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Inflorescence and Flower Development of the 'Hass' Avocado (*Persea americana* Mill.) during "On" and "Off" Crop Years

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ABSTRACT. Inflorescence and flower development of the 'Hass' avocado (*Persea americana* Mill.) were investigated at the macro- and microscopic level with three objectives: 1) to determine the time of transition from vegetative to reproductive growth; 2) to develop a visual scale correlating external inflorescence and flower development with the time and pattern of organogenesis; and 3) to quantify the effect of high ("on") and low ("off") yields on the flowering process. Apical buds (or expanding inflorescences) borne on summer shoots were collected weekly from July to August during an "on" and "off" crop year. Collected samples were externally described and microscopically analyzed. The transition from vegetative to reproductive condition probably occurred from the end of July through August (end of shoot expansion). During this transition the primary axis meristem changed shape from convex to flat to convex. These events were followed by the initiation of additional bracts and their associated secondary axis inflorescence meristems. A period of dormancy was not a prerequisite for inflorescence development. Continued production of secondary axis inflorescence meristems was observed from August to October, followed by anthesis seven months later. In all, eleven visual stages of bud development were distinguished and correlated with organogenesis to create a scale that can be used to predict specific stages of inflorescence and flower development. Inflorescence development was correlated with minimum temperature $\leq$15 ^{O}C, whereas yield had little effect on the timing of developmental events of individual inflorescence buds. However, the high

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yield of the "on" year reduced inflorescence number and increased the number of vegetative shoots. No determinate inflorescences were produced during the "on" year. For the "off" year, 3 % and 42 % of shoots produced determinate and indeterminate inflorescences, respectively.

The avocado produces two types of inflorescences: determinate, in which the primary axis develops into a terminal flower (Schroeder, 1944) and indeterminate, in which a bud forms on the primary axis that continues the growth of the shoot (Fig. 1 A and B) (Reece, 1942). With few exceptions, the indeterminate type of inflorescence is more abundantly produced (Schroeder, 1944). Both types of inflorescences consist of secondary axes (lateral panicles), which develop acropetally producing tertiary axes (cymes) which bear a terminal flower and two lateral flowers (Reece, 1942). The flower when fully open is ≈1.0 cm in width and 6 to 7 mm in length (Davenport, 1986). It is perfect, hypogynous, regular, and trimerous (Schroeder, 1952). The perianth is formed by three petals alternating with three sepals (Reece, 1939; Scholefield, 1982). However, Blanke and Lovatt (1993) proposed the use of the term tepal as sepals and petals were indistinguishable on the basis of surface morphology. Inside the perianth are three whorls of stamens and one of starninodes (Bergh, 1985). Aligned with each petal (or tepal) is one stamen and one nectar-secreting, yellow staminode. Similarly, two stamens are aligned with each sepal (ortepal), the interior one having a pair of nectaries at its base. Therefore, each flower normally has a total of nine stamens (Bergh, 1985). The simple pistil is located in the center. It has a superior ovary with one anatropous ovule (Schroeder, 1952)

Davenport (1982) proposed a visual scale to evaluate avocado inflorescence development but this scale was not correlated with anatomical changes. Existing anatomical studies of avocado inflorescence development have not documented the sequence in which vegetative apices are converted to reproductive apices. The earliest event reported is inflorescence initiation and it is reported to occur over a period of two to three months (Alexander, 1975; Davenport, 1982; Inohue and Takahashi, 1989; Reece, 1942; Schroeder 1951). Subsequent flower development to anthesis requires an additional two to three months (Reece, 1942; Schroeder, 1951), resulting in a high degree of variation in the time of anthesis.

Growth of avocado branches takes place in distinctive flushes, occurring one, two or three times during the year (i.e. spring, summer or fall flushes). Not all the branches contribute to each flush resulting in a composite canopy with leaves and shoots of various ages (Davenport, 1982; Scholefield et al., 1985; Venning and Lincoln, 1958). Since vegetative shoots of different chronological and developmental ages are present, there is considerable variation in the proportion of vegetative apices that continue the growth of the shoot or develop into inflorescences. This complexity makes it difficult to know how far inflorescence development has proceeded for the majority of the buds at a given time and makes it difficult to manipulate the flowering process with any degree

of reliability. Lord and Eckard (1985) proposed that careful documentation of the time and pattern of floral organogenesis is a necessary prerequisite to any attempts to manipulate flowering in woody perennials. Thus, in preparation for future experiments to regulate the time and intensity of avocado flowering, a study was undertaken in a commercial 'Hass' avocado orchard with the following objectives: 1) to determine the time of transition from vegetative to reproductive growth; 2) to correlate external (macroscopic) inflorescence and flower development with the time and pattern of organogenesis (microscopic), in order to develop a visual scale to evaluate the progress (stage) of inflorescence ontogeny from inflorescence initiation to anthesis; and 3) to quantify the effect of high ("on") and low ("off") yields and daily minimum temperature on inflorescence development.

Materials and Methods

PLANT MATERIAL. Twenty 10-year-old 'Hass' avocado trees on a Mexican race rootstock in a 10-acre commercial orchard in Corona, Calif. (34' N latitude), were selected for uniform yield, tree health and vigor in July 1994 (after the June fruit drop period). These trees were used during the 2 consecutive years of the study.

