least 2 layers deep and perhaps 3. The corpus was highly disorganized and approximately 5 cells deep.

Floral Apex: The first indication of flower primordia appeared in mid-August in the form of rounded primordial masses slightly flattened across the top (Figure 7-C). Ten days later the buttress had broadened-out and the shoulders of the buttress had flattened (Figure 7-D). Sepal primordia became evident by the end of August (Figure 7-E). Rapid development followed with petal and stamen primordia usually appearing simultaneously or occasionally the stamens very slightly thereafter. By mid-September the carpels were distinguishable (Figure 7-F). The perigynous flower became evident toward the end of September as the style began to elongate (Figure 7-G). The flower bud normally overwintered in either the above condition or after ovule initiation. Ovules which formed in the autumn were evident during mid-October and at the same time microsporogenesis was observed to have begun (Figure 7-H). In most flowers ovule formation, as well as microsporogenesis, was initiated during early spring. The ovule was well formed by mid-April and microsporogenesis was mostly complete (Figure 7-I).



Figure 7: Stages in the development of flower buds of Prunus glandulosa Thunb.

- A. Collateral multiple buds (vegetative bud central).
- B. Vegetative apex (approx. 40x).
- C. Flower primordia appearance (approx. 40x).
- D. Buttress surface ready for differentiation (approx. 40x).
- E. Sepal primordia (approx. 40x).
- F. Sepal, petal, stamen and carpel primordia (approx. 60x).
- G. Perigynous flower evident (approx. 40x).
- H. Ovule and microsporogenesis initiation (approx. 15x).
- I. Flower bud when growth resumed the following spring (approx. 15x).
- J. Flower several days before anthesis (approx. 15x).



Megasporogenesis was not observed at this time. The anatropous ovule was visible approximately 10 to 15 days before anthesis while megasporogenesis occurred during this time (Figure 7-J). Anthesis began from late April and continued to mid-May.

Flower initiation occurred in acropetal succession starting in mid-August. Sepals, petals, stamens and carpels were well-developed at dormancy. Ovule formation was observed to begin either in mid-October or, in most cases, when growth resumed the next spring. Microsporogenesis started approximately at the time ovule initiation was observed. Megasporogenesis began 10 to 15 days prior to anthesis. Anthesis occurred from late April to mid-May.

Pyracantha coccinea Roem. var. lalandii Dipp.
(Rosaceae Juss., Subfamily Promiodeae Focke)

Gross Morphology: Active vegetative growth began during April and continued until the end of August or early September. Buds became visible during mid-June but no distinction could be made between reproductive or vegetative buds at this time. By the end of August, the respective buds could be identified and by mid-September they were both clearly visible (Figure 8-A). As the autumn progressed the flower buds were observed to swell until the end of October after which the buds showed no change until growth resumed the next spring.

The inflorescence primordia became evident during late October but remained in a highly meristematic state through the winter. When vegetative growth commenced the next spring, this primordial mass began to expand very rapidly. Flowers were initiated and developed to anthesis during approximately 55 days. Flowers were borne on current season's wood.

Fruit development proceeded through the summer months, finally maturing in early to mid-September. The fruit was found to persist until the following February or March.

The experiments were not observed in the field. The experiments were
not visible approximately 10 to 15 days before sunset when the
experiments occurred during the night. The experiments
from late April and continued to mid-May.

There is a lot of
information about
the experiments
and the results.

The leaves remained on the plants through the winter with 75 percent abscission in February or March of the following year.

Table 11: Growth Characteristics of Pyracantha coccinea Roem. var. lalandii Dipp.

Year	Vegetative Growth Began	Flowering		Buds First Visible to Naked Eye	Date of Initi- ation	Days from Inflorescence Initiation to Flowering
		Began	Ended			
1962	4/28	5/27	6/14	5/10	Inflorescence 10/20, Flower 4/28	
1963	4/6	5/31	6/12	5/7	Inflorescence 10/21, Flower 4/18	221
1964	4/18	5/24	6/9	5/1		214

Vegetative Apex: The vegetative apex was observed to be a high concave buttress with a shallow curved surface (Figure 8-B). Leaf primordia were cut off on the flanks in an alternate arrangement. A tunica 2 cells deep was observed with a somewhat disorganized corpus approximately 5 cells deep.

Floral Apex: The primordia of the corymb inflorescence became visible in late October (Figure 8-C). At this time the apex within the floral bud was highly meristematic with little differentiation into a recognizable inflorescence, at which stage the flower bud over-wintered.

