

AN ABSTRACT OF THE THESIS OF

John Robert Kelley for the degree Master of Science

in Horticulture presented on November 14, 1979

Title An Analysis of the Effects of Plant Growth Regulators and

Boron on Flower Development in Filbert, *Corylus avellana* L.

Abstract approved:


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Three distinct stages of flower cluster abscission were identified prior to fertilization: flowers which did not begin development (stage I), flowers which had begun development (stage II) and clusters which had begun to form distinct nuts (stage III). Abscission of stages I and II coincided with a rapid increase in leaf area. Abscission of stage III coincided with the rapid increase in ovary growth.

A localized dominance effect appeared to occur among buds located in close proximity. This became evident when multiple buds occurred at the same node or when numerous buds were borne on catkin peduncles. Both 'Ennis' and 'Barcelona' averaged over one nut cluster per node when multiple flower clusters were borne on a catkin peduncle.

GA₃, 50 ppm, induced multiple budding at nodes. Developing female flowers were inhibited from maturing and abscised. Male

catkin development was also inhibited but to a lesser extent. Significantly greater numbers of female flowers differentiated in August on those branches treated the previous spring with GA₃. Nuts per cluster was increased with daminozide (2000 ppm), however, daminozide, TIBA (50 ppm) and boron (one pound actual boron per acre) reduced nut size. Daminozide, boron and TIBA did not influence the percent set at any treatment date. Ethephon (500 ppm), increased set. At all three treatment dates it increased percent set. The May 30 application increased set 18 percent above the control. There was no influence on set the year after treatment as a result of any of the sprays.

An Analysis of the Effects of Boron and Plant
Growth Regulators on Flower Development in
Filbert, Corylus avellana L.

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

November 15, 1979

Commencement June 1980

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An Analysis of the Effects of Plant Growth
Regulators and Boron on Flower Development in
Filbert, Corylus avellana L.

I. INTRODUCTION

A major production drawback of the filbert (Corylus avellana) is its biennial cropping nature. The Willamette Valley of Oregon is a small geographical area that produces 95 percent of the total U.S. filbert crop. Periodic weather conditions affecting the entire valley synchronizes most of the trees to the same biennial cropping pattern. Wide differences in annual production make it difficult to develop and maintain stable markets. Cultural management is likewise complicated by this phenomenon. Solving the biennial bearing problem would probably increase production and greatly improve marketing of the U.S. filbert crop.

This study examines the possibility of increasing yield via foliar application of selected plant growth regulators and boron. Increasing yield in the off year would level out production thereby reducing annual yield differences.

The parameters influencing yield which were examined include, pollen production, fruit set, nuts per cluster, nut size, kernel weight, blank production and floral initiation. A separate study examining the morphological development of flowers and fruit during abscission was undertaken. Such analysis permits a better understanding of flowers and fruit abscission in the filbert.

Biennial Bearing

The basis for biennial bearing in the filbert was first studied in 1925 (94). A high correlation was found to exist between shoot length and the number of female flowers. Later research established that long filbert shoots provided greater potential bearing surface (119). Detailed analysis of shoot length as related to female flower production indicated that shoots shorter than 14 cm bore substantially fewer flowers per centimeter of wood than longer wood (101, 192, 111, 113). It is hypothesized that the trees cannot bear a heavy crop and also produce vigorous stem growth to bear a second heavy crop the following year. Alternate bearing appears to be caused by alternating short and long shoot production during years of heavy and light crops respectively.

Studies examining shoot growth and bearing potential hint at a partial answer to the biennial bearing problem. Where as short shoots produce short shoots, long shoots produce long and short shoots (119). The number of female flower clusters initiated is strongly dependent on current season's shoot growth which is influenced by the vigor of the previous two years growth (Lagerstedt personal communication 1979). These results suggest that tree vigor should be maintained so as to induce consistent year to year growth.

The heavy crops in pistachio and pecan are also borne on long shoots (42). Carbohydrate depletion during kernel filling in the on year reduces winter reserves resulting in shorter shoot growth the

next year. This fluctuating carbohydrate pool affecting shoot vigor is implicated in the biennial bearing problems of pecan and pistachio.

Abundant pistachio female flower buds develop in spring, however a majority of them abscise during kernel development in the on year (42). Removal of nuts and increase in leaf area per fruit both promote flower bud initiation (38, 41). These findings imply an inadequate carbohydrate supply as a cause of floral abscission. It is supported by the fact that bearing branches enter winter with lower carbohydrate reserves than non-bearing branches resulting in less reserves for shoot growth in the off year (37, 39).

A hormonal interaction has also been hypothesized as there is sufficient soluble sugars in the nut bearing branches during kernel development for starch synthesis (39). Flower bud abscission on de-fruited branches does not occur until 63 percent defoliation (38). Either the flower buds require low levels of carbohydrates or the leaves are producing and exporting a flower bud abscission inhibitor. This does not appear to be auxin as an application of para-chlorophenoxyacetic acid (PCPA) only delayed abscission (41).

Pecan kernels mature during mid August to mid October. Starch is not accumulated in the tree until the fruit requirement is met. As a result the tree enters winter with low carbohydrate reserves (132, 152, 153). Accordingly weak inferior flowers are formed terminally on the next years growth which is characteristically short (130). This results in massive flower drop up to and during the time of fertilization. It is not known if any aborted flowers have been successfully fertilized.

Hormone imbalance in the pecan flower is not implicated as during flowering auxin concentrations are high and abscisic acid levels are low (78).

A heavy filbert crop reduces shoot growth in the year it is borne (101). Rapid ovary development on heavily bearing trees in mid-May could initiate serious substrate competition resulting in early growth cessation. Cluster set is ten percent greater in the off year than in the on year (101). Superior set appears to be due to reduced substrate competition during the cluster set period assuming that the flowers initiated in the on and off year have equal vitality. Growth cessation two weeks earlier in the on year could account for the observed reduced growth.

Floral Initiation and Differentiation

Floral differentiation has been observed in several Italian filbert cultivars. Staminate catkin primordia were found between June 20-30 in the cultivar 'Santa Maria di Gesù' (126). Pistillate flower clusters were reportedly differentiating from mid-May to June 30. In this cultivar both the male and female flowers were differentiating at the same time.

The cultivar 'San Giovanni' began pistillate cluster development at the end of June or beginning of July, while another reported cultivar initiated cluster development at the end of June--beginning of August (144, 7). First to differentiate were flowers borne at nodes, while flowers on catkin peduncles developed later. It was hypothesized that initiation occurred in mid to late June.

In 1875 Baillon reported finding the first pistillate flower primordia on June 15 in France (61). Examination of a filbert shrub growing in a Munich conservatory in 1892 determined that staminate differentiation began between June 10-20 with pistillate differentiation occurring during the first week of September (Albert 1892).

The 'Barcelona' filbert in the Willamette Valley begins staminate catkin differentiation in mid-May while pistillate cluster primordia are not visible until the last week in August (139). This would indicate that in Oregon 'Barcelona' male flower initiation occurs during active shoot growth and female flower initiation occurs after shoot growth has ceased.

Walnut catkins differentiate in late spring at a time when gibberellin bud levels are high and levels of auxin and abscisic acid are very low (76). Female flowers begin initial differentiation in late summer when GA levels are very low and auxin and abscisic acid concentrations are quite high. This hormonal relationship during male and female flower differentiation has been reported in numerous crops (129, 105, 68, 55). This relationship between GA, IAA and ABA concentrations during flower differentiation would appear to be occurring in the 'Barcelona' filbert as it differentiates its male and female flowers as approximately the same time.

Filbert flowers male and female, develop in axillary buds of current season wood. Female flowers may also develop proximally on the newly formed catkin peduncles (103, 109).

A recent study has shown that there is a cultivar difference in the relative proportion of female flowers borne on catkin peduncles or singly at nodes (75). 'Ennis' (81 percent), 'Butler' (69 percent) and 'Lansing' (67 percent) bear a majority of their total female flower production on catkin peduncles. 'Barcelona' flower production on the other hand is more evenly divided between catkins peduncles (41 percent) and large single flowers at nodes (48 percent).

Male and female flower production occurs on the same biennial cycle. Catkins are borne laterally at nodes on previous years growth. Therefore, large shoot growth the previous season provides a greater number of nodes from which catkins can be initiated. By the same token more catkin peduncles are formed increasing female flower production.

In Oregon, the male catkin is visible during the first week of July as it emerges from the axillary leaf bud. The female flower remains hidden behind the bud scales until bloom in December. An average of eight flowers are borne in the 'Barcelona' bud cluster (104)..

Floral Development

The ontogeny of female bloom, pollination, fertilization and subsequent ovule development has been extensively examined (109, 61, 144, 108, 112, 140, 26). The wind-pollinated filbert does not require showy visual or olfactory attractants for pollination. Early female flowers emerge from axillary buds in December with full bloom generally

occurring in February. Emergence and full bloom varies with cultivar (109). The stigma is receptive from its emergence in December until it is black and withered in March (141). The longevity of pecan stigmas decreases with low relative humidity, high temperature and wind (146). The long receptivity of the filbert stigma on the other hand is probably due to the cool temperatures, high relative humidity and low wind velocity during the winter bloom period.

Male Flower

The male catkin is made up of multiple bracts attached to a central vascular strand. Each bract is subtended by eight anther sacs. In early winter, in Oregon, elongation of the catkin's central vascular system separate the bracts exposing the anthers. The anthers dehisce in response to low relative humidity. The dry, smooth, small (20.2 x 24.8) pollen grains may drop onto the bract below and be blown away by the wind to land on a stigma (65, 1).

Elongation of the catkins occur in January and February with catkins at various stages of elongation at any one time. This ensures that pollen is not released all at one time but on numerous occasions. It reduces the possibility of pollen damage by cold or moisture and dispersion in only one direction. Dehiscence spread over a one to two month period ensures pollination of any late blooming female flowers.

The 'Barcelona' is a self sterile cultivar, i.e., it requires cross pollination with a compatible pollinizer (95). The pollinizer must also bloom at the same time thereby complicating the selection of a good pollinizer.

Filbert pollen grains burst in the presence of free water due to excessive osmotic uptake of moisture. A survival mechanism has developed whereby the anthers dehisce after a drop in relative humidity. This generally occurs when it is not raining. Pecans have developed a similar mechanism. They will not dehisce at high relative humidities or at temperatures over 85°F. This eliminates pollen destruction by rain or dessication.

Cool temperatures, high relative humidity and lack of excessive winds during winter pollination allow the filbert bloom to be extended over a two month period. A warm winter on the other hand will markedly reduce the catkin bloom period by increasing the rate of elongation and dehiscence (24). The bloom period of the female flower on the contrary does not seem to be affected by temperature. When all the pollen is shed the catkin shortly thereafter turns brown.

Within two days of pollination the pollen germinates. The pollen tube travels down the style stopping short of the base of the style. Here the tube and two generative nuclei encyst because the ovary has not yet developed. In mid-June, four to five months after pollination, the embryo sac matures and a second pollen tube is generated. Fertilization then ensues.

Female Flower

At the time of pollination, January or February, the major portion of the female flower is hidden in the bud. Two red stigmatic styles protude about 0.3 cm from the bud tip. They are joined at their base

by a small amount of rudimentary ovarian tissue. This is a unique aspect of filbert floral biology as the embryo sac in most flowering plants are essentially mature at the time of pollination.

The ovary differentiates from a growing intercalary zone beneath the styles and perianth (61). The encysted pollen nuclei and placental tissue are raised during ovarian differentiation so that fertilization and embryo development occurs in the apex of the nut.

The ovules are nurtured by a vascular strand which differentiates from the intercalary zone as the developing ovules are elevated with ovarian growth (61). A meristematic region in the vascular bundle where it crosses the intercalary zone can not function completely as vascular bundle cells while in a meristematic condition. Hagerup suggests that the kernel does not begin development until the ovary has reached full size and the vascular bundles can function properly.

The filbert ovary begins development in late April early May, being only two to four mm in diameter by the end of May (140). At this time some ovaries begin a rapid growth. In mid-June these ovaries are eight to ten mm in diameter at which time the embryo sac is mature and fertilization takes place four to five months after pollination.

The ovary contains two parietal placenta each bearing two ovules (61). Typically only one, or occasionally two, of these will develop into a seed. The bracts are located below the intercalary zone. They develop independently into the enveloping involucre.