ANATOMICAL STUDY. Ten of the twenty trees were used for both years of the anatomical study. Two apical buds from summer shoots were collected weekly from each tree to obtain buds through the end of shoot elongation (July) and biweekly from August through April of each year. For each sampling date, buds and subsequent inflorescences were visually sorted based on shape and degree of expansion. For each category, 20 buds and/or inflorescences were externally described and microscopically analyzed. Anatomical sectioning was practiced to 20 buds from each category and the number of structures observed by longitudinal serial sections up to the central axis was counted. Thus, for each sampling date the proportion of buds at each developmental stage (both macro- and microscopic) was quantified. Buds were fixed in FAA (5 formalin : 5 acetic acid : 90 ethanol solution, by volume), dehydrated via sequential transfer through a series of aqueous ethanol solutions (70%, 85%, and 95% ethanol), infiltrated and embedded in glycol methacrylate (LKB 2218-500 Historesin). Infiltration was done in a graded 25 Historesin : 75 ethanol (95%) series (by volume) (two changes in 24 h), 50: 50 and 75 : 25 (24 h each), and 100 : 0 (one change at 24 h and then left for 5 days). Embedding in Historesin was done according to the instructions. Serial sections were made on a H/I Bright 5030 rotary microtome at 6 µm, mounted in water on glass slides, heated until dry, stained by flooding in 0.05% toluidine blue (O'Brien and McCully, 1981), and photographed with Kodak Technical Pan 2415 film on a compound microscope. For description of the anatomical sections the terms primary axis meristem, secondary axis meristem, and tertiary axis meristem were used to designate the shoot apical meristems of the corresponding axes (Fig. 1).

FLOWERING INTENSITY. Five branches 1 m in length and 6 to 10 cm in diameter were selected evenly around each of the 10 remaining trees not used in the anatomical study. At the end of the flowering period, the number of inflorescences (including determinate and indeterminate), vegetative shoots, and inactive buds on each branch were counted.

In addition, flowering intensity was estimated on all 20 tree replications using a visual rating of the amount of canopy covered by inflorescences: 1 = no inflorescences; 2 = ≤25%; 3 = ≤50%; 4 = ≤75%; 5 = 76% to 100%.

YIELD DATA. Yield per tree was obtained for all 20 tree replications in July 1995 and May 1996, which were "on" and "off 'crop years, respectively.

STATISTICAL ANALYSIS. A randomized complete block design with 20 single-tree replications was used to obtain yield and flowering intensity at the tree level. For the anatomical study and the quantification of flowering intensity per branch, 10 single-tree replications were used. Before analysis of variance, data expressed as percentages were transformed by arcsin of the square root of the observation (Steel and Torrie, 1980). Depending upon normality, a t test or a Mann-Whitney rank sum test was used to compare two independent means at P = 0.05, therefore, significant differences are presented at this probability.

Results

At the macroscopic level, 11 distinct sequential stages of bud, inflorescence and flower development were identified (Fig. 2) and described macro- and microscopically in Table 1.

INFLORESCENCE INITIATION. Close to the end of the expansion of the summer vegetative flush (23 July), apical buds were at Stage 1, having convex primary axis meristems and one or two young secondary axis inflorescence meristems in the axils of bracts (Fig. 3A). Also present in the axils of the bud scales, as illustrated in Fig. 1A, were five to seven axillary shoot meristems, each with a convex apex covered by bracts (data not shown). These meristerns remained dormant for almost two months. After that, they produced more bracts and returned to dormancy.

Stage 2 buds could be distinguished on mature summer shoots by the end of July. The buds were pointed and closed (Fig. 2-2). At this stage, a flat (low convex) shoot apical meristem with separated bracts was evident plus one to three secondary axis meristems (Fig. 3B). By 30 Aug. buds reached Stage 3 and the bud scales started to abscise (Fig. 2-3). The primary axis meristem. was convex and four secondary axis meristems were present in the axils of inflorescence bracts (Fig. 3C). A decreased rate of secondary axis meristern production was observed in Stage 3. By 30 Oct. first buds at Stage 4 were observed and were characterized by the separation of bud scales (often only scale bases), revealing the expanded inflorescence bracts (Fig. 2-4). At this stage the primary axis meristem had become flattened and an average of 10 secondary axis inflorescence meristems were present, with the basal six having produced bracts (Fig. 4A). At Stage 5, there was a clear increase in bud dimensions and bud scales were more separated (Fig. 2-5). Elongation of secondary axis inflorescence meristems had occurred and tertiary axis meristems were apparent at this stage (Fig. 4B).

INFLORESCENCE AND FLOWER DEVELOPMENT. The beginning of flower organ development, initiation of the perianth, was observed for terminal flowers of secondary and tertiary axes at Stage 5 (Figs. 2-5 and 4B). Buds at Stage 6 had a rounded shape and inflorescence bracts, enclosing secondary axes of the inflorescence, were evident (Fig. 2-6). The secondary axes of the inflorescence were completely formed, with each bearing several cymes of flowers, equivalent to the tertiary axis (Fig. 4C). At this stage, terminal flowers (of both secondary and tertiary axes) had complete perianth and sporogenous tissue was evident in anthers. The gynoecium was at the early stage of locule formation (Fig. 4D). At Stage 7, the inflorescence had started to emerge from the bud (Fig. 2-7), the flowers were more developed (Fig. 5A); i.e., the ovule was initiated (Fig. 5B) and pollen mother cells and a tapetum were visible in the anthers (Fig. 5C). Stage 8, also known as cauliflower stage (Lovatt, 1994), was first observed by 28 Feb. and corresponded to an obvious elongation of the secondary axes of the inflorescence (Fig. 2-8). Meiosis had occurred in the anther locules and microspores were evident. Integuments were forming on the ovule (Fig. 5D). Stage 9 was designated as the point when elongation of the tertiary axes (cymes) was observed. Microspores with well developed exine layers (Fig. 6A) and ovules in the anatropous position with megaspore present were characteristic of Stage 9 (Fig. 6B). At this stage, the vegetative bud emerging above the inflorescence (containing up to seven leaf primordia) was visible (Fig. 2-9), but bud break did not occur until Stage 11I (anthesis). At Stage 10, flowers were fully differentiated but unopened (Fig. 2-10). Microspore mitosis had given rise to the two-celled pollen grains; sexual organs were mature and ready for anthesis (Fig. 6C). Stage 11 corresponded to the flower at anthesis where the stigma is receptive and pollen may be shed Fig. 2-11). At this stage, bud break at the apex of indeterminate inflorescences initiated the spring vegetative flush.