About the time vegetative growth resumed in the spring, individual flower initiation became evident. The first indication was a definite flattening of the meristematic buttress (Figure 8-D). Sepals became apparent 10 days later in the uppermost flower of the corymb (Figure 8-E). Flower parts were formed in acropetal succession with the petals

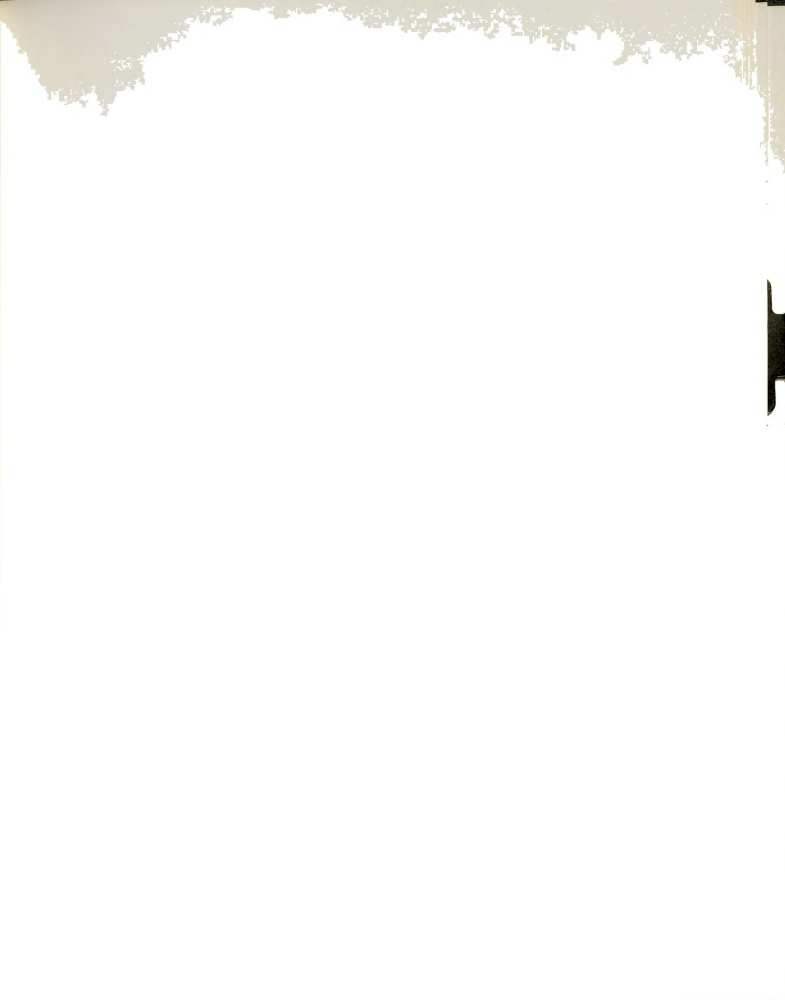
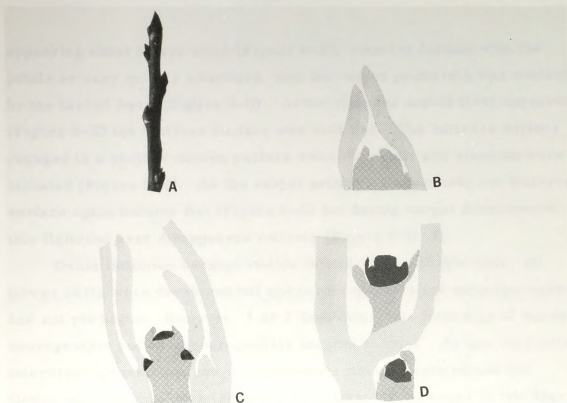


Figure 8: The development of floral buds in Pyracantha coccinea Roem. lalandii Dipp.

- A. Vegetative (upper) and flower buds (lower).
- B. Vegetative apex (approx. 40x).
- C. Inflorescence initiation (approx. 40x).
- D. Individual flower primordia appearance (approx. 40x).
- E. Sepal primordia (approx. 40x).
- F. Petal primordia (approx. 40x).
- G. Stamen and carpel primordia (approx. 40x).
- H. Carpel development in late spring (approx. 40x).
- I. Ovule and microsporogenesis initiation (approx. 30x).
- J. Microsporogenesis complete, megasporogenesis starting (approx. 20x).



appearing about 9 days later (Figure 8-F), stamens formed with the petals or very quickly afterward, and the carpel primordia was evident by the last of April (Figure 8-G). At the time the sepals first appeared (Figure 8-E) the buttress surface was still flat. The buttress surface changed to a shallow convex surface when the petals and stamens were initiated (Figure 8-F). As the carpel primordia appeared, the buttress surface again became flat (Figure 8-G) but during carpel development this flattened area disappeared entirely (Figure 8-H, I).