The shell of the nut results from lignification of the ovary wall. The tissue filling the ovary prior to seed growth consists of

large thin walled parenchyma cells (61). The vascular bundle also develops from this tissue.

Embryo Development

There are initially four ovules but two develop to the mature embryo sac stage. Only one generally develops into a seed, the other aborting. Occasionally two seeds are present. In Oregon Embryo growth is rapid beginning around the first of July and ending five to six weeks later (139). Maturation of the embryo continues in August and September with differentiation of leaf primordia, vascular strands and root cap. Separation of the nut from the tree occurs at the intercalary zone. Nut fall is delayed until the involucre reflexes releasing the nut.

Floral Abscission

The filbert annually drops more than 80 percent of its flowers (109, 140). In an effort to determine if this is due to improper pollination, Thompson examined the styles of 'Barcelona' flowers under fluorescent microscopy. Over 90 percent of the flowers examined from trees in the Willamette Valley had pollen tubes in their styles. A similar Italian study on 'Tonda Gentile della Langhe' reported 28 to 52 percent had pollen tubes (112). Pollen tubes within the stylar tissue represents successful cross pollination, because most filberts are self sterile. Selfed pollen does not germinate on its own style.

After pollination there is a quiescent period, then ovary growth begins slowly. Non-pollinated ovaries do not initiate growth (140). During mid-May pollinated filbert flowers begin rapid ovarian growth. However 70 to 80 percent cease growth after attaining three-fourths to two mm diameter (109, 140). Unpollinated ovaries do not develop beyond 0.5 mm diameter, implying that growth cessation in May is not due to a lack of pollination.

If one embryo in a multiple cluster maintains development, the cluster will remain on the tree until nut fall in October. However if all the embryos in a cluster cease growth, then the cluster will abscise. The 'Barcelona' normally sets about 2.2 nuts per cluster while other cultivars set up to four (140, 74). Schuster suggests that the number of nuts set per cluster is a maternal characteristic, while percent cluster set is dependent on the pollen parent (122).

Blanks

A portion of the filbert flowers mature into nuts containing no developed kernel. Up to 25 percent of the 'Barcelona' nut production may be blanks (96). In a three year study, 97 percent of the blanks examined contained small aborted embryos, indicating fertilization had taken place and initiated development (98). The remaining three percent had no visible embryo, suggesting that fertilization may not have occurred. It would appear that stimulative parthenocarpy is a rare if ever event in filbert. The walnut on the other hand is known to produce apomictic fruit (117). In fact the tendency towards apomixis has

been observed in all taxons of the Juglandaceae (58). This has not been reported in filbert.

Fertilizer trials with NPK and Mg had no effect on blank production and would seem to rule out association of blanks with mineral nutrition (98). Nor were blanks preferentially associated with either short, medium or long shoots (120).

An Italian study comparing tillage and irrigation on blank nut production determined that tillage significantly reduced blank production (156). The combination of tillage and irrigation was even superior. Irrigating a cultivated Oregon orchard did not reduce blank count over the non-irrigated control (75). This orchard was located on deep fertile soil and might therefore have had adequate stored soil moisture. The Italian paper did not report average rainfall distribution or soil depth. Irrigation and the elimination of weeds would significantly improve the soil moisture content in a shallow soil with long intervals between rainfall. It is possible that under such stress moisture conservation practices would reduce blank production.

It was originally felt that poor pollination was the basis for blanks (121). In hand-pollinated controlled crosses masses of compatible pollen have been applied to receptive styles. The percentage blank production was not reduced, indicating that inadequate pollination may not be the cause of blanks (98).

Blanks do not seem to be related to lack of compatible pollinizers. In 'Barcelona' orchards with up to five different compatible pollinizer varieties the blank percentage is not reduced (98). However in a limited study evaluating potential pollinizers for 'Barcelona' there

was limited evidence that the number of blanks varied with the male parent (155). This suggests that blank production is influenced by the pollen parent. Selfing produces few nuts and most of these are blanks (7, 123, 155).

The necessity for pollinizers was first recognized in 1905 (118). Work by Schuster showed that trees 17 meters away or farther produce smaller crops (124). Schuster also noted that orchards with few or no pollinizers are characterized by high blank counts (121). Research has not supported the idea that the pollen parent influences blank nut production.

Filbert wind pollination has prompted studies examining: distance pollen travels, deposition density over distance, and pollen type over distance (4, 104). In a 24 hour period with wind averaging two m/sec, round pollen did not carry over 18 meters, while shrunken poor quality pollen grains traveled up to 34 meters. Yield drops and blank count rises with increasing distance from a pollinizer due to reduced pollination.

Cytological studies of the Corylus genus (and *avellana* specifically) revealed tri and quadrivalent chromosomes, cytotoxicity and nondisjunction during meiosis in the pollen mother cells (116, 151, 85, 70). The resulting microspores that contain an odd chromosome number develop into abnormal, empty pollen grains. Kasapliligi suggests that these may cause blanks (70). However, in a study involving controlled crosses, the percentage abnormal pollen of an essentially sterile male parent could not be associated with blank nut production on another cultivar. Open pollination of the male sterile hybrid produced 85 percent blanks

suggesting that similar meiotic abnormalities may be occurring in megasporogenesis.

Flowers of Kerman pistachio undergo degeneration of the megaspore mother cell, megaspores or embryo sac which results in flower abscission (35, 16). Whether it was due to meiotic abnormalities or rootstock influence was not stated. Blank production due to embryo abortion has been associated with seedling rootstocks of Pistacia atlantica (34, 40). Filbert rootstocks have not been implicated in blank production.

The pollen of six Turkish filbert cultivars and three native types could be divided into three categories: round, convex, and ellipsoid (4). Round turgid pollen grains were assumed to be viable. Their germination percentages in this study, although following a trend, did not match the observed round pollen percentage. This demonstrates the difficulty in developing good germination techniques. Different techniques produce different results confounding evaluation of germination studies. There is a need for an accurate uniform germination test so that the pollen quality of different cultivars can be evaluated.

Pollen Production

The stigma provides an extremely small target for the pollen. The filbert must therefore produce copious numbers of pollen grains. Various estimates of the number of pollen grains released by a single catkin range from 1.2 to 5 million (109, 86, 52, 154, 103). Multiplying these figures by the number of catkins per tree reveals the immense sperm production of the filbert.

Nut Weight and Nuts Per Cluster

There is an inverse relationship between the number of nuts per cluster and the individual nut weights (120, 113). Long shoots average more nuts per cluster and larger kernels. It appears obvious that this is due to the greater leaf area the flowers and kernels can mobilize substrates from. However, no direct effect of subtending leaf area has been observed on nut weight (120, 111).

Fruit Set

Soil analysis has revealed a deficiency of boron in some Willamette Valley soils. Schuster and Stevenson while conducting extensive walnut fertilizer trials included limb injections of borax on filbert (125). Two annual soil applications of 0.44 pounds of boron per filbert tree induced toxicity (100). Reducing the rate to 0.03 and 0.06 pounds per tree did not produce any consistent trends (99). However an increase in yield, nut weight and percent kernel weight were reported in various years.

In a separate study soil boron applications of six pounds per acre have increased cluster set 25 percent (9). This treatment has been effective in orchards reporting 50 ppm in August leaf analysis. Filbert leaf boron levels of 50 ppm are not deemed deficient at this time (136).

Spring sprays of boron at one pound per acre have also increased cluster set (9, 10, 11). Treatment late in the spring had the most pronounced effect, with the May 30 application increasing cluster set

30 percent. It is felt that boron's effect is not due to a classical deficiency but to the inability of the soil, root-absorption, and translocation to supply adequate boron during a critical stage of flower development.

A boron deficiency in pear was found to be caused by an inability of tree roots to take up boron from cold soil in early spring causing blossom blast (13). 'Barcelona' filbert begins leafing out in late March with flower abscission occurring in mid-May. Soil temperatures at this time are warmer than at pear blossoming but still may be sufficiently cool to cause a similar problem.

A post harvest spray of boron on 'Italian' plum was substantially superior to a prebloom spray in enhancing fruit set (22). Post-harvest sprays increased flower boron content above a prebloom spray and both increased boron levels above control. Boron concentration in filbert flower parts has not been examined.

Large female flower clusters borne singly on nodes produce a greater number of nuts per cluster and set a greater percentage of clusters than medium, small or catkin peduncle borne flowers. These large flower clusters exhibit greater vitality than other clusters however they amount to only one quarter the total number of flowers produced on 'Ennis', 'Lancing' and 'Butler'. The greater number of peduncle flowers ultimately bear a greater proportion of the nuts. A significant increase in yield is potentially possible if a greater number of peduncle borne flower clusters could be induced to set.

Growth Regulators

Previous plant growth regulator studies in the filbert have centered around sucker control and nut drop acceleration (107, 73). There is no mention of any side effects on fruit set or floral initiation as a result of these treatments.

There is a single Italian study reporting the effects of gibberellic acid on fruiting of filberts (83). Gibberellic acid (GA_3) (10 ppm) was applied at the four to five leaf stage and 50 days later when the embryo was beginning to form. Their results indicate that an early gibberellic acid application increases yield and marketability of the filbert due to increases in nuts per cluster, nut weight and nut volume. Roundness of nut and kernel was also improved. The late GA_3 application increased the production of blank nuts. There was no original flower count so it can not be determined if this was due to increased embryo abortion or to the retention of nuts whose embryos had aborted. The use of a single concentration and two treatment dates so widely apart do not warrant any definitive conclusions. It would be of interest to know the results of gibberellic acid applications at various concentrations and intervals during ovary development and fertilization.

An Oregon pilot study was conducted in 1965 to evaluate the effects of daminozide and 2, 4, 5-TP on cluster size, yield and blank percentage (97). Multiple sprays applied to 'Barcelona' trees January 10, February 10, and June at an unspecified concentration did not result in any

significant effects. As would be expected 2, 4, 5-TP prevented nut drop as the husks remained green.

Fruit set of pecan was not affected by June or July sprays of GA_3 (131). There was an increase in shuck and shell weight as well as nut density.

Parthenocarpy is generally promoted by GA_3 applications during blooming of pear, apple, Valencia orange, figs, grapes and stone fruits (15, 91, 45, 36, 43, 31). This is a desirable effect where the ovary is the primary edible part of the fruit. However, with parthenocarpy there is no embryo development. Parthenocarpy would result in the production of nuts with little or no kernel development.

Daminozide applications during or shortly after bloom has promoted fruit set in apple, pear, pomegranate and grape (47, 79, 93, 49, 54, 51, 51, 84, 60, 21, 138). However, the expected increase in yield did not materialize as there appeared to be a negative effect on fruit size (12, 114, 89). The reduction in fruit size was related to daminozide concentration. There appears to be a threshold effect on fruit size reduction the year following treatment as rates below 250 ppm had no effect (147).

There are no reports of ethephon or 2, 3, 5-Trichlorobenzoic acid (TIBA) promoting set in the year applied. Both have increased fruit set in apple the following year (135). However this is not observed in all cases (57).

Flower Initiation

Gibberellic acid treatments prior to floral initiation inhibit flower formation in numerous crops: Valencia orange, apple, pear, peach, plum, apricot, sour cherries, and almond (59, 90, 46, 30, 33). Sprays after floral initiation has occurred results in flower production (32).

Gibberellic acid-induced inhibition of flowering appears to be an all or none process as no flower primordia develop if applied prior to initiation (17). In mango, GA₃ has no inhibitory effect once flower primordia are formed (69). A similar situation occurs in Pecan where inhibition of catkin formation is directly related to concentrations of GA₃ applied in June and July (131). August and September applications had no effect as the catkins were well developed by this time. Apple flower bud differentiation is also sensitive to exogenously applied GA₃. Applications two weeks after full bloom or earlier were inhibitory (142, 143). Those treatments administered three weeks or more after full bloom had no effect.

Studies comparing the influence of seeded versus seedless apple fruit on flower bud formation have confirmed the inhibitory effects of GA₃ (29, 64). Seeded fruit exerts a significant inhibitory effect on flower bud formation whereas seedless fruit do not. Seedless parthenocarpic 'Bartlett' pears export significantly lower levels of gibberellins when compared to seeded 'Bartlett' yet both have comparable internal levels of gibberellins (56). In this case floral inhibition

is directly related to the amount of gibberellins moving down the fruit peduncle.

