

FLOWERING OF AVOCADO (*Persea americana* Mill.). I. INFLORESCENCE AND FLOWER DEVELOPMENT

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SUMMARY

A study of inflorescence and flower development of the 'Hass' avocado (*Persea americana* Mill.) was undertaken in California, USA. Eleven macroscopic stages of external bud and subsequent inflorescence development were correlated with microscopic organogenesis for subsequent use in predicting specific stages of inflorescence development to schedule cultural practices in a commercial orchard. Transition from vegetative to reproductive growth on summer shoots occurred in July-August and was followed by inflorescence initiation from August to October. Anthesis occurred seven months later. A period of dormancy was not required for transition to flowering. At the time of transition, apical buds of mature vegetative shoots consisted of a convex primary axis meristem with two lateral, secondary axis inflorescence meristems lacking apical bracts. Under floral-promoting conditions (low temperature), apical buds fully committed to flowering were not distinguishable anatomically from those that were not committed to flowering. Avocado inflorescence development was correlated with night temperature ≤ 15 °C. Crop load influenced the proportion of determinate and indeterminate floral shoots and vegetative shoots produced during spring bloom.

ADDITIONAL KEY WORDS: alternate bearing, commitment to flowering, gibberellic acid, floral development, organogenesis, yield.

FLORACIÓN DEL AGUACATE (*Persea americana* Mill.). I. DESARROLLO DE LA INFLORESCENCIA Y FLOR

RESUMEN

En California, EUA se estudió el desarrollo de la inflorescencia y flor del aguacate 'Hass' (*Persea americana* Mill.). Se diseñó una escala que correlaciona 11 estados de desarrollo externo de la yema y desarrollo posterior de la inflorescencia con la organogénesis microscópica para ser usada en la predicción de estados específicos de desarrollo de la inflorescencia que ayuden a programar prácticas culturales en huertos comerciales. La transición del crecimiento vegetativo al reproductivo ocurrió en julio-agosto en brotes de verano y fue seguida por la iniciación de la inflorescencia en agosto-octubre. La anthesis ocurrió siete meses más tarde. La transición a la floración no requirió de un periodo de reposo. Al momento de la transición, las yemas apicales de brotes maduros presentaron un meristemo del eje primario convexo, con dos meristemos laterales de ejes secundarios que carecían de brácteas apicales. Bajo condiciones que promueven floración (baja temperatura) no se detectaron diferencias anatómicas entre yemas apicales completamente determinadas a reproductivas y aquellas que no lo estaban. El desarrollo de la inflorescencia se correlacionó con temperaturas nocturnas ≤ 15 °C. La cantidad de fruta influenció la proporción de inflorescencias determinadas, indeterminadas y brotes vegetativos producidos en la floración de primavera.

PALABRAS CLAVE ADICIONALES: alternancia de producción, determinación a la floración, ácido giberélico, desarrollo floral, organogénesis, rendimiento.

INTRODUCTION

Research on reproductive physiology has resulted in the development of commercial strategies to manipulate flowering of subtropical and tropical fruit crops like citrus (Monselise and Halevy, 1964; Iwahori and Oohata, 1981; Guardiola *et al.*, 1977) and mango (*Mangifera indica*) (Kachru

et al., 1972; Nunez-Elisea and Davenport, 1991; Bally *et al.*, 2000; Salazar-Garcia *et al.*, 2000). Avocado (*Persea americana* Mill.) is an important crop for both tropical and subtropical regions; however, little information on its reproductive physiology is available in such a manner that would make possible the development of field management strategies to modify the date and intensity of bloom to escape

from undesirable environmental conditions, shift the harvest season to avoid seasonal peaks, and minimize alternate bearing, among others. In preparation for future research to manipulate vegetative and reproductive growth of 'Hass' avocado, results of a series of studies performed on field and controlled environment are presented. The objective of this paper is to present critical stages of inflorescence and flower development, as well as the effect of tree's fruit load on the expression of a series of studies performed on field and controlled environment are presented. The objective of this paper is to present critical stages of inflorescence and flower development, as well as the effect of tree's fruit load on the expression of flowering of 'Hass' avocados in California, USA.