Ovule initiation became visible in mid-May. At this time, all flower parts were developed but microsporogenesis and megasporogenesis had not yet begun. However, 1 or 2 days later, the first sign of microsporogenesis and megasporogenesis became evident. By late May both microsporogenesis and megasporogenesis were completed and the flower was ready to open (Figure 8-J). Anthesis occurred in late May.

The first evidence of flower formation began in late October when inflorescence primordia were seen. Over-winter, this primordium remained in a highly undifferentiated state and began to expand as vegetative growth resumed the following spring. Sepals were initiated 10 days later, and carpels approximately 3 days later. By early May, all flower part primordia were present. Ovule initiation was evident in Mid-May with microsporogenesis and megasporogenesis limited to the latter half of May. Anthesis occurred in very late May.

Rosa multiflora Thunb. (Rosaceae Juss.,
Subfamily Rosoideae Focke.)

Gross Morphology: With the commencement of vegetative growth in early April, growth was rapid until mid to late May. During mid-May growth began to decrease as the flowers emerged from the bud. Growth had ceased by the last of May, 5 to 8 days before flower anthesis.

appearing about 7 days later (Figure 3-4), when we learned that the
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 by the last of April (Figure 3-4). In the last few weeks that appeared
 (Figure 3-4) the business system was still flat. The business system

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Vegetative buds were first visible in early July and continued to enlarge until dormancy. Over wintering buds were vegetative only (Figure 9-A).

Floral development began 10 days after vegetative growth.

Flowers were initiated and developed during active vegetative growth.

Anthesis began in early June on current season's vegetative growth.

Fruit development occurred through the summer reaching maturity during early September.

Table 12: Growth Characteristics of Rosa multiflora Thunb.

Year	Vegetative Growth Began	Flowering		Flower Bud First Visible to Naked Eye	Date of Initi- ation	Days from Initiation to Flowering
		Began	Ended			
1962	4/4	6/1	6/28	5/15	4/28	33
1963	3/31	6/7	6/19	5/16	4/18	49
1964	4/14	6/4	6/20	5/14		

Vegetative Apex: The vegetative apex appeared to be flat with a slight concave surface. The cells of this region were highly disorganized so that a definite tunica and corpus were not distinguishable. Leaf primordia arose on the flanks of the buttress in an alternate fashion (Figure 9-B).

Floral Apex: The individual flower primordia became evident 6 to 10 days after the commencement of vegetative growth. The buttress of these primordial masses was highly concave in shape with leaf primordia as well as flower primordia being cut off on the flanks of the terminal primordia mass (Figure 9-C and D). The miniature corymb and flower primordial continued rapid development until the buttress started to flatten out approximately 18 to 30 days after vegetative growth began

Vegetation plots were first established in 1951 and continued to 1954.
 until 1954. These following plots were established in 1955 and 1956.
 Total development in 1955 to 1956 was 100%.
 There were no other plots established during this period.

Vegetation plots

Final data

1955

(Figure 9-E). At this time the flowering stem began elongating more rapidly but was not observed outside of the enclosing immatured leaves.

Several days later at the time of the appearance of flower initiation the buttress was a very shallow convex surface enclosed with very small sepals (Figure 9-F). First, most terminal flower began development followed by further flower development in an acropetal fashion. By the end of April petal primordia appeared as small swellings just below the developing sepal primordia (Figure 9-G). During the early part of May the stamens were initiated. Ten days after petal development began, the first signs of carpel formation were evident (Figure 9-H). At this time, the stamens were somewhat higher, slightly overhanging the carpel primordia, and the flower buds were beginning to become visible to the naked eye.

In mid-May a definite epigynous flower could be recognized (Figure 9-I). Both the sepals and petals were well developed but the stamen and carpel primordia were still strongly meristematic. Carpel primordia were observed to nearly triple in height in a matter of 8 or 9 days.

Ovule development was observed during late May (Figure 9-J) at a time when the corymb was expanding rapidly and all flower buds were visible.