An increase in bloom density resulting from previous season post June-drop sprays of ethephon has been reported by numerous authors (80, 18, 148, 48). However, ethephon may both increase floral initiation and induce fruit abscission in the season applied. Its effects depend on time of application (physiological stage of fruit development) and concentration. With high concentrations more fruit abscise. Ethephon, applied shortly after June drop generally does not induce fruit abscission. There is no year to year guarantee that such a treatment will not result in excessive fruit drop (57). Late May and early June sprays of ethephon has also promoted precocious flowering of young non-bearing apple trees (148, 72).

An extensive amount of work has been conducted with daminozide in hopes of increasing flower initiation in apple. Successful results have occurred with treatments applied ten days to six weeks after full bloom (106, 20, 148, 48, 44, 137, 28, 135). Applications five weeks after full bloom or later have a diminishing influence on floral initiation (53). The flowering response increases with increasing rates up to 6000 ppm. On the other hand tree growth diminishes as the concentration rises (106, 145).

Floral bud development in sour cherry and cranberry is improved with daminozide applications ranging from 1000 to 8000 ppm (3, 77). Similar successful treatments are described for plum, sweet cherry and pear (87, 28, 115). No effect was observed in orange after treatment with 3000 ppm daminozide (92).

Induction of precocious flowering has not always been successful in apple. Young 'Wayne' apple trees treated with 2000 ppm three to six weeks after full bloom did not significantly increase flowering although shoot growth was reduced (71). A combined spray of daminozide and ethephon successfully increased flowering.

Selected apple varieties have responded with increased flowering as a result of TIBA treatments applied one month after full bloom (19, 50, 49). Precocious flowering has been induced on one year old Johnathon apple trees with 35 ppm TIBA applied late in the growing season (134).

Daminozide, ethephon and TIBA are all effective in promoting flower initiation on apple when applied one month after full bloom. It would appear that growth cessation or retardation is the essential common feature in the treatments. However, this does not appear to be the case with young 'Cox's Orange Pippin' apple stems placed horizontally after growth cessation. Such stems initiate as many flowers as those treated with daminozide, TIBA, and ethephon (142, 143). This suggests that an endogenous hormonal change underlies increased flowering as a result of SADH, TIBA, and ethephon applications.

Sex Expression

Male walnut catkins differentiate in lateral buds at a time when gibberellic acid is present at high levels with no indolacetic acid activity present (76, 128). A similar relationship exists during flower differentiation of Zea mays (129). Female Cannabis sativa

plants can be induced to form male flowers with GA_3 treatment (105). This change in sex expression is concentration dependent which implies that a hormonal balance is operating. The maleness of the Cucurbitaceae can in general be increased by treatments with GA_3 (149, 55, 133, 110, 24).

Whereas gibberellins promote maleness in the Cucurbitaceae ethephon promotes femaleness (25, 82, 66, 6, 5, 127). With ethephon treatment at the four leaf stage female flowers are formed at earlier nodes and in greater numbers. The effect is not permanent as the vines grow out of ethephon induced femaleness. Gibberellic acid reduces the ethephon's effect on femaleness. The interaction is not significant thereby suggesting that they operate independently rather than antagonistically (133, 62).

Daminozide has promoted female flower production in muskmelon (62). A later study on an andromonoecious cucumber line resulted in fewer male flowers. However an increase in female flower number was not observed (81).

A 25 ppm spray of TIBA on young cucumber seedlings has resulted in an increase in the ratio of pistillate to staminate flowers (150). Sex expression of young papaya (Carica papaya), a weakly dioecious plant, became more female after treatment with TIBA (67). This growth regulator has also extended the period during which male walnut catkins are initiated and differentiate (76). The TIBA inhibited basipetal transport of auxin from the apex resulting in low auxin levels in lateral walnut buds. Male catkins differentiate in the presence of GA_3 and absence of auxin.

Growth regulators have been successfully used in numerous tree crops to improve set and floral initiation. Yields have been increased in some cases. Following are the results of attempts to increase set and influence floral initiation in the Filbert via applications of Boron, TIBA, daminozide, GA₃, and ethephon.

II. MATERIALS AND METHODS

Growth regulators applied to filbert branches in the spring of 1977 were: daminozide, 2000 ppm; GA₃, 50 ppm; ethephon, 500 ppm; TIBA, 50 ppm and 100 ppm; and boron, applied as sodium pentaborate at the rate of one lb. boron per acre. A pilot study in 1976 established that GA₃ at 250 ppm applied May 6 was excessive. As a result the rate was lowered to 50 ppm in 1977. Each treatment was applied without surfactant, but the foliage was wetted thoroughly. Each treatment consisted of three single tree replicates. Four limbs per tree were sprayed (approximating N, S, E, W orientations). Sprays were applied one week before flower cluster drop (April 29), during maximum cluster drop (May 15) and as cluster drop declined (May 29). The last spray of TIBA 100 ppm was delayed until June 20 in an effort to influence female flower initiation.

Female cluster counts were made the previous winter so as to be able to determine percent cluster and nut set during the 1977 growing season. Treatment effects on yield, the percent set, number of nuts per cluster, percent blanks, nut size, and kernel weight were also evaluated for each treatment.

Limb diameters were taken at the base of bearing wood. Cross-sectional area for these stems was computed ($D^2 \times 0.7854 = \text{cm}^2$). A ratio of flower clusters and nuts per cm^2 cross-sectional area served as a means of comparing treatments effects on fruit set and flower initiation. Effects on fruit set were determined in August 1977 prior

to blank drop. To determine if there was any carry over effect as a result of the spring 1977 sprays the percent set on the treated branches was established in the summer of 1978 prior to blank drop.

Leaf length and width measurements were made weekly between April 5 and June 5, 1977. Measurements terminated when all leaves were fully expanded and the terminal bud had set. Four uniform limbs per tree oriented N, S, E, W on two trees were selected for leaf area measurements. These limbs averaged 68.9 cm in length and had a basal diameter of 0.766 cm. They represented vigorous lateral bearing wood.

The relationship between the actual leaf surface area and a rectangle made by the leaf length and width measurements was established. A Li-Cor Model 3100 photosensitive area meter was used to determine the actual leaf surface.

From a separate group of 'Barcelona' trees, the rate of ovary growth was determined by collecting ten flower clusters weekly between April 5 and August 11. This time span covers the period of greatest ovarian growth. The 'Barcelona' filbert is spherical, best described as a prolate spheroid. Ovary height and diameter measurements were taken. These figures were then incorporated into the following equation which approximates the volume of a prolate spheroid $(4/3)(\pi)(1/2 H)(1/2 D)^2$. As numerous ovaries were arrested in early development the approximate volume of those exhibiting substantial growth were averaged weekly to estimate ovary size.

A separate study was made to determine pollen production of the pollinizer Daviana. Individual anthers were carefully excised and mounted suture up on a cover slip coated with Scotch Spray Mount [®]

adhesive. The coverslip was then inverted and mounted on a glass cylinder one cm in diameter and one cm long. After the anther had dehisced, usually within 30 minutes, the cover slip was tapped to jar loose any remaining pollen. The anther was removed and examined under a dissecting microscope (25x). Any pollen remaining in the anther was counted. The coverslip was then examined under a microscope (100x) and the adhering pollen grains counted. The temperature in the laboratory where the process was performed was 23°C with a relative humidity of 25 percent.

Two or three drops of a hot 0.7 percent agar solution was pipetted onto the pollen. The slide was then quickly shaken to spread the agar solution over the slide and disperse the pollen grains. Upon drying, the pollen grains remained embedded in a thin film of agar. The entire agar surface was then scanned with a microscope (100x) and all of the pollen grains counted. The pollen of 11 anthers was counted.

The number of bracts per catkin was determined by individually pulling off each bract from 30 catkins. The number of anthers per bract was found by excising bracts individually and counting the anthers under a dissecting microscope (20x). Two entire catkins and nine catkin ends were counted in this manner.

The average number of female flowers per cluster was determined. Twenty five clusters were randomly selected from each side of a tree. Four trees were sampled thusly. These were dissected and the number of individual flowers tabulated.

A separate study was established to categorize seasonal bud drop. This was done by anchoring a plastic catching sheet beneath two trees and making weekly collections of vegetative buds and reproductive buds from April 24 to November 22. Following bud break, the vegetative growing points and female flower clusters were collected.

Female flower clusters occur singly on stems and up to seven in number on catkin peduncles. In an effort to determine the set of female flower clusters on catkin peduncles, 57 peduncles on 'Barcelona', bearing two or more clusters were tagged. Cluster set was determined the following August.

To more clearly establish which peduncle cluster would force and bear nuts, 44 peduncles on 'Ennis' were also tagged. Clusters were disbudded so that each peduncle had three clusters. These were examined during fruit set and the position of the clusters setting nuts was noted.

III. RESULTS

Leaf Area

Bud break occurred during the first week of April, 1977. Leaf area increased gradually for the first three weeks (Table 1). It rapidly increased from late April through May, the time during which most shoot extension takes place (Figure 1). Maximum leaf area was attained by mid-July. At this time the growing point abscised and the most distal axillary bud became the terminal bud.

A constant was formulated which allowed the conversion of leaf length and width measurements to actual leaf surface area (Table 2). The formula used was $a \times b \times 0.755$ where a = width and b = length.

Ovary Growth

A gradual increase in ovary growth rate began in mid-May (Table 3). During the first week in June those ovaries destined to develop into mature nuts entered into a very rapid period of growth (Figure 2). Full size was attained during the third week of July. These results are similar to those obtained by Thompson (139).

Pollen Production

Examination of the pollination capabilities of the Daviana pollinizer indicate that pollen production was immense. The mean number of bracts per catkin was 212 (Table 4). In the 30 catkins examined, there was an average of 7.56 anthers per bract, with eight

Table 1. Average leaf area of four vigorous lateral branches on each of two 'Barcelona' trees.

date	tree #1 (cm ²)	tree #2 (cm ²)	average leaf area (cm ²)
4/5/77	N - 0.58	N - 0.58	4/5/77 = 0.44
	S - 0.58	S - 0.58	
	E - 0.58	E - 0.58	
	W - 0.58	W - 0.58	
4/12/77	N - 1.2	N - 0.79	4/12/77 = 0.84
	S - 1.01	S - 1.25	
	E - 0.89	E - 1.23	
	W - 1.38	W - 1.18	
4/19/77	N - 1.62	N - 2.50	4/19/77 = 1.66
	S - 2.00	S - 2.02	
	E - 2.48	E - 2.43	
	W - 2.17	W - 2.35	
4/26/77	N - 4.96	N - 6.39	4/26/77 = 4.34
	S - 5.81	S - 6.16	
	E - 6.41	E - 5.37	
	W - 4.83	W - 6.12	
5/3/77	N - 11.54	N - 10.64	5/3/77 = 8.04
	S - 9.96	S - 10.34	
	E - 9.28	E - 11.62	
	W - 11.09	W - 10.79	
5/10/77	N - 12.98	N - 14.11	5/10/77 = 10.42
	S - 15.39	S - 12.30	
	E - 14.56	E - 12.37	
	W - 13.28	W - 15.54	
5/17/77	N - 18.56	N - 16.60	5/17/77 = 13.24
	S - 16.83	S - 19.39	
	E - 16.60	E - 17.35	
	W - 18.71	W - 16.37	
5/25/77	N - 20.75	N - 19.24	5/25/77 = 15.02
	S - 21.13	S - 18.41	
	E - 19.39	E - 19.24	
	W - 18.34	W - 22.71	
5/31/77	N - 23.09	N - 21.00	5/31/77 = 16.02
	S - 20.83	S - 21.13	
	E - 20.22	E - 24.44	
	W - 18.41	W - 21.13	

Table 1. Cont.

date	tree #1 (cm ²)	tree #2 (cm ²)	average leaf area (cm ²)
6/7/77	N - 22.35	N - 23.84	6/7/77 = 16.97
	S - 22.33	S - 21.49	
	E - 21.96	E - 26.33	
	W - 21.53	W - 20.07	
6/14/77	N - 28.40	N - 23.53	6/14/77 = 18.52
	S - 25.51	S - 22.51	
	E - 22.61	E - 27.03	
	W - 22.66	W - 24.17	