Development of the secondary axes of the inflorescence within the bud proceeded in an acropetal fashion, so a developmental range was observed in a single inflorescence with the most advanced secondary axes (i.e., at perianth differentiation) at the base and the youngest (i.e., at initial elongation of the meristem) just below the primary axis meristem. However, on an individual secondary axis, development was basipetal with the terminal flowers (lacking subtending bracts) differentiating and maturing first as is typical in a cyme.

In our study, avocado flower morphology was similar to what is reported in the literature (Bergh, 1985; Blanke and Lovatt, 1993; Davenport, 1986; Reece, 1939; Scholefield, 1982; Schroeder, 1952).

Macroscopic grading was very reliable for predicting the microscopic stage of inflorescence development. The degree of variation at each sampling date for a given year is illustrated in Fig. 7. Variation in the collection of Stages 1 to 3 was nil. From 30 Oct. to 30 Mar. the variation was never greater than one developmental stage.

EFFECT OF CROP LOAD ON INFLORIESCENCE DEVELOPMENT. Average yield (n = 20 trees) was 66.1 ± 5.6 kg/tree and 18.3 ± 4.9 kg/tree for the "on" and "off ' crop years, respectively. The average length of time from the initiation of an inflorescence

bud (August) through end of Stage 4 was approximately the same during the "on" and "off" crop years (Fig. 7). After this period, an increased rate of inflorescence development was observed for trees in the "off" crop year which reached the cauliflower stage earlier. However, anthesis (Stage 11) was reached by ≈ 15 Apr. in both years.

To determine if the faster speed of development from Stage 6 to 10 during the "off" crop year was related to crop load or to temperature, inflorescence development was related to maximum and minimum air temperatures. Inflorescence development correlated well with minimum temperature $\leq$15 ^{o}C, which was first recorded on 4 and 1 July of the "on" and "off" crop year, respectively. Beginning 1 Aug., 81 and 77 d with temperature $\leq$15 ^{o}C, were accumulated by Stage 4 (30 Nov.) for the "on" and "off" crop years, respectively (Fig. 7). A total of 198 and 196 d $\leq$15 ^{o}C accumulated in the "on" and "off" crop year, respectively by Stage 10, and 213 and 210 d to Stage 11 (anthesis), respectively (Fig. 7). The delay in inflorescence development observed by 15 Mar. of the "on" crop year was probably the only difference attributable to crop load, because there was no significant difference in the number of days $\leq$15 ^{o}C between the two cropping years from 1 Aug. to 15 Mar. (Fig. 7).

EFFECT OF CROP LOAD ON FLOWERING INTENSITY. The high yield during the "on" crop year (average of 66.1 kg/tree) significantly reduced flowering intensity for the next year's crop. This reduction was associated with a decreased production of inflorescences (13.3% of the total shoots/branch) which was accompanied by a higher production of vegetative shoots (71.9% of the total shoots/branch) (Table 2). The opposite was found for the "off' crop year (average of 18.3 kg/tree), where inflorescences were produced on 45.7% of the total shoots and vegetative shoots on only 38.3% (Table 2). No determinate inflorescences were produced during the "on" crop year. For the "off" crop year, 3.5% and 42.2% of total shoots produced determinate and indeterminate inflorescences, respectively. The proportion of inactive buds was not affected by yield (Table 2). Similar to the results obtained for branches, a reduction in flowering was observed at the tree level during the "on" crop year, 20% of the trees produced less than 50 inflorescences or had no flowering at all. Tree flowering intensity (percent canopy covered with inflorescences) was slightly higher than 25% per tree (Table 3). For the "off" crop year, all trees had a flowering intensity >75%.

Discussion

TRANSITION FROM VEGETATIVE TO REPRODUCTIVE GROWTH. Venning and Lincoln (1958) documented a predictable pattern of vegetative growth in avocado illustrative of a genetically predetermined transition from the formation of bracts to leaves of increasing size. After a specific number of nodes, leaf size decreased and leaves became bract-like, presumably leading to the initiation of bracts and their associated secondary axis meristems for reproductive growth. So, the primary axis meristern plays two roles in avocado; one is to produce inflorescence bracts and the other is to produce leaf primordia. We found that the presence of a convex primary axis meristem indicated an active apex, producing one or the other. Secondary axis inflorescence meristems form in the axils of bracts just below the primary axis meri stem