Two or three days before anthesis in early June, microsporogenesis and megasporogenesis were completed (Figure 9-K). By this time, the styles were observed to have grown through the open area formed by the basal tissue of the sepals, petals and stamens. All flower parts were initiated during the period of the most active vegetative growth and in acropetal succession. Sepals were initiated approximately 20 days after vegetative growth started. Petals and stamens were initiated 8 to 10 days later with the carpel primordia evident by mid-May.

Figure 9: Development of flower buds in Rosa multiflora Thunb.

- A. Vegetative buds .
- B. Vegetative apex (approx. 35x).
- C. Inflorescence primordia, early stage (approx. 30x).
- D. Inflorescence primordia, late stage (approx. 30x).
- E. Individual flower buttress flattening (approx. 30x).
- F. Sepal primordia (approx. 70x).
- G. Petal initiation (approx. 50x).
- H. Stamens present, carpel primordia (approx. 50x).
- I. Epigynous flower with developing carpels (approx. 40x).
- J. Ovule development (approx. 15x).
- K. Flower 1 to 2 days before anthesis (approx. 10x).



Microsporogenesis and megasporogenesis did not become evident until 10 to 12 days before anthesis. The inflorescence and flower parts developed in acropetal succession.

Spiraea thunbergi Sieb. (Rosaceae Juss.,
Subfamily Spiraeoideae Focke.)

Gross Morphology: Vegetative growth began at the time of flower anthesis or slightly after anthesis. Growth continued to expand rapidly until mid-August at which time flower and vegetative buds were distinguishable (Figure 10-A). The small, slender stems tended to die back quite a little during the winter months, especially the terminal 3 or 4 inches.

During the latter part of August floral buds can be distinguished by being round and blunt at the apex (Figure 10-A). The flowers were initiated and developed up to microsporogenesis and megasporogenesis before dormancy. Some flowers developed to anthesis during early to mid-October depending upon existing weather conditions. In general, microsporogenesis and megasporogenesis were initiated and completed after growth had resumed the following spring. Flowers were borne on previous season's wood and were usually produced over a period of 1 or 2 months.

Fruit maturity was reached in late May or early June when the follicles split open and dispersed the seed.

Table 13: Growth Characteristics of Spiraea thunbergi Sieb.

Year	Vegetative Growth Began	Flowering		Flower Bud First Visible to Naked Eye	Date of Initi- ation	Days from Initiation to Flowering
		Began	Ended			
1962	4/24	4/27	5/17	7/27	9/30	
1963	3/29	3/30	5/19	8/6	9/4	181
1964	4/14	4/21	5/19	7/23		229

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Vegetative Apex: The vegetative apex presented a rather flattened buttress with leaf primordia cut off in an alternate arrangement (Figure 10-B). The buttress showed a slightly curved surface made up of a 2 layered tunica and a corpus 2 or 3 cells deep.

Floral Apex: The first indication of flower formation became evident in early September at which time several raised areas of meristematic cells were visible (Figure 10-C). These highly meristematic cells continued to differentiate rapidly until approximately mid-September when individual floret primordial masses could be distinguished (Figure 10-D). These primordial masses were rounded in shape with a slight flattening of the apex. A definite flattening of the buttress was not evident, however, until approximately 5 days later (Figure 10-E). The primordial mass was still highly meristematic with activity in the lower part of each floret decreasing. Cell division and expansion did not stop entirely until the floret peduncles had been differentiated.

A few days after the buttress flattened out the sepals first became evident at a time when the buttress was a slight concave, dish-shape (Figure 10-F). Although the stamen primordia followed the petal primordia within 3 days in early October, the undifferentiated buttress surface continued to be slightly concave (Figure 10-G). Protuberances indicating carpel primordia became evident within 2 or 3 days after the stamen primordia (Figure 10-H), at which time meristematic activity continued rapidly with carpels and minute ovules formed by late October (Figure 10-I). Also, microsporogenesis was noticed to be proceeding rather rapidly. Each floret was complete in all flower parts at this time except for completion of microsporogenesis and megasporogenesis. Normally microsporogenesis was not completed and megasporogenesis apparently did not begin until growth resumed in the spring (Figure 10-J).