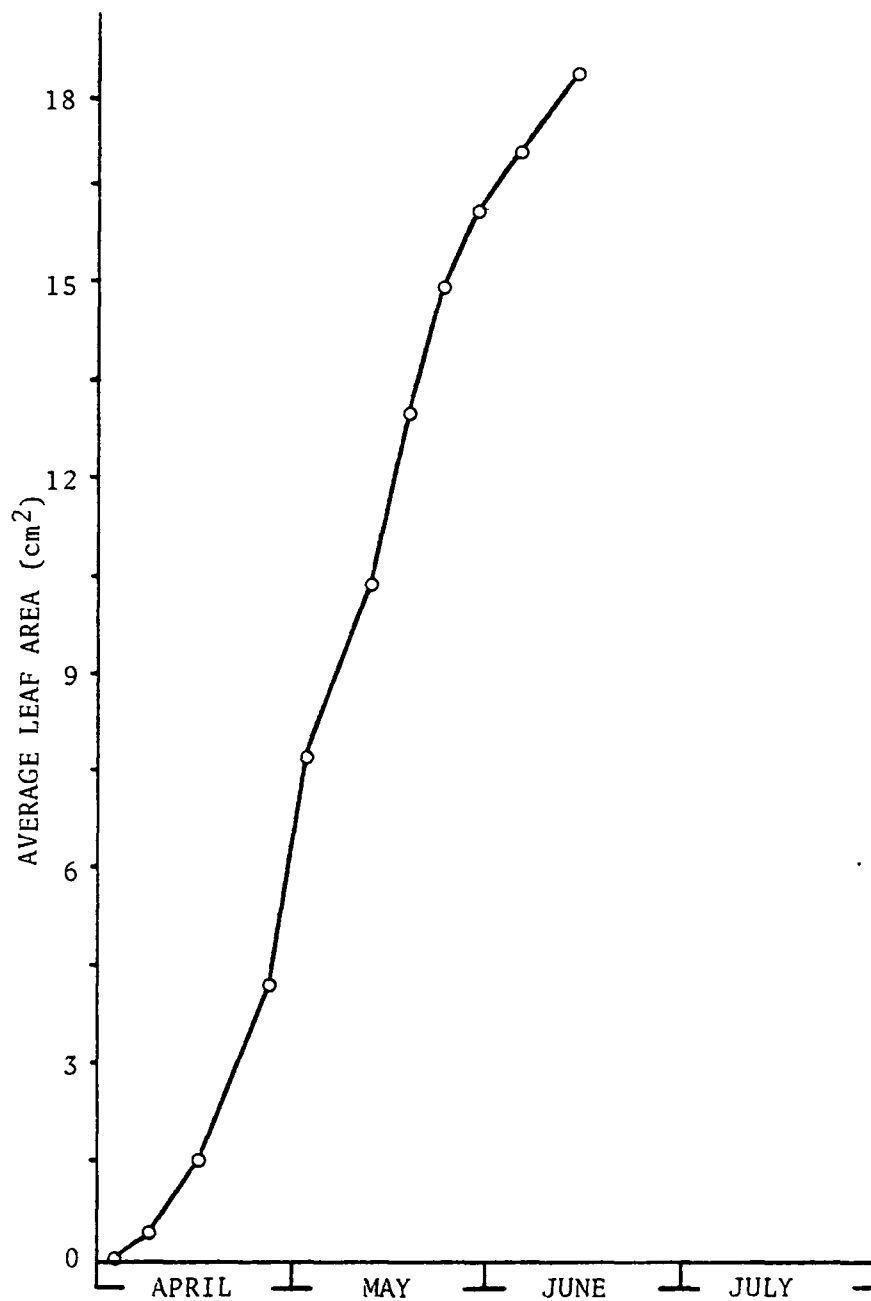


Figure 1. Expanding individual leaf area of four (north, south, east, west) one-year-old vigorous lateral branches of two 'Barcelona' trees.

Table 2. The actual leaf surface area is compared to the rectangular area established by length and width measurements of 'Barcelona' leaves.

length cm	width cm	rectangular area cm ²	Actual area cm ²	$\frac{\text{actual area cm}^2}{\text{rectangular area cm}^2}$
7.5	7.0	52.50	40.58	.773
2.6	2.4	6.24	4.77	.764
4.0	2.7	10.80	8.88	.822
12.2	10.0	122.00	92.50	.758
10.0	8.2	82.00	59.30	.723
6.5	5.2	33.80	24.45	.723
6.3	4.6	28.98	22.00	.759
8.6	7.3	62.78	47.40	.755
8.5	6.8	57.80	40.95	.652
11.8	9.4	110.92	77.93	.703
10.0	11.5	115.00	84.30	.733
8.8	6.0	52.80	34.35	.651
10.5	9.5	99.75	73.55	.737
13.5	10.2	137.70	95.69	.695
2.6	2.4	6.24	3.62	.580
7.5	5.3	39.75	28.63	.720
8.8	7.0	61.60	47.00	.763
8.6	7.5	64.50	46.00	.713
10.2	8.7	88.70	62.94	.709
7.4	5.5	40.70	29.00	.713
9.6	8.3	79.70	62.30	.782
10.4	8.7	90.50	66.70	.737
7.4	5.5	40.70	29.00	.713
9.6	8.3	79.70	62.30	.782
10.4	8.7	90.50	66.70	.737
5.8	4.4	25.52	17.80	.697
6.2	5.0	31.00	24.73	.798
9.0	6.6	59.40	43.79	.737
5.5	4.3	23.65	17.00	.719
4.5	3.3	14.85	10.36	.698
10.5	8.8	92.40	67.59	.731
11.0	9.0	99.00	74.98	.757
12.5	11.3	141.00	107.20	.759
10.3	9.0	92.70	77.90	.840
10.5	9.0	94.50	70.58	.747
5.6	4.6	25.76	17.58	.682
7.4	6.3	46.62	34.80	.746
4.0	3.3	13.20	9.26	.702
5.0	4.3	21.50	17.10	.795
3.6	3.1	11.16	8.40	.753
7.0	5.8	40.60	32.50	.800
4.5	3.5	15.80	12.50	.794
9.2	7.5	69.00	56.00	.812
9.2	10.8	99.40	80.40	.809

Table 2. Cont.

length cm	width cm	rectangular area cm ²	actual area cm ²	$\frac{\text{actual area cm}^2}{\text{rectangular area cm}^2}$
10.5	11.0	115.50	95.60	.828
9.0	8.8	79.20	63.00	.795
5.8	4.8	27.80	21.58	.775
11.0	11.5	126.50	98.50	.779
7.8	6.8	53.00	43.60	.822
6.0	4.8	28.80	20.60	.715
3.8	2.5	9.50	7.69	.809
10.0	9.0	90.00	71.40	.793
9.8	9.6	94.10	71.90	.764
7.5	5.8	43.50	33.45	.769
8.2	6.4	52.50	39.18	.743
9.4	8.1	76.10	62.00	.814
9.3	7.2	67.00	54.34	.812
11.8	9.3	109.70	83.70	.763
4.6	3.5	16.10	12.55	.780
6.4	5.0	32.50	25.70	.791
9.2	8.0	73.60	55.60	.755
5.8	4.8	27.80	22.69	.814
10.5	9.8	102.90	83.50	.811

$$\bar{X} = 0.7545$$

$$SD = 0.0478$$

Table 3. Growth of developing 'Barcelona' ovaries is estimated by determining the volume of a corresponding prolate spheroid $(4/3) (\pi) (1/2 \text{ height}) (1/2 \text{ diameter})^2$.^Z

date	Diameter (mm)	Width (mm)	Height (mm)	Volume (mm)
4/5/77	.165	.29	.249	.004
4/12/77	.238	.383	.466	.013
4/19/77	.311	.495	.689	.035
4/26/77	.351	.523	.660	.043
5/3/77	.524	.819	1.063	.153
5/10/77	.825	1.278	1.497	.533
5/17/77	.899	1.433	1.617	.684
5/24/77	1.48	2.28	2.443	2.80
6/9/77	2.3	3.69	3.93	10.89
6/14/77	3.31	5.02	5.4	30.90
6/24/77	7.5	10.28	9.27	273.9
6/26/77	8.77	11.9	12.09	486.9
7/20/77	18.95	21.68	20.27	3809.4
7/28/77	18.09	20.0	19.97	3387.8
8/11/77	8.99	19.63	20.28	3429.4

^ZDiameter and height were used to compute the volume.

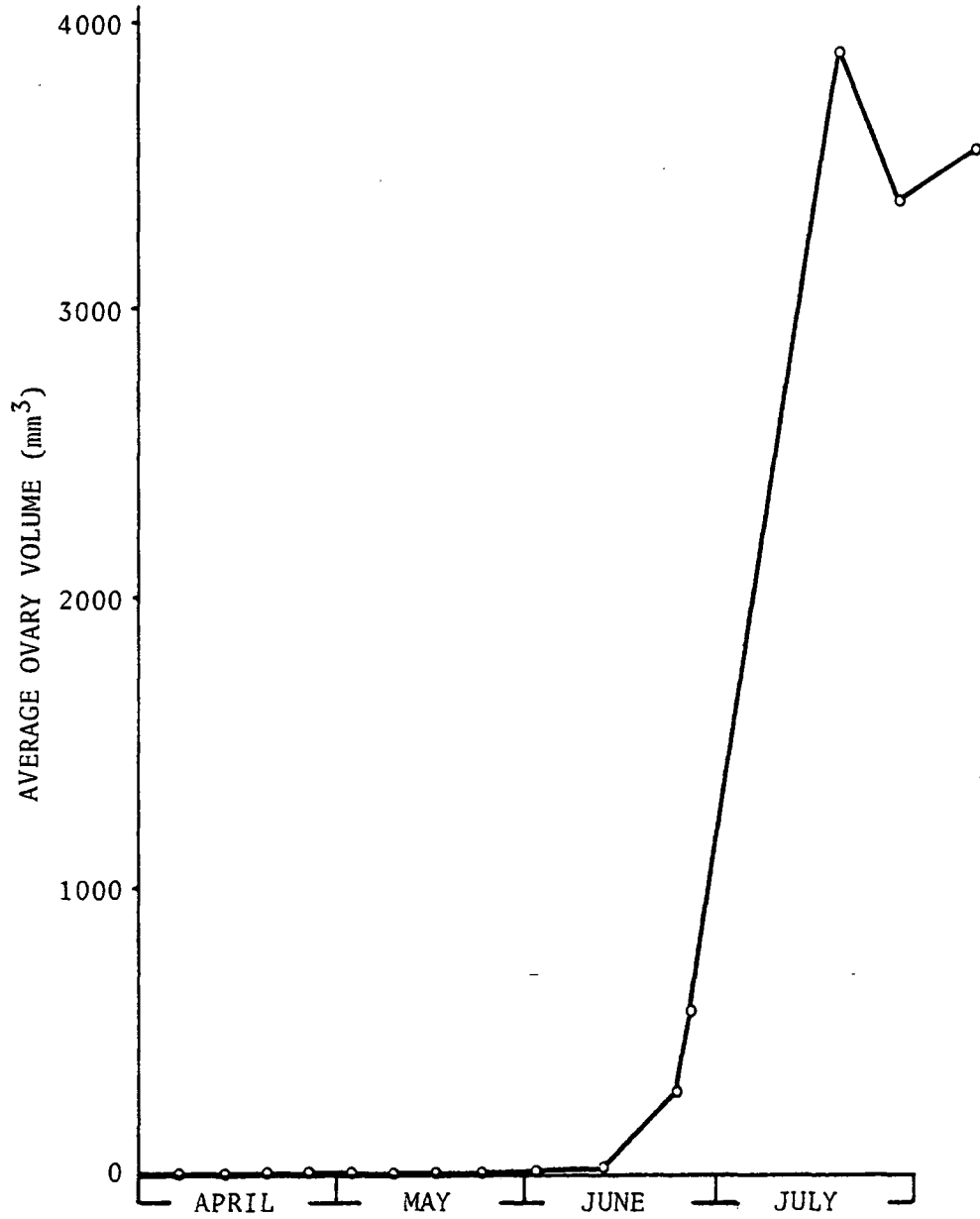


Figure 2. Growth of developing 'Barcelona' ovary. Volume was estimated by determining the volume of a corresponding prolate spheroid $(4/3)(\pi)(1/2 H)(1/2 D)^2$.

Table 4. Bracts per catkin of the Daviana cultivar. Each number represents the total bracts of one catkin.