(Stage 1). These axillary meristems typically formed inflorescences. But, as reported for other species (Bernier et al., 1981), we find flowering in avocado is not obligatory at this point, but depends on environmental conditions. After initiation of these secondary axis meristems the primary axis meristern becomes flattened and its activity decreases (Stage 2), but at no time was dormancy detected. We observed in a sample of 20 buds per developmental stage that the primary axis meristem changed shape from convex to flat to convex during the period from the end of July through August and that after these events, the primary axis meristem initiated new bracts in the axils of which additional secondary axis inflorescence meristems were formed. We propose this to be the critical stage in reproductive development and refer to it as the transition phase. A flattened meristem is associated with the transition to the reproductive condition in many species, of which the best studied are those of the Compositae (Bernier et al., 198 1). If environmental conditions promoting vegetative growth had prevailed, the growth of the apical two secondary axis inflorescence meristems formed prior to the transition phase would have been suppressed by the production of new leaf primordia on the primary axis meristem. However, under conditions optimal for flowering, these meristems develo ed into the basal lateral cymes of the inflorescence and the other es were produced by the new activity of the primary axis menstem. This is the first time that this transition stage has been documented in the primary axis meristem of avocado. It is our working hypothesis that the flattening of the primary axis meristem during this period is associated with the potential for a full transition from vegetative to reproductive development and that the subsequent formation of additional secondary axis inflorescence meristems, which was evident by 30 Aug., is consistent with commitment of the primary axis meristem to flowering. Our results suggest that commitment to flowering may occur earlier an previously reported for avocado (Thorp et al., 1994). The environmental conditions contributing to this transition remain unknown. It may even be the case that the primary axis meristem oscillates between the vegetative and reproductive state but only flowering promoting conditions allow flowering to be fully expressed. In this study we found a good correlation between inflorescence development and night temperature $\leq$15 ^{o}C, but whether such conditions play a role in the transition, commitment or initiation of reproductive growth is not known. It is of interest, however, that days with temperature $\leq$15 ^{o}C were recorded in early July for the 2 years of study. We do not consider this temperature inductive, but rather promotive of flowering expression. Buttrose and Alexander (1978) obtained maximum flowering with 20 ^{o}C, 15-h day and 15 ^{o}C, 9-h night, but also reported that exposure of buds to 30 ^{o}C interrupted flowering. A negative effect of maximum temperatures on inflorescence initiation was not found in this study. Furthermore, the population of buds collected on any sampling date, never contained buds that had reverted to vegetative growth despite the occurrence of high temperatures (27 to 42 ^{o}C) during the inflorescence initiation period (August to October), providing strong evidence of commitment to flowering early in this period. With further research, it seems likely that temperature based models can be developed to predict inflorescence development in avocado growing regions similar in climate to southem California.

CORRELATION BETWEEN MACROSCOPIC AND MICROSCOPIC INFLORESCENCE AND FLOWER DEVELOPMENT. Development of axillary shoot meristems (those

formed in the bud scales) observed at Stage 1 have not been reported in previous studies. These meristems remained dormant in the presence of an active primary axis meristem. We observed that when the primary axis meristem was destroyed or removed (frost damage or pruning) at the time environmental conditions promoting vegetative growth were present, the axillary shoot meristems continued the vegetative growth of the shoot. Similarly, if the developing apical inflorescence was removed they may produce inflorescences. After inflorescence expansion (Stage 9), these arrested axillary meristems were visible at the macroscopic level as small inflorescence buds in the bud scale scars below the inflorescence.

External characteristics of buds in Stages 1, 2, and 3 have been described previously as buds in rest (Davenport, 1982). However, at the microscopic level one to two secondary axis inflorescence meristems were formed during stages 1 and 2 and by Stage 3, two additional secondary axis inflorescence meristems had been formed. Hence, this period from the end of July through August can be considered the beginning of inflorescence initiation. Thus, inflorescence initiation of the 'Hass' avocado occurred earlier than previously reported for other cultivars in Califomia and other avocado producing regions (Alexander, 1975; Davenport, 1982; Inohue and Takahashi, 1989; Reece, 1942; Schroeder, 1951). The earlier onset of inflorescence initiation for 'Hass' avocado protracted the period required to reach anthesis (seven and a half months) and was much longer than the 2 to 4 months previously reported (Reece, 1942; Schroeder, 195 1). The use of the term floral initiation may be the cause of this discrepancy as it has been used both to designate the presence of secondary axis meristems of the inflorescence and the presence of flower meristems.

The 11 visual stages of inflorescence and flower development distinguished in this study may prove to be a useful tool to predict the microscopic stage of reproductive growth at the branch or tree level. The ability to reliably predict avocado inflorescence development each year should prove of practical benefit for scheduling orchard management practices at specific stages of inflorescence development. For example, any attempts to manipulate inflorescence initiation should be done before buds reach Stage 4. However, if flower organ development is the target (e.g., pollen orovule viability), treatments at Stage 5 to 9 would be more appropriate.

EFFECT OF HIGH ("ON") AND LOW ("OFF") YIELDS ON FLOWERING. Yield had little effect on the timing of developmental events of the inflorescence or flower through anthesis. However, a higher yield in the "on" crop year correlated significantly with reduced flowering intensity and increased production of vegetative shoots. In addition, the vegetative shoots produced during the spring from indeterminate inflorescences bearing fruit through maturity did not produce summer or fall flushes. Thus, there was a reduced number of shoots that could actually produce inflorescences as a result of the "on" crop. A similar reduction in the number and intensity of vegetative flushes apparently caused by a heavy crop has been reported by Lahav and Kalmar (1977) and Schaffer et al. (1991). In our study, despite the presence of mature fruit the next spring, the vegetative shoot apices from indeterminate inflorescences flushed, suggesting that mature fruit did not repress the growth of the apical bud. Seed-produced gibberellic acid

(GA_3) has been hypothesized to prevent the formation of floral buds during the "on" crop year in other fruit trees (Ebert and Bangerth, 1981; Garcia-Luis et al., 1988; Jonkers, 1979). Also, increasing ABA levels have been detected in avocado fruit as they reach maturity (Wolstenholme et al., 1985). It may be that such growth regulator effects are operating in avocado but these hypotheses have not yet been tested.