1. The first part of the report is a general introduction to the project.

2. The second part of the report is a detailed description of the project.

3. The third part of the report is a discussion of the results of the project.

4. The fourth part of the report is a conclusion and recommendations.

5. The fifth part of the report is a list of references.

6. The sixth part of the report is a list of appendices.

7. The seventh part of the report is a list of figures.

8. The eighth part of the report is a list of tables.

9. The ninth part of the report is a list of abbreviations.

10. The tenth part of the report is a list of symbols.

Figure 10: Stages in the development of Spiraea thunbergi Sieb. flower buds.

- A. Vegetative (middle) and flower buds (upper bud).
- B. Vegetative apex (approx. 40x).
- C. Floret initiation, first appearance (approx. 40x).
- D. Individual florets visible (approx. 40x).
- E. Floret buttress flattened (approx. 40x).
- F. Sepal primordia (approx. 80x).
- G. Petal and stamen primordia (approx. 40x).
- H. Carpel primordia (approx. 40x).
- I. Ovule development (approx. 40x).
- J. Flower before anthesis (approx. 40x).



A few flowers were observed to bloom in late October, depending upon weather conditions, with microsporogenesis being completed but it was not determined whether megasporogenesis had been completed.

Anthesis started in the early spring after 5 or 6 days of warming weather. The period of bloom extended over a 1 to 2 month period.

Flower initiation began in early September after approximately 125 days of vegetative growth. Three to five rounded primordial masses were at first evident, eventually becoming flattened. Sepals, petals, stamens and carpels were initiated in acropetal succession from late September to mid-October. Microsporogenesis began several days later. Megasporogenesis was not observed in the fall but appeared to be completed a day or 2 before anthesis the following spring. Anthesis normally occurred early in the spring, although it did also occur during the fall months.

Viburnum dentatum L. (Caprifoliaceae Vent.,
Section Odontotinus Rehd.)

Gross Morphology: The period of vegetative growth started from mid to late April and continued uninterrupted until mid-July. Buds during this time were small and flower and vegetative buds were not distinguishable. Toward the end of July, growth began to decrease and the terminal buds began to enlarge. Large plump buds were evident from early August until shortly before vegetative growth commenced the following spring (Figure 11-A).

During the fall and early spring inflorescences were developing in the terminal buds. Shortly after vegetative growth commenced in the spring, the mostly undifferentiated floral primordia continued to develop at the same time as stem growth. By the time of anthesis, the vegetative stem growth had elongated about 5 inches. At the same time, the



cymose inflorescence continued development until anthesis in early to mid-June.

Most fruit had matured and abscised by the time floral initiation becomes evident.

Table 14: Growth Characteristics of Viburnum dentatum L.

Year	Vegetative Growth Began	<u>Flowering</u>		Flower Buds First Visible to Naked Eye	Date of Initi- ation	Days from Inflorescence Initiation to Flowering
		Began	Ended			
1962	4/24	6/8	6/23	9/15	Inflorescence 9/3, Flower 4/14	
1963	4/17	6/12	6/28	9/4	Inflorescence 9/10, Flower 4/16	282
1964	4/18	6/8	6/23			271

Vegetative Apex: The typical vegetative apex showed a shallow convex buttress. The tunica of the apex consisted of 2 layers with a rather disorganized corpus approximately 4 cells thick and located immediately below the tunica. Leaf primordia are oppositely arranged and arose on the flanks of the buttress (Figure 11-B).

Floral Apex: Inflorescence initiation became evident during early September approximately 38 days after the previous bloom. At first the buttress was shallow with somewhat more width than the vegetative apex (Figure 11-C) but soon began to rise rapidly in the center. The primordial mass grew rather rapidly until individual floret primordia were evident in a highly undifferentiated state (Figure 11-D and E). At this time the visual appearance of the flower bud produced a compressed, plump

appearance and all flower primordia remained in this condition until resumption of growth the following spring.

Upon resumption of growth (mid-April), the "ball" shaped inflorescence began to expand and soon emerged from the bud scales. At the same time the pedicels of the cymose inflorescence expanded causing the "ball" shaped primordial mass to expand in width; individual flower initiation could be observed (Figure 11-F). The typical buttress surface became shallow and concave in shape and the individual cymes of the compound inflorescence were conspicuous. The sepals became evident at the same time or within a few days.

The sepals, petals and stamens followed in rapid succession (Figure 11-F, G, and H) so that by early to mid-May these floral parts were well-developed. Initiation of the petals and stamens was observed to be either simultaneous or the stamens followed in quick succession. While the sepals, petals and stamens were forming, the inflorescence branching system was also expanding to its maximum width (Figure 11-G).

Carpel development could be observed during early May with ovule formation evident during mid-May (Figure 11-I).