145	196	207	231	233
157	198	208	232	238
159	198	212	232	241
190	199	215	232	241
191	200	215	232	253
193	201	225	233	261

$$\bar{X} = 212.4$$

$$SD = 27.16$$

anthers per bract the predominant figure (Table 5). Nine anthers per bract were never observed. On the basis of anther number per bract, the catkin can be divided into two parts; the larger proximal part with predominately eight anthers per bract, and a smaller distal part with less than eight anthers per bract (Figure 3).

There was an average of 2754 pollen grains per anther in the 11 anthers examined (Table 6).

The total calculated number of pollen grains released by an average *Daviana* catkin would be 4,413,891. This figure was arrived at by multiplying the average number of the component parts of the catkin: 2754 pollen grains/anthers x 7.56 anthers/bract x 212 bracts/catkin.

Microscopic examination of '*Daviana*' pollen grains revealed that many appeared clear or empty, that is having only a pollen grain wall. No cytoplasm was evident. The actual percentage of defective pollen grains per anther was not determined, but was estimated to be close to 50 percent.

Catkin elongation develops in such a manner so as to expose the anthers near the proximal end first (Figure 4, 5). The distal portion of the catkin is the last to elongate and expose the anthers. Anthers must undergo a physiological change to enable them to dehisce as only those anthers near the separating bracts were capable of laboratory induced dehiscence. These combined mechanisms allow for a timed release of the pollen over a period of days since dehiscence

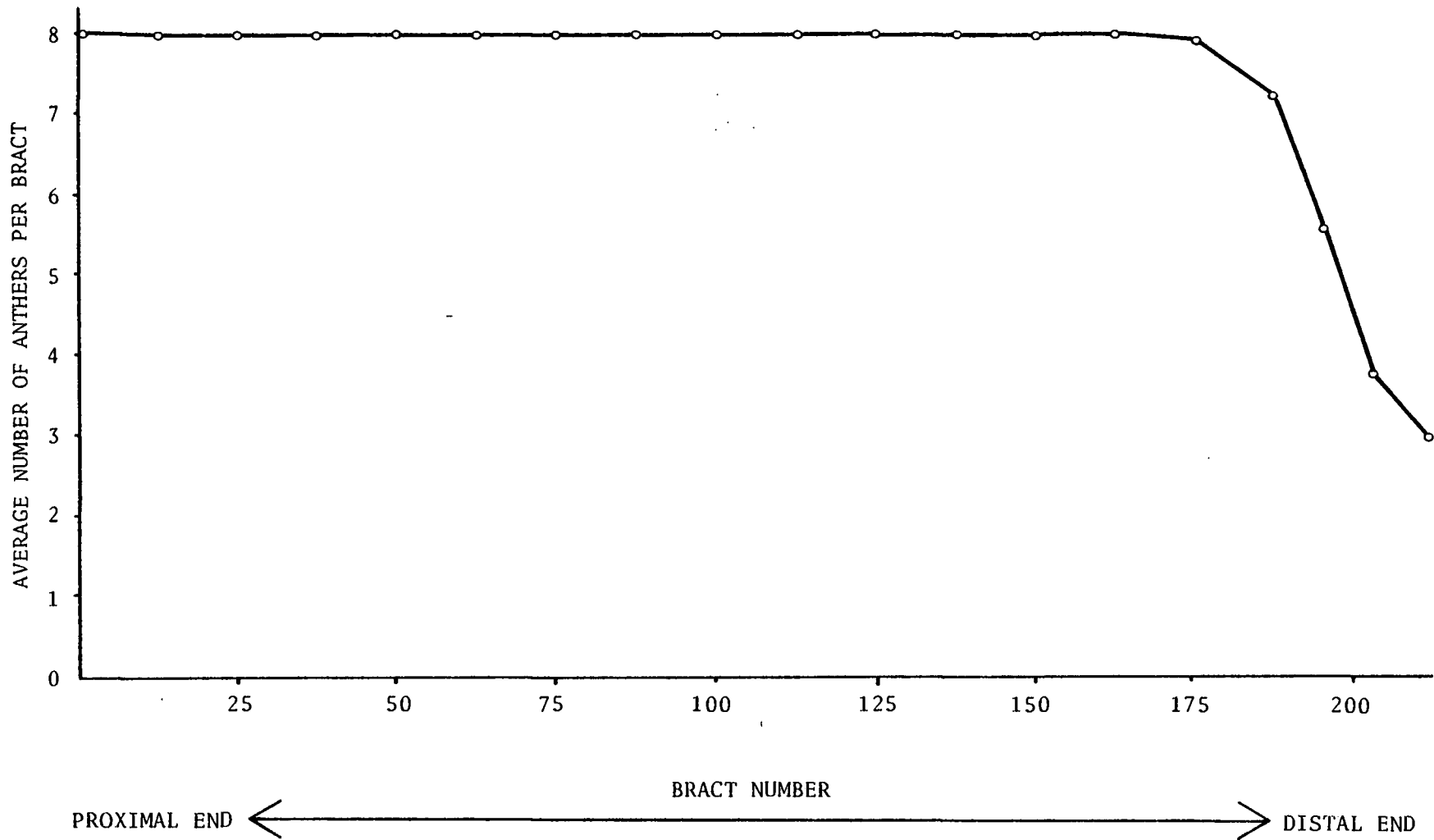


Figure 3. Average number of anthers per bract on 'Daviana'. Mean number of anthers per bract = 7.56 .

Table 6. Number of pollen grains per anther in catkins of the *Daviana* cultivar. Each number represents the total number of pollen grains in one anther.

1853	2636	3235
2106	2722	3423
2273	2916	3621
2587	2918	

$$\bar{X} = 2784$$

$$SD = 546$$



Figure 4. Elongating catkin of 'Daviana'.



Figure 5. Close-up of the elongating 'Daviana' catkin in Figure 4.

follows catkin elongation and anther exposure. In this study 'Barcelona' female flower clusters averaged 8.56 flowers per cluster (Table 7). Another researcher has noted 8.0 flowers per cluster in 'Barcelona' (140).

Flower Cluster Drop

Female flower clusters began to drop during the last week in April, 1977, and increased to a maximum a week later (Figure 6). The drop gradually declined to a low at the end of May, followed by a modest increase from the middle of June to the middle of July. The fewest number of clusters fell during July and August.

Female flower cluster drop occurred during three morphologically distinct stages: I clusters which did not begin development, that is, did not increase in size (May 1-25), II clusters which did begin development (May 15-June 10), and III clusters whose ovaries had begun to develop (June 24-July 20) (Figures 7 and 8). These individual morphological stages accounted for 56.6 percent, 27.2 percent, and 14.2 percent, respectively, of the total female flower cluster drop before the drop of matured nuts. Over half of the clusters fell as undeveloped flower clusters (stage I). The blank drop occurring in the last half of August is not evident as Table 5 represents a composite of abscising clusters. In late August blanks and immature nuts fell at the same time.

Cluster drop during stages I and II coincided with a rapid increase in leaf area (Figure 9). Abscission of clusters bearing

Table 7. Number of flowers per 'Barcelona' cluster.

North				South				East				West			
1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
10	10	7	8	10	7	8	8	8	8	6	10	10	6	10	11
10	8	10	6	10	9	6	6	10	10	7	12	13	8	8	8
10	10	7	10	10	6	6	10	8	6	5	10	8	6	7	5
10	9	10	8	10	10	8	7	12	6	6	10	10	10	7	8
14	10	10	8	10	10	10	9	9	8	6	10	12	8	8	8
8	8	9	12	12	8	6	7	8	10	6	10	11	6	10	10
8	10	6	6	8	10	9	8	10	10	6	10	12	6	12	8
8	7	6	8	10	6	8	10	8	10	7	10	11	7	10	8
8	11	10	8	10	6	12	9	10	10	8	6	10	8	10	10
6	10	10	6	7	8	8	8	6	8	8	10	10	10	8	12
10	2	10	8	10	8	10	8	10	8	8	12	8	10	8	8
12	10	6	11	10	8	12	7	8	9	6	8	8	8	7	8
10	15	10	8	6	9	7	8	8	8	6	8	8	6	8	4
8	6	8	6	8	8	7	8	8	8	6	10	12	8	8	8
9	8	10	8	10	8	8	7	6	8	6	8	8	8	8	10
8	8	8	10	10	8	8	8	8	8	10	10	8	8	8	7
8	10	6	10	8	8	10	9	10	8	8	10	10	8	10	8
14	7	6	6	10	8	8	8	8	10	8	10	10	6	7	10
10	10	7	10	8	8	10	5	8	8	8	12	10	8	11	7
10	12	8	8	10	6	10	8	8	9	8	10	10	6	6	6
8	12	8	8	10	8	9	8	8	7	8	8	10	6	8	7
10	8	6	10	8	10	6	4	8	8	8	8	8	5	10	8
8	6	8	8	8	6	8	10	7	9	8	10	10	10	10	12
7	10	8	10	10	6			9	6	8	8	10	10		12
8	8	12	8	10	8				9	6	8	10	10		9
										6	10				8
															10

$$\bar{X} = 8.54$$

$$SD = 1.71$$

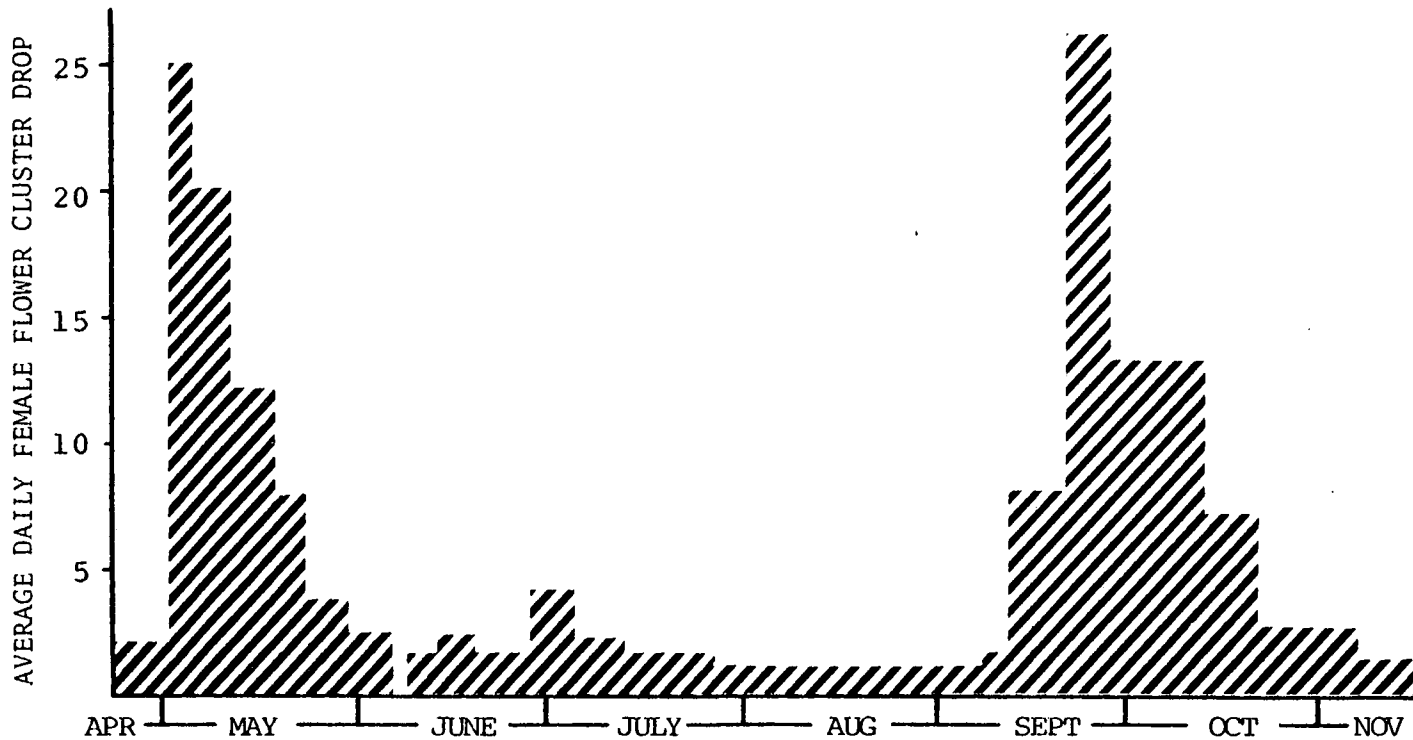


Figure 6. Female flower cluster drop throughout the growing season in 'Barcelona' filbert. Average daily flower cluster and nut cluster drop counts were made throughout the growing season. Total drop was evaluated in periods varying from 4 to 14 days and averaged to obtain daily drop counts.