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Table 1. Developmental stages designated for apical inflorescence buds on summer shoots of the 'Hass' avocado in Corona, California (see Figs 2 to 6)

Stage	Macroscopic description	Microscopic description[z]
1	Closed pointed bud within the most distal two nonexpanded leaves of the shoot.	Convex primary axis meristem with bracts. One or two secondary axis meristems in the axil of bracts.
2	Closed pointed bud, most distal two leaves are expanded and mature.	Flat primary axis meristem with separated bracts. One to trhee secondary axis meristems in the axils of bracts.
3	Closed pointed bud. Partial senescence of bud scales.	Convex primary axis meristem. Four secondary axis inflorescence meristems.
4	Bud scales separated. Inflorescence bracts expand to all sides of the bud.	Flat primary axis meristem. Ten secondary axis inflorescence meristems.
5	Increase in bud dimensions. Sclaes distrinctly separated.	Elongation of oldest secondary axis with tertiary axis meristems present. Initial development of perianth to terminal flowers of secondary and tertiary axes.
6	Rounded bud. Bases of outermost scales remain. Inclorescence bracts enclosing inflorescence are present.	Elongation of youngest secondary axis meristems. Oldest secondary axes are completely formed, including cyme of flowers. Flowers have complete perianth, and anthers with sporogenous tissue are present. Genoecium is at early locule formation.
7	Opening of inflorescence bracts. Inflorescence starts emerging.	Continued development of stamen and gynoecium. Pollen mother cells and a tapetum are evident in the anthers. Ovule is initiated.
8	Obvious elongation of secondary axes (cauliflower stage). Tertiary axes still covered by subtending bracts. Small closed flowers occur.	All flower parts are present. Meiosis has occurred in the anther locules and microspores are evident. Integuments are forming on the ovule.
9	Elongation of teriary axes. Cyme of flowers is evident. Vegetative bud at the inflorescence apex is visible.	Microscpores with well developed exine layers. Ovule in the anatropous position with megaspore present.
10	Flowers are fully differentitated but unopened.	Complete flower with mature sexual organs and ready for anthesis. Microspore mitosis has given rise to the two-celled pollen grains.
11	Flower at anthesis. Bud break of vegetative bud at the apex of indeterminate inflorescences, initiating the spring vegetative flush.	Stigma may be receptive and pollen may be shed.

[z] Description is for an intact bud and was calculated by counting the number of structures observed by longitudinal serial sections up to the central axis. N = 20 buds or inflorescences for each developmental stage.

Table 2. Production of vegetative and reproductive growth (±SE) by 'Hass' avocado trees during an "on" and "off" crop year.

Cropping year	Yield (kg/tree)	Total shoots (no. branch)	Type of growth[Z] (% total shoots)		
			Inflorescences	Vegetative shoot	Inactive bud
"On" (1994-1995)	66.1±5.6 a[Y]	17.6±2.9	13.3±2.5 b	71.9±4.4 a	14.9±2.7 a
"Off" (1995-1996)	18.3±4.9 b	21.0±3.2	45.7±8.6 a	38.3±6.4 b	15.1±5.2 a

[Z] Means ± SE were obtained from 20 tree replications for yield and 10 tree replications of five branches I in long per tree for type of growth.

[Y]Mean separation in columns by t test, P = 0.05.

Table 3. Flowering intensity of 'Hass' avocado trees during an "on" and "off" crop year[Z].

Cropping year	Trees with >50 inflorescences	Avg flowering intensity[Y]
"On" (1994-95)	80	2.2 ± 0.2 b[X]
"Off'(1995-96)	100	4.2 ± 0.2 a

[Z] Means ± SE were obtained from 20 tree replications, except for flowering intensity in the "on" crop year in which only ten replications were used.

[Y] Visual scale (amount of the canopy covered by inflorescences): 1 = no inflorescences; 2 =≤25%; 3 =≤50%; 4 =≤75%; 5 = 76% to 100%.

[X] Means separation in columns by Mann-Whitney rank sum test, P 0.05.

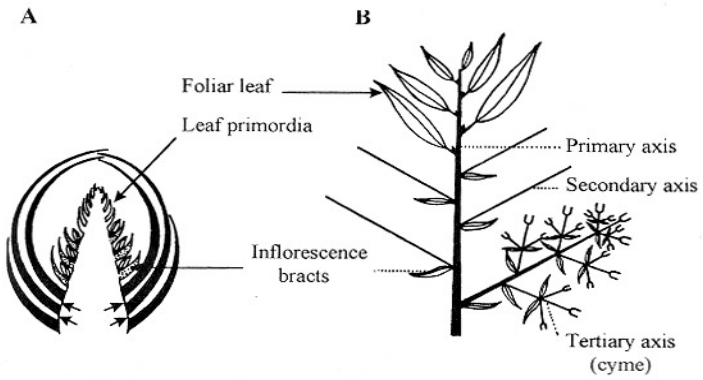

Fig. 1. (**A**) Morphology of a reproductive bud (indeterminate) of 'Hass' avocado in diagrammatic longitudinal section showing foliar appendages and inflorescence meristerns (not drawn to scale). Short arrows = place where axillary shoot meristems are produced; Bud scales= solid black; Inflorescence bracts= stippled; Secondary axis meristerns = hatched; Leaf primordia = white (redrawn from Thorp et al., 1994). (**B**) Diagram of reproductive and vegetative growth in an indeterminate avocado inflorescence (from Reece, 1942).