Microsporogenesis and megasporogenesis were limited to the last 2 weeks of development immediately preceding anthesis (Figure 11-J).

Inflorescence initiation and development occurred after vegetative growth had ceased during early to mid-autumn. The flower primordial mass over-winters in an undifferentiated state. Soon after vegetative growth commenced in the spring individual floret initiation began (mid-spring). Sepals, petals, stamens and carpels were initiated rapidly in acropetal succession. Microsporogenesis and megasporogenesis were limited to the last 2 weeks of flower development.

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been steadily increasing in number and importance.

The first of these institutions was the "Board of Education," which

was established in 1901, and has since that time

been steadily increasing in number and importance.

The second of these institutions was the "Board of

Education," which

was established in 1901, and has since that time

Figure 11: Stages of flower development in Viburnum dentatum L. and V. lentago L.

- A. Exterior of flower buds; V. dentatum left and V. lentago right.
- B. Vegetative apex (approx. 35x).
- C. First indication of floral initiation (approx. 35x).
- D. inflorescence primordia (approx. 30x).
- E. Floret primordia (approx. 30x).
- F. Sepal initiation (approx. 45x).
- G. Petal and stamen primordia simultaneous or stamens somewhat later (approx. 40x).
- H. Carpel initiation (approx. 40x).
- I. Ovule formation (approx. 35x).
- J. A day or two before anthesis (approx. 15x).



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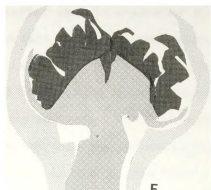
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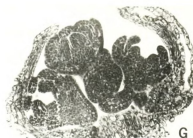
D



E



F



G



H



I



J



Viburnum lentago L. (Caprifoliaceae Vent.,
Section Lentago DC)

Gross Morphology: The period of vegetative growth began in mid-April and continued until the end of July. During the early stages of development flower and vegetative buds were not distinguishable. By the end of June the basal area of the terminal bud began to swell indicating floral development had begun. This swollen area continued to enlarge until it was approximately one-quarter inch in diameter by the onset of dormancy. The bud remained in this condition until vegetative growth started in the spring (Figure 11-A)

Inflorescence development commenced during mid to late summer with floret development beginning during early autumn. With the commencement of vegetative growth the following spring, the inflorescence and flowers continued development until anthesis in mid to late May. Flowers were borne on previous season's wood. Current season vegetative growth surmounted the inflorescence by mid-June.

Fruit development and the development of the inflorescence proceeded at the same time with the fruit reaching maturity at approximately the same time individual flowers were initiated.

Table 15: Growth Characteristics of Viburnum lentago L.

Year	Vegetative Growth Began	<u>Flowering</u>		Flower Bud First Visible to Naked Eye	Date of Initi- ation	Days from Inflorescence Initiation to Flowering
		Began	Ended			
1962	4/9	5/19	5/27	7/10	Inflorescence 6/23, Flower 7/16	
1963	4/2	5/19	6/5	7/20	Inflorescence 6/19, Flower 7/24	330
1964	4/16	5/17	5/28	7/2		333

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Vegetative Apex: Similar to the vegetative apex of Viburnum dentatum L. (Figure 11-B).

Floral Apex: Inflorescence initiation was observed from mid to late June approximately 20 days after the previous bloom (Figure 11-C). Development of the inflorescence primordial mass was like that of Viburnum dentatum L. (Figure 11-D). Floral primordia became evident by late July when the inflorescence mass appeared to flatten in shape and segregate into individual flowers (Figure 11-E). Cymes were well-developed by early August with sepals apparent (Figure 11-F). Petal initiation followed 18 days later and the primordia of the petals and stamens appeared to arise either simultaneously or in quick succession (Figure 11-G and H). The carpels did not appear to be completely formed at the time dormancy set in. At this time the visual appearance of the flower bud produced a candle-like appearance with a swollen base. The inflorescence and individual flowers remained in this condition until growth resumed the following spring.

With the resumption of growth the next spring, the cymose inflorescences expanded rapidly until they had become flattened in shape 16 days preceding anthesis. During the time of inflorescence expansion the individual flowers completed development.

Ovule development was observed to be well underway 14 days after resumption of growth and 30 days preceding anthesis (Figure 11-I). The beginning of megasporogenesis and microsporogenesis, however, was not observed until approximately 16 days preceding anthesis (Figure 11-J).