Figure 7. Example of the flower clusters abscising during three distinct stages of ovary development.

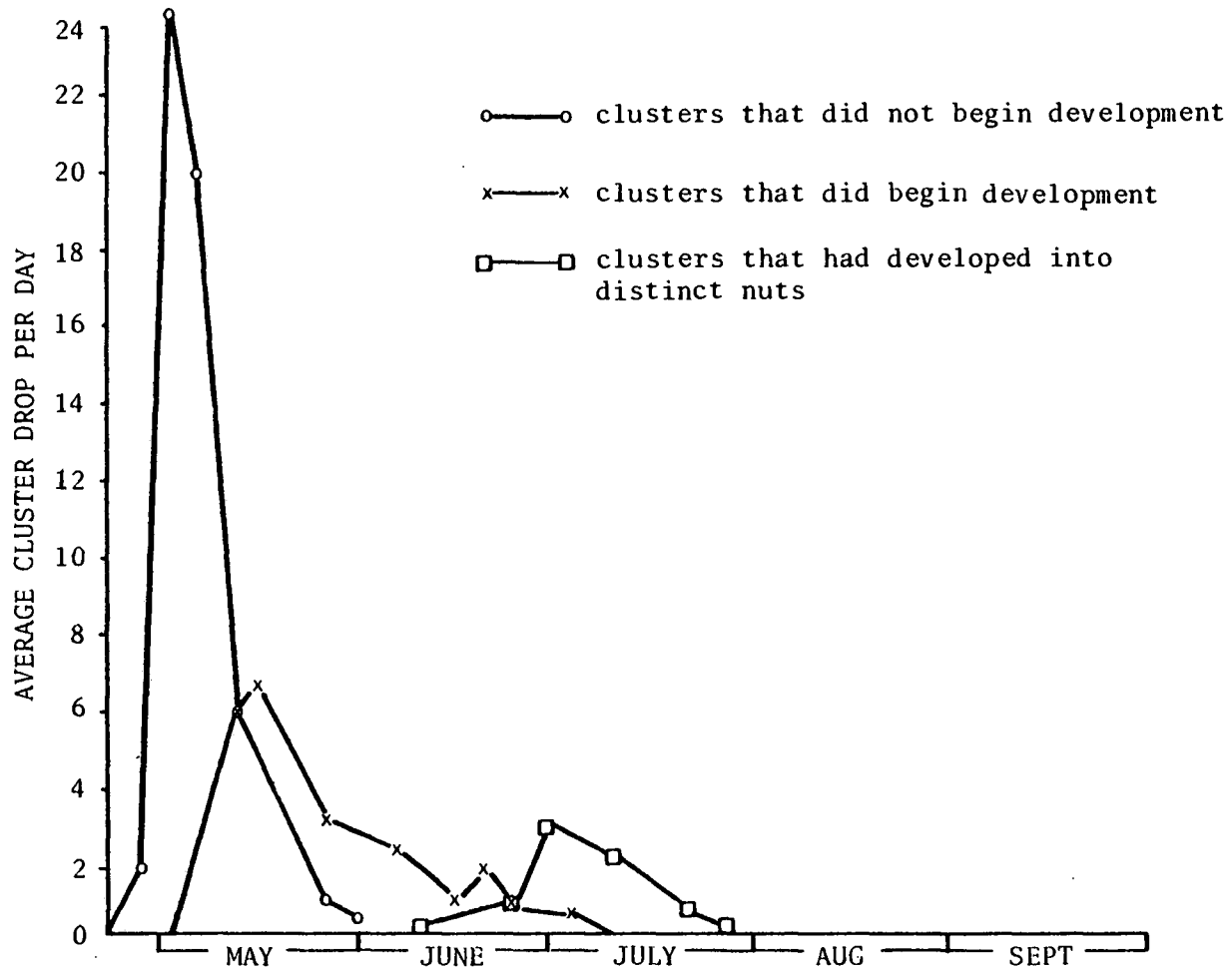


Figure 8. Average daily cluster drop of three morphologically distinct stages of ovary development.

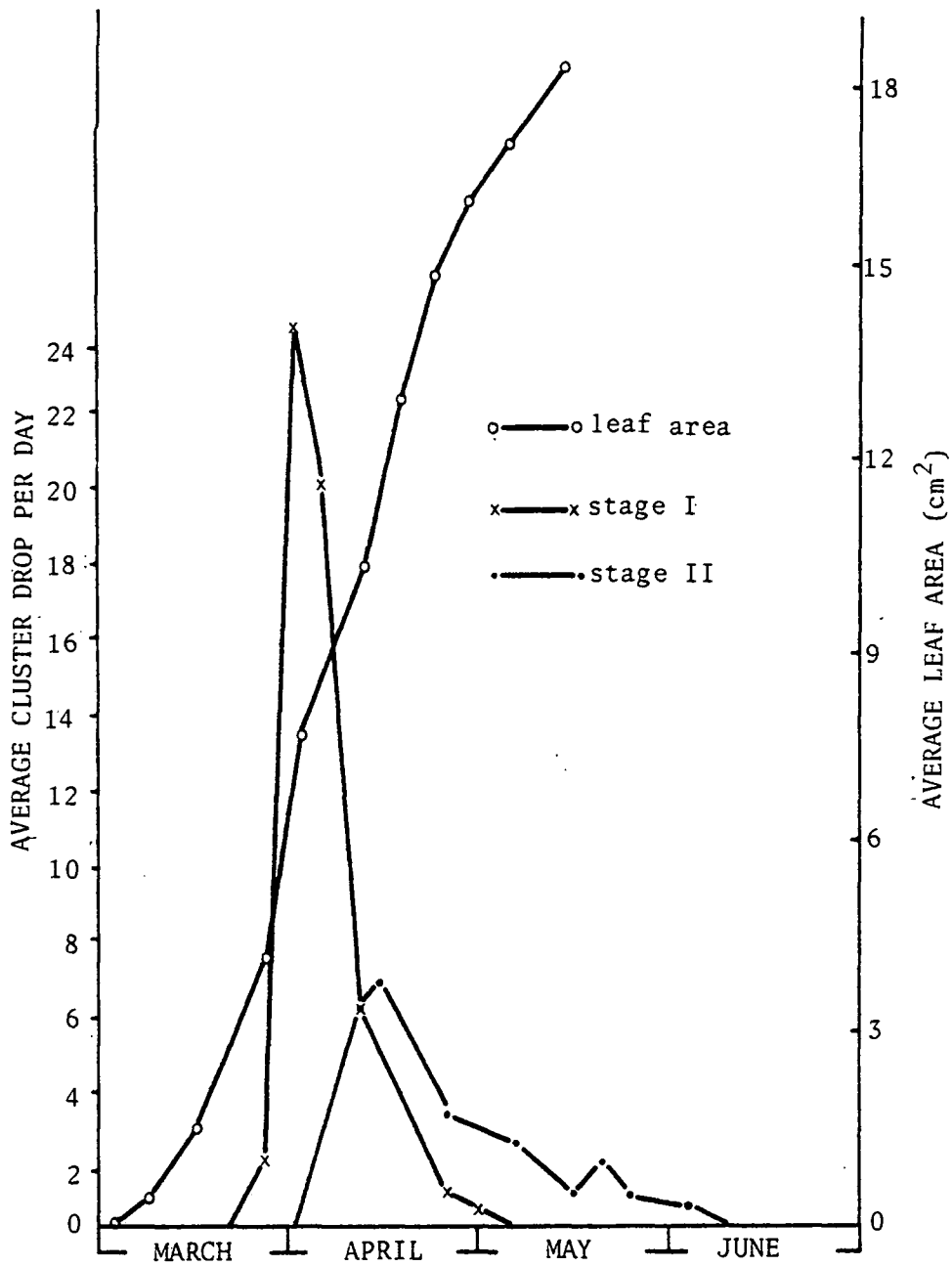


Figure 9. Female flower cluster drop (stages I, II) and expanding leaf area.

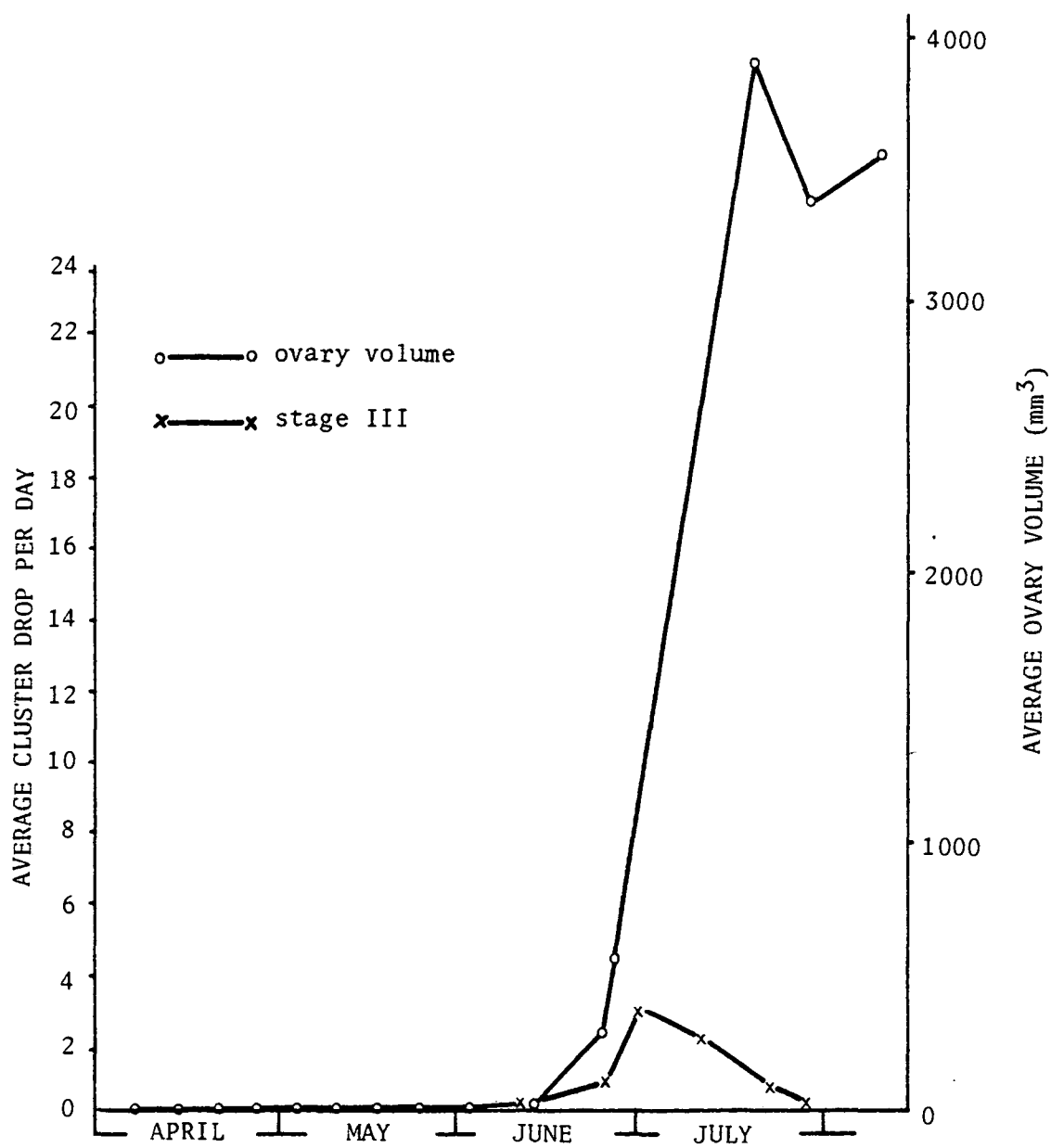


Figure 10. Female flower cluster drop (stage III) and ovary volume.

distinct nuts (III) occurred during this period of maximum ovary growth (Figure 10).

Vegetative terminal bud drop paralleled flower cluster drop during the first half of the growing season (Figure 11). The drop of vegetative buds was minimal during July and August, reflecting a cessation of stem growth.