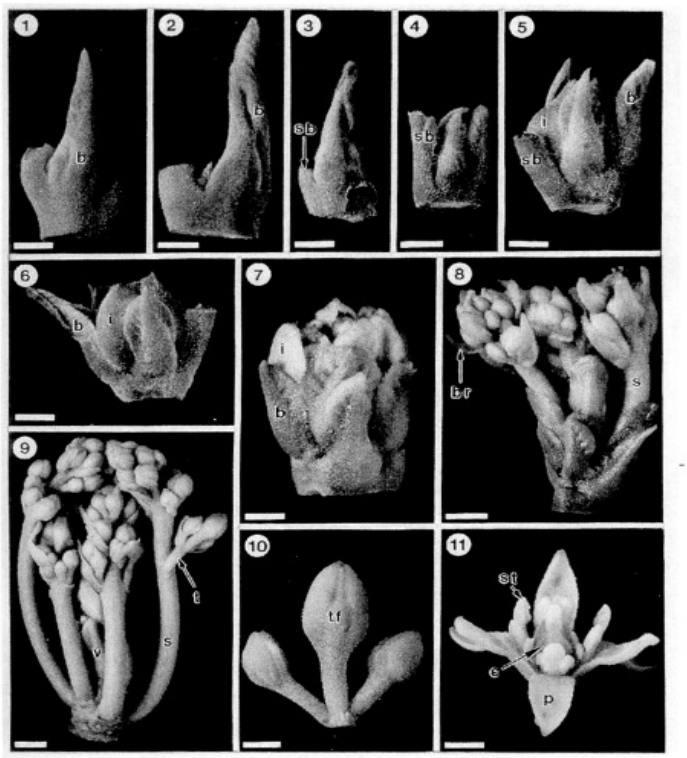

Fig. 2. Macroscopic views of inflorescence development (labeled Stages 1 to 11) of apical buds of summer shoots of the 'Hass' avocado. See Table 1 and Figs. 3 to 6 for a detailed macroscopic and microscopic description of each stage, respectively. Abbreviations: b = bud scale, br = bracteole of tertiary axis, c = carpel, i = inflorescence bract, p = perianth, s = secondary axis inflorescence, sb = bud scale base, st = stamen, t = tertiary axis, tf = terminal flower of secondary axis, v = vegetative bud. Bars = 2 mm (I to 7 and 10 to 11) and 3 turn (8 and 9).

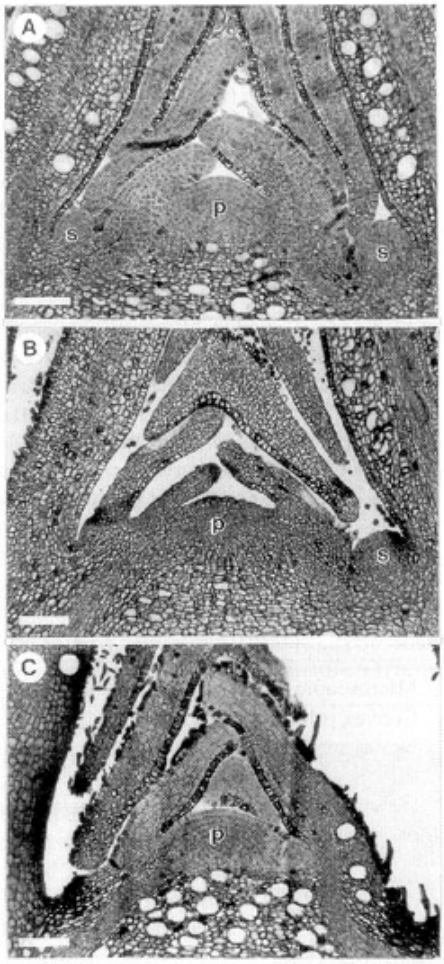

Fig. 3. Microscopic views of inflorescence development (Stages 1 to 3) showing the transition from vegetative to reproductive state of apical buds of summer shoots of 'Hass' avocado (**A**) Stage 1: convex primary axis meristem, one or two secondary axis inflorescence meristems present. (**B**) Stage 2: flat primary axis meristem. (**C**) Stage 3: convex primary axis meristem, four secondary axis inflorescence meristems present (not in view)/. See Table 1 and Fig. 2 for a detailed macroscopic and microscopic description of each stage. Abbreviations: p = primary axis meristem, s = secondary axis inflorescence meristem. Bars = 100 µm (**A**-**C**).