Initiation of the inflorescence occurred in mid-summer as vegetative growth began to slow up. Flower initiation began 35 days after the inflorescence was initiated. Sepals, petals and stamens were laid down in early fall and were fairly well developed when cold weather began. Carpels apparently made little development in the fall but

developed rapidly after growth resumed the following spring. Floral parts were initiated in acropetal succession. Microsporogenesis and megasporogenesis were limited to the 16 days preceding anthesis.

Information on the use of the
equipment is available in the
manual. The equipment is
designed to be used in the
laboratory.

developed rapidly after growth resumed the following spring. Floral parts were initiated in acropetal succession. Microsporogenesis and megasporogenesis were limited to the 16 days preceding anthesis.



CONCLUSION

In Table 16 a comparison of vegetative growth, flower bud formation and flowering periods is made for all the species examined.

Vegetative growth in all plants was found to start during late April or early May regardless of the time of flowering. In agreement with Goff (1899, 1900, 1901) vegetative growth was observed to have ceased when flower buds became visible to the naked eye except in Hibiscus syriacus L. and Indigofera potanini Craib.

Flower bud formation and flowering, on the other hand, were found to vary with the time flowering first occurred.

All the spring flowering plants--Hamamelis vernalis Sarg., Cornus mas L., Forsythia ovata Nakai., Prunus glandulosa Thunb., Spiraea thunbergi Sieb. and Viburnum lentago L.--except Prunus glandulosa Thunb. and Spiraea thunbergi Sieb., were found to initiate flowers during the early part of the previous summer. Both Prunus glandulosa Thunb. and Spiraea thunbergi Sieb. initiated flowers during the latter part of summer similar to several other genera of rosaceous plants (Goff, 1899, 1900, 1901; Drinkard, 1909; MacDaniels, 1922; Tufts and Morrow, 1925; and Hirai, Nakagawa, Nanjo and Hirata, 1961).

Summer flowering plants--Pyracantha coccinea Roem. var. lalandii Dipp., Rosa multiflora Thunb., Viburnum dentatum L., Hibiscus syriacus L. and Indigofera potanini Craib.--were found to vary considerable in the time of flower initiation. Hibiscus syriacus L. and Rosa multiflora Thunb. initiated flower buds in late April or early May, resembling the spring flowering plants. Time of flower initiation for Rosa multiflora Thunb. was similar to that found by Grainger (1939)

CONCLUSION

As Table 10 shows,

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TABLE 16: SUMMARY OF VEGETATIVE GROWTH, FLOWER BUD FORMATION AND FLOWERING



— Vegetative growth and flower bud formation.

---- Flowering period.