By collecting every flower cluster that fell and knowing the average number of flowers per cluster (8.56), it was possible to calculate the reproductive potential. The two trees produced only 11.4 percent of their reproductive potential, and of the nuts produced, 8.8 percent were blanks (Table 8). The actual harvest of sound nuts was 10.2 percent of the reproductive potential for the year.

Peduncle Flower Clusters

The distal female flower cluster on 'Barcelona' and 'Ennis' catkin peduncles was largest and in general formed earliest. Subtending flower clusters on the peduncles in many cases did not initiate growth. By the middle of May these small subtending clusters turned yellow and began to fall off. Fifty-six 'Barcelona' peduncles bearing from two to seven flower clusters were tagged (Table 9). An average of 1.1 clusters set per peduncle. A number of peduncles bore no clusters. As the number of clusters per peduncles increased there was an associated increase in the number of clusters set.

Forty-two 'Ennis' peduncles bearing three flower clusters were tagged. An average of 1.4 nut clusters set per peduncle (Table 10).

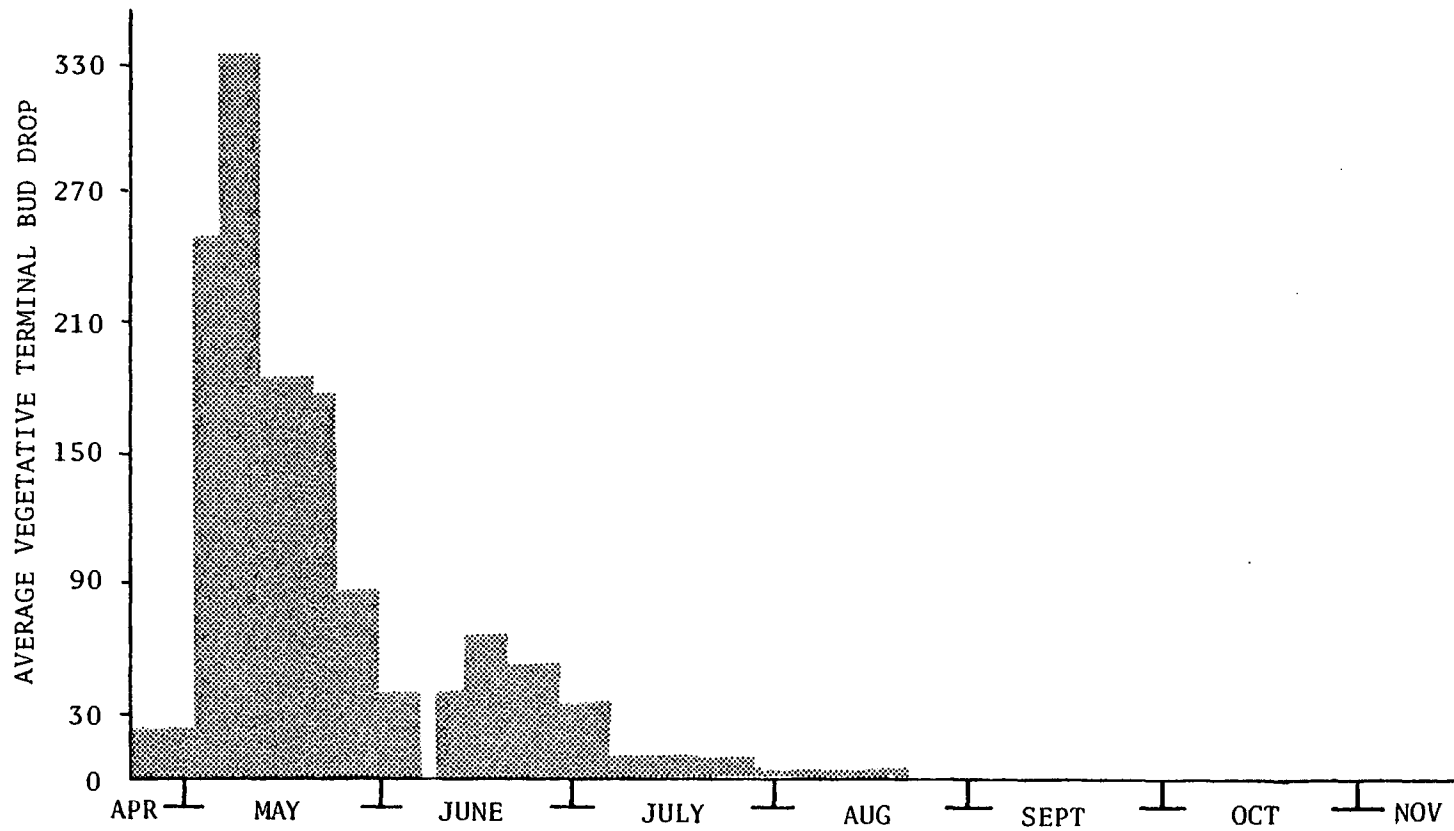


Figure 11. Vegetative terminal bud drop during period of shoot growth in 'Barcelona' filbert. Vegetative bud drop was evaluated in periods varying from 4 to 14 days and averaged to obtain daily drop counts.

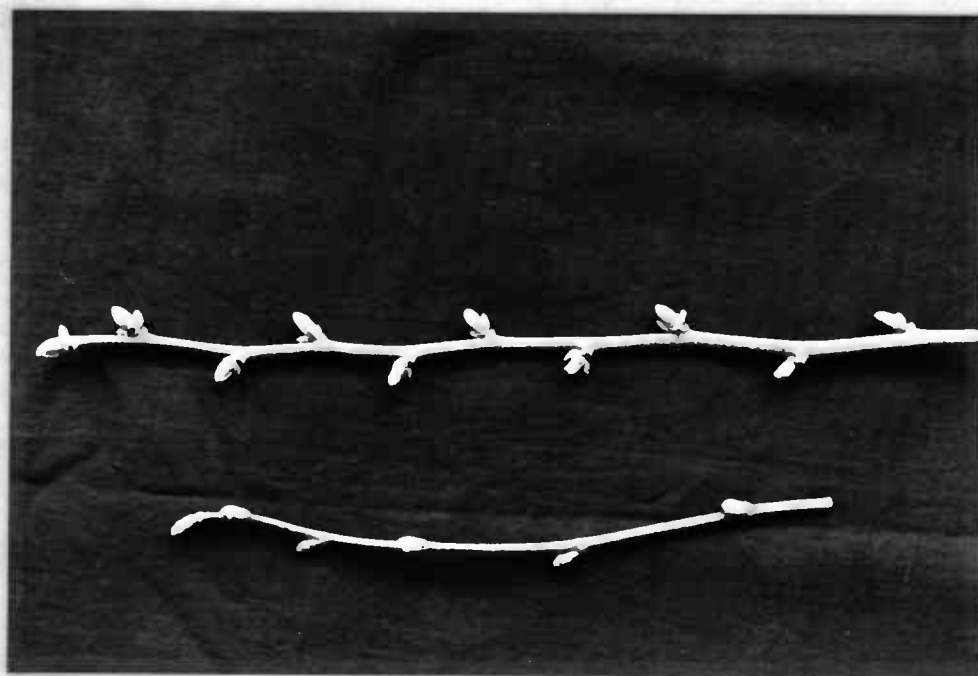


Figure 12. Multiple budding induced by GA_3 50 ppm (top).

Table 8. Filbert cropping potential.

Total number of female clusters ^Y -----	2259
Total number of flowers ^Z -----	19336
Total nut harvest -----	2250
Total kernel count -----	1984
Flower set -----	11.7%
Percent blanks of total nuts produced -----	8.8%
Percent sound kernels resulting from initial flower number -----	10.2%

^YAll flower clusters borne on two 'Barcelona' trees, one eight the other nine years old.

^ZBased on 8.56 flowers per cluster.

Table 9. Flower cluster set on 'Barcelona' catkin peduncles bearing from two to seven flower clusters.^Y

	3-0				
	3-0				
	3-0				
	3-1				
	3-1				
	3-1				
	3-1				
	3-1				
2-0	3-1	4-0	5-0		
2-0	3-1	4-0	5-1		
2-0	3-1	4-1	5-1		
2-0	3-1	4-1	5-1		
2-1	3-1	4-1	5-1		
2-1	3-1	4-2	5-1	6-1	
2-1	3-2	4-2	5-1	6-2	
2-1	3-2	4-2	5-1	6-2	7-1
2-1	3-2	4-2	5-2	6-2	7-2
2-1	3-2	4-2	5-2	6-2	7-2
$\bar{x}=0.6^Z$	$\bar{x}=1.06$	$\bar{x}=1.3$	$\bar{x}=1.3$	$\bar{x}=1.8$	$\bar{x}=1.7$

^YThe first number in a column represents the number of flower clusters present on a given peduncle. The second number indicates the number of flower clusters which set.

^ZAverage number of flower clusters set per peduncle

$$\bar{X} = 1.1$$

$$SD = 0.68$$

Table 10. Flower cluster set on 'Ennis' catkin peduncles bearing three flower clusters.^Z

3-1	3-1	3-1	3-2
3-1	3-1	3-1	3-2
3-1	3-1	3-1	3-2
3-1	3-1	3-1	3-2
3-1	3-1	3-1	3-2
3-1	3-1	3-1	3-2
3-1	3-1	3-2	3-2
3-1	3-1	3-2	3-2
3-1	3-1	3-2	3-2
3-1	3-1	3-2	3-2
		3-2	3-2

$\bar{X}=1.38$

SD=0.49

^ZThe first number in a column represents the number of flower clusters on a given peduncle. The second number indicates the number of flower clusters which set.

On almost every peduncle the terminal bud forced and set nuts. In numerous instances both the terminal and middle cluster set nuts.

Effects of Growth Regulators

Results of a preliminary growth regulator study in 1976 indicated that GA_3 , at a concentration of 250 ppm was excessive. It caused extensive stem elongation, low cluster set, and complete inhibition of male flower initiation; in this study, however, female flower initiation was not affected.

In the 1977 application the rate of GA_3 was reduced to 50 ppm. Gibberellic acid inhibited ovary development and cluster set for each application date, resulting in an average set of only 15 percent of the control (Tables 11, 15, 19). The few nuts produced on GA_3 treated branches were normal (Tables 12, 13, 16, 19, 20, 21). Shoot growth was estimated to be greater with each subsequent GA_3 application. The earliest GA_3 application did not reduce male flower development significantly. However, each subsequent spray reduced catkin formation to a greater extent than the previous one, with the May 29 treated branches having only one-half as many catkins as the control (visual observation).

Branches treated with GA_3 (in 1976 and 1977) produced multiple buds, both vegetative and female, on elongated stems (Figure 12). Usually only the largest bud developed into a lateral branch. The subtending buds abscised by mid-May.

Table 11. Percent set following April 24 growth regulator treatment on 'Barcelona'.

GA ₃ -----50 ppm -----	5.2% ^{Z**}
TIBA -----50 ppm -----	42.1
TIBA -----100 ppm -----	42.7
Ethephon -----500 ppm -----	45.9
Sodium pentaborate ---1#/a -----	46.7
Control -----	40.6

^ZBased on Duncan's multiple range test.

**LSD .01

Table 12. Percent blanks following April 24 growth regulator treatment on 'Barcelona'.

GA ₃ -----50 ppm -----	5.6%
TIBA -----50 ppm -----	9.9
TIBA -----100 ppm -----	12.1
Ethephon -----500 ppm -----	11.1
Sodium pentaborate ---1#/a -----	6.8
Control -----	10.3

Table 13. Average kernel weight following April 24 growth regulator treatment on 'Barcelona'.

GA ₃	-----50 ppm	-----1.0g
TIBA	-----50 ppm	-----1.1
TIBA	-----100 ppm	-----1.2
Ethephon	-----500 ppm	-----1.1
Sodium pentaborate	----1#/a	-----1.1
Control	-----	-----1.2

Table 14. Averaged nuts per cluster following April 24 growth treatment on 'Barcelona'.

GA ₃	-----50 ppm	-----2.3
TIBA	-----50 ppm	-----1.9
TIBA	-----100 ppm	-----2.1
Ethephon	-----500 ppm	-----2.2
Sodium pentaborate	----1#/a	-----2.1
Control	-----	-----2.2

Table 15. Percent set following May 15 growth regulator treatment on 'Barcelona'.