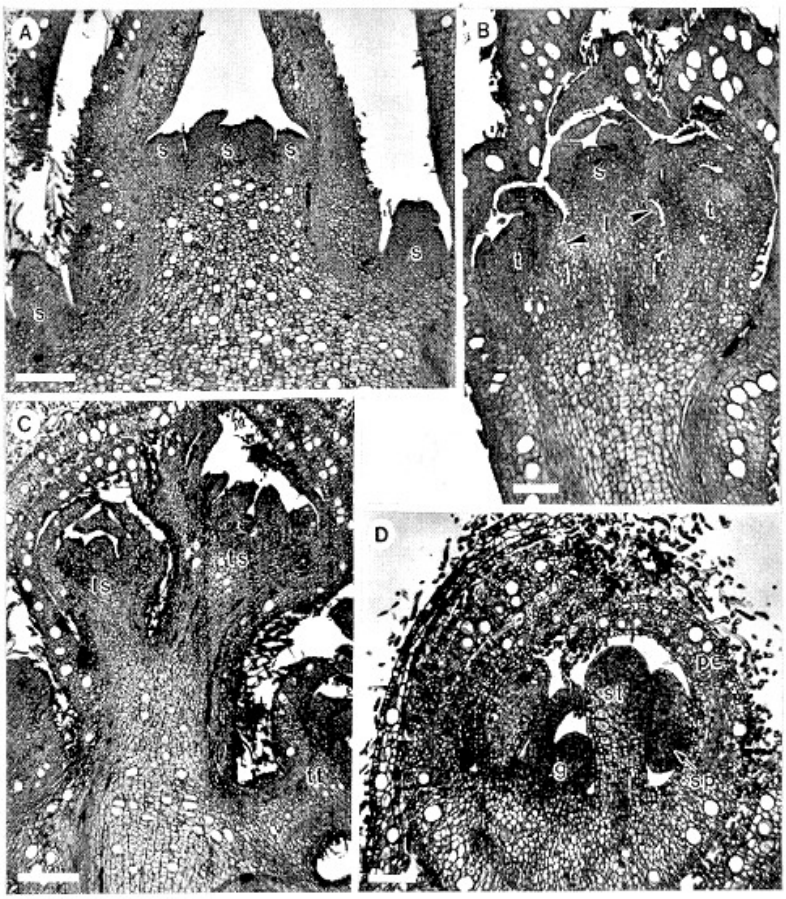

Fig. 4. Continued microscopic views of inflorescence and flower development (Stages 4 to 6) of apical buds of summer shoots of 'Hass' avocado. (**A**) Stage 4 with a full set of secondary axis inflorescence meristems. (**B**) Development of secondary and tertiary axis at Stage 5. (**C**) Secondary axis at Stage 6 with a terminal and a lateral flower of the terminal cyme (top of picture); the two lowest flower structures belong to a different cyme each. (**D**) Closeup of developing flower at Stage 6. See Table I and Fig. 2 for a detailed macroscopic and microscopic description of each stage. Abbreviations: g = gynoecium, I = lateral flowermeristem, Is =lateral flowerof secondary axis, pe =perianth; s = secondary axis inflorescence meristem, sp = sporogenous tissue, st = stamen, t = tertiary axis meristem, is = terminal flower of secondary axis inflorescence, tt = terminal flower of tertiary axis. Bars = 200 Vin (**A** and **C**) and 100 gm (**B** and **D**).

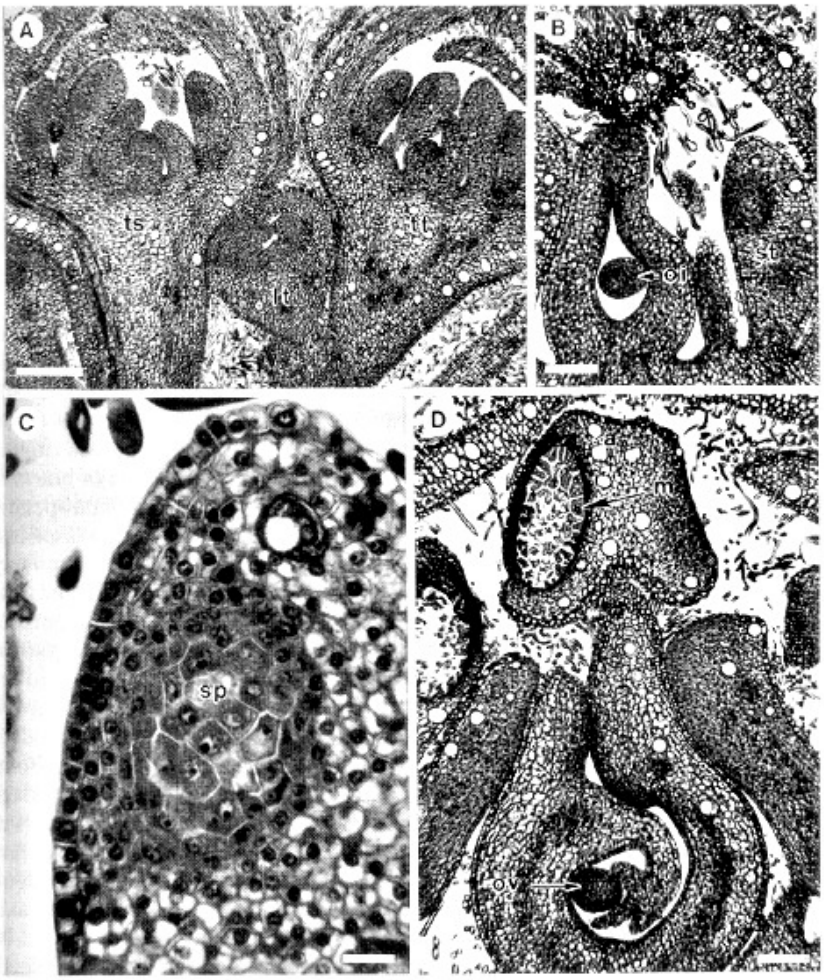

Fig. 5. Continued microscopic views of flower development (Stages 7 and 8) in apical buds of summer shoots of 'Hass' avocado. (**A**) Stage 7. (**B**) Initiated ovule at Stage7. (**C**) Closeup of anther at Stage 7 showing sporogenous tissue. (**D**) Stage 8 Fig. 6. Continued microscopic views of flower development (Stages 9 and 10) of (cauliflower stage), microspores in anther. See Table 1 and Fig. 2 for a detailed macroscopic and microscopic description of each stage. Abbreviations: lt = lateral flower of tertiary axis, m = microspores, oi = ovule initiating, ov = ovule with integuments, sp = sporogenous tissue, st = stamen, ts = terminal flower of secondary axis, tt = terminal flower of tertiary axis. Bars = 200 pm (**A**), 100 Itm (**B** and **D**), and 20 pm (**C**).