CONCLUSION

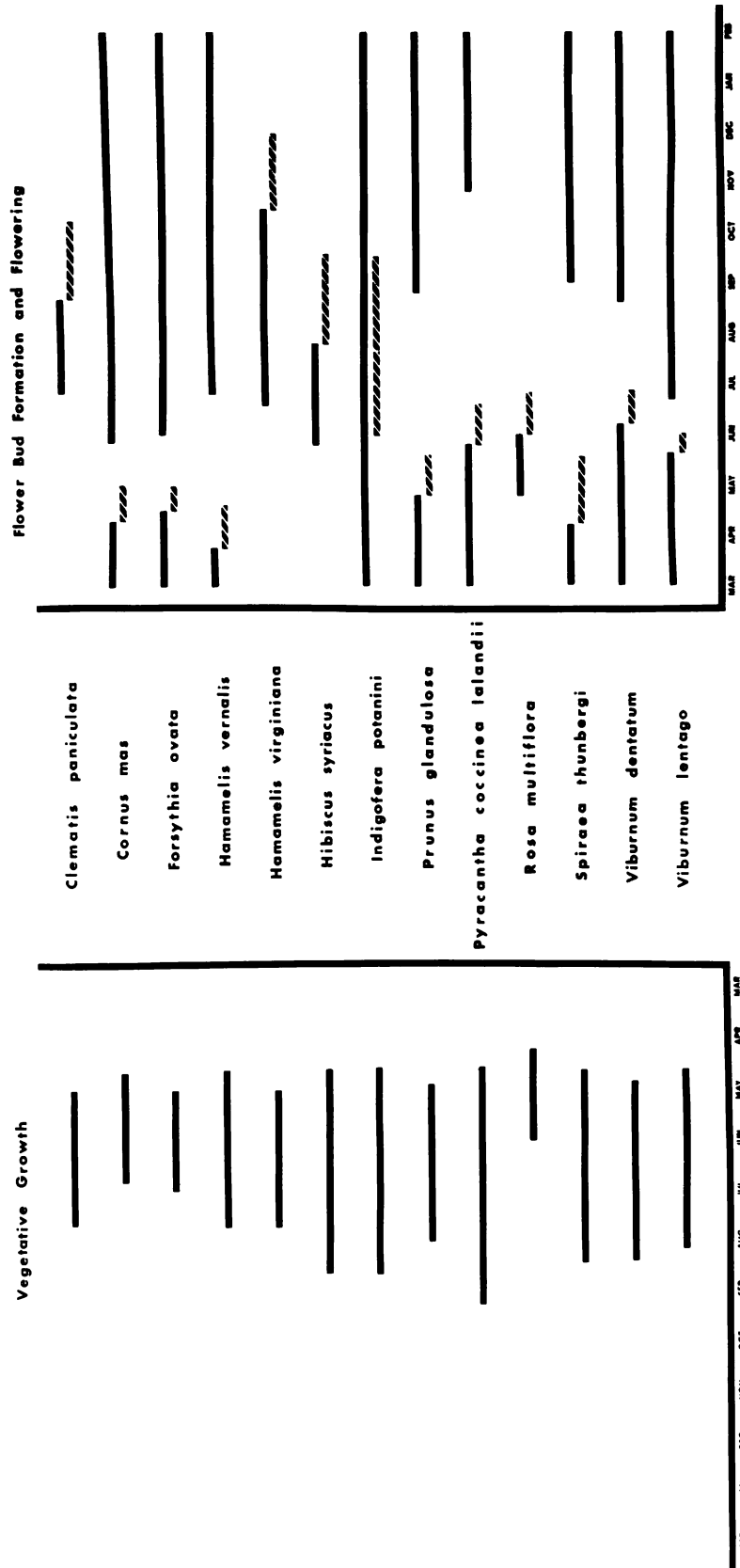
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— Vegetative growth and flower bud formation.

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for Rosa canina L. in England. Both plants initiated flowers in late April and flowered from mid to late June. Viburnum dentatum L. and Pyracantha coccinea Roem. var. lalandii Dipp. which flowered during early summer were found to initiate inflorescence primordia in late summer and late autumn, respectively, but did not initiate floret primordia. Inflorescence and flower initiation and development of Pyracantha coccinea Roem. lalandii Dipp. was found to correspond with results found by Reisch, Chadwick and Hildreth (1961) and Girouard (1962).

Flower initiation and development in Indiogfera potanini Craib. were most interesting. Although this plant flowered all summer the majority of flowers were borne during the first 3 or 4 weeks of the season, the amount of flowering decreased from that point until flowering stopped in late September. In addition, flower primordia were formed throughout the flowering period and into the autumn. Within the multiple winter buds as well as within individual racemes 2 or 3 stages of development of miniature flower primordia were found. Microscopic examination of these buds revealed that the order of flower part succession was similar to that found by Goebel (1887).

The length of time over which vegetative growth progressed was a factor in the initiation of flower buds in plants which flowered in the autumn. The amount of vegetative growth of Hamamelis virginiana L. and Hamamelis vernalis Sarg. were similar. Vegetative growth of H. vernalis Sarg. was more vigorous and flower buds appeared to develop more abundantly under cultivation than those of H. virginiana L. Although H. virginiana L. flowered in mid to late autumn and H. vernalis Sarg. flowered in very early spring, the time of flower bud initiation of each species was within 5 or 10 days of one another. Fruits of H. vernalis Sarg. matured the same year as anthesis and fruits of H. virginiana L. mature 1 year after the flowers opened.

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Results obtained in this study generally agree with the order of succession in papilionaceous legumes (Goebel, 1887), rosaceous fruit crops (Goff, 1899, 1900, 1901), loquat (Smock, 1937), cranberry (Lacrois, 1936), lowbush blueberry (Bell and Burchill, 1955), Gaultheria species (Chou, 1952) and Populus species (Nagarij, 1952).

The results of the present investigation were intended to serve as a guide for experiments on cultural methods similar to those for tree fruits (Ruth, 1921; Harley, Masure and Magness, 1932; Crane and Dodge, 1935; and Edgerton and Harris, 1950). In addition these data were prepared as a beginning for further work on the ecology of flowering of woody ornamentals to aid the understanding of their responses to various environments.

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