Daminozide	-----2000 ppm	-----39.4%
GA ₃	-----50 ppm	-----9.5**Z
TIBA	-----50 ppm	-----41.7
TIBA	-----100 ppm	-----44.8
Ethephon	-----500 ppm	-----44.1
Sodium pentaborate	-----1#/a	-----42.3
Control	-----	-----36.6

Z Based on Duncan's multiple range test.

LSD .01**

Table 16. Percent blanks following May 15 growth regulator treatment on 'Barcelona'.

Daminozide	-----2000 ppm	-----10.6%
GA ₃	-----50 ppm	-----7.7
TIBA	-----50 ppm	-----10.9
TIBA	-----100 ppm	-----10.0
Ethephon	-----500 ppm	-----9.5
Sodium pentaborate	-----1#/a	-----9.2
Control	-----	-----9.1

Table 17. Average kernel weight following May 15 growth regulator treatment on 'Barcelona'.

Daminozide	-----2000 ppm	-----1.1g
GA ₃	-----50 ppm	-----1.2
TIBA	-----50 ppm	-----1.1
TIBA	-----100 ppm	-----1.0
Ethephon	-----500 ppm	-----1.0
Sodium pentaborate	-----1#/a	-----1.2
Control	-----	-----1.2

Table 18. Average nuts per cluster following May 15 growth regulator treatment on 'Barcelona'.

Daminozide	-----2000 ppm	-----2.5
GA ₃	-----50 ppm	-----1.9
TIBA	-----50 ppm	-----2.0
TIBA	-----100 ppm	-----2.0
Ethephon	-----500 ppm	-----2.1
Sodium pentaborate	-----1#/a	-----2.2
Control	-----	-----2.1

Table 19. Percent set following May 29 growth regulator treatments on 'Barcelona'.

Daminozide	-----2000 ppm	-----45.2%
GA ₃	-----50 ppm	-----8.9** ^Z
TIBA	-----50 ppm	-----43.6
Ethephon	-----500 ppm	-----52.6*
Sodium pentaborate	-----1#/a	-----42.5
Control	-----	-----44.1

^ZBased on Duncan's multiple range test.

**LSD .01

*.05

Table 20. Percent blanks following May 29 growth regulator treatments on 'Barcelona'.

Daminozide	-----2000 ppm	-----11.4
GA ₃	-----50 ppm	-----18.2
TIBA	-----50 ppm	-----10.4
Ethephon	-----500 ppm	-----8.3
Sodium pentaborate	-----1#/a	-----10.3
Control	-----	-----11.2

It was evident that the production of multiple buds was a direct result of the GA_3 application. The April 24 treatment produced multiple buds in the basal third of the shoot. The May 15 treatment resulted in mid-shoot multiple buds while the May 30 treatment produced multiple buds in the top third of the shoot.

Growth of lower lateral stems was severely inhibited and developing buds on these laterals were killed. Most growth took place in the upper half of the GA_3 treated branches, leaving the lower half with twigs and dead buds. This effect was most pronounced with the later treatments.

Of the three GA_3 sprays the April 24 treatment had the least influence on vegetative growth but promoted initiation of a significantly greater number of female flowers than the control branches (Table 24). The two later GA_3 sprays, May 15 and 30, affected vegetative growth to a greater extent than the early spray. These treatments produced a large but not significant number of flowers per limb cross-sectional area. The high density of flowers became visually evident for as the nuts matured the branches were bowed from the weight of the heavy nut crop. The other treatments did not influence bloom density.

The June 20 TIBA 100 ppm treatment caused death of buds and resulted in low bloom density (Table 24). The June 20 application of TIBA 100 ppm appeared to arrest ovary growth; nuts and kernels were significantly smaller than those of the controls (Table 23). Kernel growth was not impaired and these smaller nuts filled normally. Percent cluster set was considerably lower due to severely underdeveloped nut clusters which were not counted. The upper half of the TIBA treated branches were most severely affected as evidenced by defoliation and

Table 21. Average kernel weight following May 29 growth regulator treatments on 'Barcelona'.

Daminozide	-----2000 ppm	-----1.2g
GA ₃	-----50 ppm	-----1.1
TIBA	-----50 ppm	-----1.1
Ethephon	-----500 ppm	-----1.1
Sodium pentaborate	-----1#/a	-----1.1
Control	-----	-----1.1

Table 22. Average nuts per cluster following May 26 growth regulator treatments on 'Barcelona'.

Daminozide	-----2000 ppm	-----2.6* ^Y
GA ₃	-----50 ppm	-----1.6* ^Z
TIBA	-----50 ppm	-----2.2
Ethephon	-----500 ppm	-----2.3
Sodium pentaborate	-----1#/a	-----2.1
Control	-----	-----2.2

^YBased on Duncan's multiple range test.

^ZSample size excessively small for accurate determination

*LSD .05

Table 23. Effects of June 23 application of TIBA 100 ppm.

Percent Set	
TIBA -----	24.0%* ^Z
Control -----	44.1
Percent Blanks	
TIBA -----	15.3%
Control -----	11.2
Average Kernel Weight	
TIBA	0.7g**
Control	1.1
Average Nuts Per Cluster	
TIBA	2.0
Control	2.2

^ZBased on Duncan's multiple range test.

*LSD .05

** .01

Table 24. Bloom density following previous spring growth regulator treatment.^Y

Control	4/24	20.4
Sodium pentaborate	4/24	20.5
TIBA 50 ppm	4/24	27.8
TIBA 100 ppm	4/24	28.2
GA ₃	4/24	56.6* ^Z
Ethephon	4/24	21.9
Control	5/15	20.6
Sodium Pentaborate	5/15	19.7
TIBA 100 ppm	5/15	26.3
TIBA 50 ppm	5/15	30.6
GA ₃	5/15	33.4
Ethephon	5/15	22.1
Control	5/30	22.7
Sodium Pentaborate	5/30	25.0
TIBA 50 ppm	5/30	21.4
GA ₃	5/30	33.6
Ethephon	5/30	21.6
TIBA 100 ppm	6/23	5.0*

^YFlowers per cm² branch cross-sectional area

^ZBased on Duncan's multiple range test

*LSD .05

Table 25. Fruit set the year following spring growth regulator treatments.

Control	4/24	29.9%
Sodium pentaborate	4/24	30.9%
TIBA 100 ppm	4/24	27.6%
TIBA 50 ppm	4/24	25.3%
GA ₃	4/24	30.3%
Ethephon	4/24	38.4%
Daminozide	4/24	24.9%
Control	5/15	26.7%
TIBA 100 ppm	5/15	24.8%
TIBA 50 ppm	5/15	32.3%
GA ₃	5/15	29.0%
Ethephon	5/15	30.8%
Daminozide	5/15	41.3%
Control	5/30	33.2%
Sodium pentaborate	5/30	31.2%
TIBA 50 ppm	5/30	30.7%
GA ₃	5/30	31.8%
Ethephon	5/30	38.5%
Deminozide	5/30	35.9%
TIBA 100 ppm	6/23	30.5%

death of buds. Sprays of either TIBA 50 ppm or sodium pentaborate did not significantly alter percent cluster set, percent blanks, kernel weight, or number of nuts per cluster as compared to controls (Tables 11-22). Sodium pentaborate, TIBA at 50 and 100 ppm, and daminozide tended to produce smaller nuts. There was an increase in nuts per cluster with daminozide (Table 22). The low number of nut clusters produced on GA₃ treated branches eliminated the possibility of making valid statements regarding GA₃ effect on nuts per cluster (Table 22).

Ethephon treatments did not alter nut size, kernel weight, nuts per cluster, or percent blanks (Tables 11, 22). However, it increased cluster set. The May 29 spray caused a significant increase of 18 percent (Tables 11, 15, 19). It appears that the May 29 treatment of ethephon improved the set of female flower clusters that had begun to develop into distinct nuts. Based on the treatment date (May 29) it may be assumed that ethephon treated branches set 72 percent of the stage III clusters which normally would have abscised in June and July. There were no detrimental effects of ethephon treatments on parameters influencing yield. The effect heightens the potential of ethephon to increase yield by promoting cluster set.

No treatments influenced fruit set during the year following application (Table 24). Nor were any trends evident.

IV. DISCUSSION

Fruit set was improved as a result of the plant growth regulators applied in this study. Complimentary studies, conducted as a part of the growth regulator work, have contributed to the general knowledge of filbert floral biology.

Roughly 50 percent of filbert flower clusters mature and develop into nuts. The lost flower clusters are principally inhibited from developing beyond the flower bud cluster stage (Stage I). Two other distinct flower drops occurred (Stage II, Stage III). This would suggest that the basis for floral abscission might be different in each case. Abscission of flower clusters that had begun development (Stage II) coincided with a rapid increase in leaf area. Abscising clusters that had begun to form distinct ovaries (Stage III) fell during the period of initial rapid ovary growth. The possibility exists that rapid leaf area increase and ovarian growth are related respectively, to stage II and stage III flower cluster abscission. The cause of stage III flower cluster abscission might be arrived at by examining the physical and hormonal relationship between abscising flower cluster and successfully maturing ones.

The filbert does not appear to exhibit marked apical dominance. Single vegetative or reproductive buds located at separate nodes on the same stem do not show apical dominance. However, when more than one bud cluster is located at a node or in extremely close proximity, as on a catkin peduncle, apical dominance becomes evident.

Gibberellic acid treatment induced multiple budding at nodes. In this case, the terminal or central bud of a given node was largest and forced earliest; the remainder of the buds did not develop. A primary source-sink relationship and low level production of hormones would have inhibited development of bud clusters located immediately below the terminal bud. A similar interaction may take place when bud clusters occur in close proximity on catkin peduncles.

Female flowers borne on catkin peduncles set an average of slightly more than one nut cluster per node in both 'Ennis' and 'Barcelona' cultivars. In contrast, when a single flower cluster is located on a node, a much lower number of nut clusters set per node.

There is a cultivar difference in the number of catkin peduncles bearing female flower clusters. By examining the tendency towards bearing female flower clusters on peduncles, together with the percent set of those flowers, it may be possible to select the more productive seedlings in a filbert breeding program.

Both male and female flowers are sensitive to GA_3 applications at 50 ppm. All three treatment dates were equally effective at inhibiting ovary development and causing floral abscission. Male flowers appear less sensitive than female flowers to GA_3 treatment. It may be possible that a concentration of GA_3 could be applied which would inhibit development of off-type pollinizer nuts while at the same time not significantly affecting catkin production or pollen quality. The reduction in yield may be economically feasible if a premium were paid for uniform nut lots.

All three GA₃ treatments induced a substantial increase in the number of female flower clusters. In several other crops, GA₃ promotes maleness while inhibiting femaleness. In this study, the reverse was true. Whether the observed increase of female flower clusters resulted from a greater number of nodes or from a greater proportion of nodes bearing flower clusters is not known.

Since female flower premordia develop in August, growth regulator sprays designed to influence this phenomenon should be applied in late July or early August. Triiodobenzoic acid would be a candidate as it has promoted flower initiation in other crops. The deleterious effects resulting from the June 23 application of TIBA 100 ppm probably resulted from a mixing error rather than from a plant response to the concentration. If indeed it were a plant response then much lower rates would be necessary in future studies attempting to influence floral initiation with this plant growth regulator.

Multiple budding induced by GA₃ 50 ppm, initially appeared to be a method for increasing lateral branching and increase leaf surface area. Unfortunately, as a result of a possible localized dominance effect, only the central or terminal bud cluster forced, thereby eliminating any potential gain in leaf surface area.

Foliar treatments with TIBA or boron did not appreciably affect parameters influencing yield. Nuts per cluster was increased with daminozide which could result in increased yields. However the potential yield increase may have been negated by a reduction in nut size. The number of jumbo grade nuts was reduced by all treatments except ethephon.

Ethephon showed the most promise of any of the plant growth regulators for increased set. Relative to the control, ethephon increased nut set at all three treatment dates. No other parameters of yield were negatively affected. Further studies involving spray timing and concentration might improve ethephon's setting potential.

To solve the biennial bearing problem via plant growth regulators, it would be necessary to promote floral initiation in the "on" crop year and increase cluster set in the "off" year. The growth regulator sprays in this study were assumed to be applied too early to directly influence floral initiation. Additional research into regulating flower initiation and cluster set is vital to controlling the biennial bearing nature of the filbert.

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