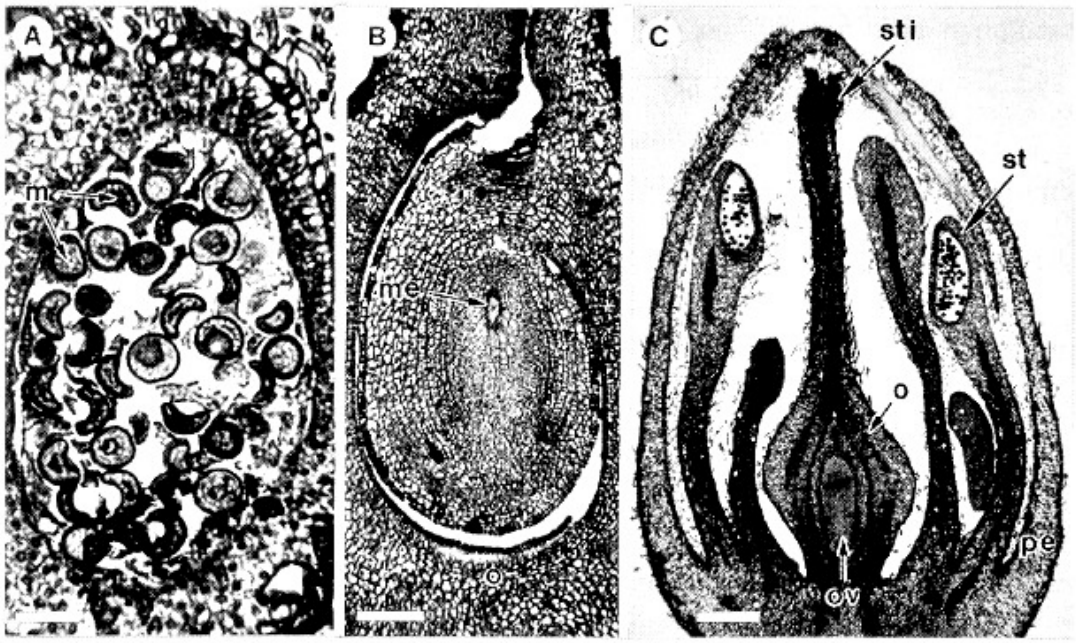

Fig. 6. Continued microscopic views of flower development (Stages 9 and 10) of apical buds of summer shoots of 'Hass' avocado. (**A**) Anther with microspores at Stage 9. (**B**) Ovule at Stage 9, note megaspore. (**C**) Mature terminal flower at Stage 10. See Table 1 and Fig. 2 for a detailed macroscopic and microscopic description of each stage. Abbreviations: m = microspores, me = megaspore, o = ovary, ov = ovule, pe = perianth, st = stamen with pollen grains, sti = stigma. Bars = 30 µm (**A**), 100 µm (**B**), and 500 µm (**C**).

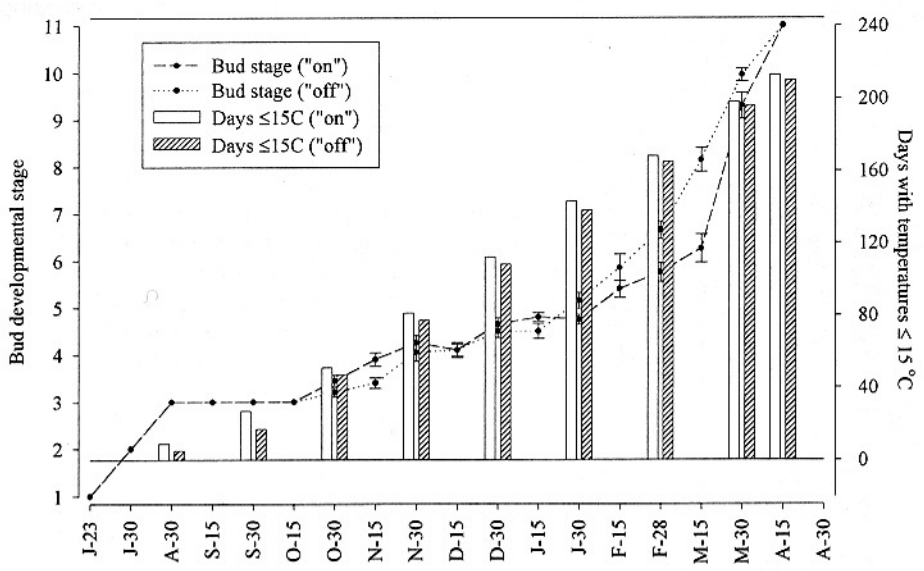

Fig. 7. Cumulative number of days with temperature ≤15 ^{o}C and macroscopic inflorescence development of apical buds of summer shoots of 'Hass' avocado in Corona, Calif., during "on" (1994-95) and "off" (1995-96) crop years. Visual scale: 1 = Closed pointed bud within the most distal two nonexpanded leaves of the shoot, 8 = cauliflower stage, 11 = anthesis.