CRITICAL STAGES OF INFLORESCENCE DEVELOPMENT

Transition from vegetative to reproductive growth

The period of transition from vegetative to reproductive growth was determined in 10-year-old 'Hass' avocado trees selected for uniform yield and vigor in a commercial avocado orchard in Southern California, (Salazar-García *et al.*, 1998). Apical buds from summer shoots were collected and serially sectioned weekly from each tree to obtain buds through the end of shoot elongation for two consecutive years. To describe the anatomical sections the terms primary axis meristem (PAM), secondary axis meristem (SAM), and tertiary axis meristem (TAM) were used to designate the shoot apical meristems of the corresponding axes. The results of Salazar-García *et al.* (1998) showed that close to the end of the expansion of the summer vegetative flush (23 July), apical buds had a external pointed shape and had a convex PAM and one or two young secondary axis inflorescence meristems in the axils of bracts. By the end of July the buds were pointed and closed. At this stage, a flat (low convex) shoot apical meristem with separated bracts was evident plus one to three SAMs. By 30 of August bud scales started to abscise. The PAM was convex and four secondary axis meristems were present in the axils of inflorescence bracts. A decreased rate of SAM production was observed in this stage.

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. Thus, the PAM 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 PAM. These axillary meristems typically formed inflorescences. But, as reported for other species (Bernier *et al.*, 1981), we found that

flowering in avocado is not obligatory at this point, but depends on environmental conditions. After initiation of these secondary axis meristems the PAM becomes flattened and its activity decreases, but at no time was dormancy detected. We observed that the PAM changed shape from convex to flat to convex during the period from the end of July through August and that after these events, the PAM initiated new bracts in the axils of bract 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. 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. 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.*, 1981). 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 PAM. However, under conditions optimal for flowering, these meristems developed into the basal lateral cymes of the inflorescence and the other cymes were produced by the new activity of the PAM (Salazar-García *et al.*, 1998). The subsequent formation of additional secondary axis inflorescence meristems, which was evident by 30 of August, is consistent with commitment of the primary axis meristem to flowering. The environmental conditions evoking this transition remain unknown.

Irreversible commitment to flowering

At some point in the transition from vegetative to the reproductive condition, which is apparently different for different species, the process is no longer reversible and the PAM is committed to flowering (McDaniel, 1994). In the avocado, only some apexes flower; others continue the vegetative growth of the tree. Thus, in order to manage vegetative and reproductive growth to improve avocado yield, it is critical to know when a PAM is irreversibly committed to be a floral shoot. Due to the lack of experimental evidence, it was assumed that a PAM had reached commitment to flowering when the two apical bracts (microscopic level) were extended over the secondary axis inflorescence meristem, which is indicative of the initiation of the terminal flower in the triplet (Thorp *et al.*, 1994). However, the results of Salazar-García *et al.* (1998) showed that this stage occurs very late in the development of the avocado inflorescence, whereas commitment to flowering is an early event.

Temperature is an additional factor known to inhibit or enhance floral initiation in avocado that can be used to help identify an anatomical change associated with commitment to flowering. Buttrose and Alexander (1978)

and Nevin and Lovatt (1989) used as little as four weeks of low temperature (LT) treatment ($\leq 15\text{ }^{\circ}\text{C}$) with daylength of $\leq 10\text{ h}$ to successfully cause flowering in 'Fuerte' and 'Hass' avocado, respectively. Trees maintained at $24\text{ }^{\circ}\text{C}$ day/ $19\text{ }^{\circ}\text{C}$ night and 12-h photoperiod (Nevin and Lovatt, 1989) or at a constant minimum temperature $> 20\text{ }^{\circ}\text{C}$ did not produce inflorescences (Buttrose and Alexander, 1978).

A series of growth chamber experiments using container-grown two- and three-year-old 'Hass' avocado scions grafted on Duke 7 clonal rootstock were performed by Salazar-García *et al.* (1999). The objective was to identify an early anatomical change at the macro- and microscopic levels before which the developmental fate of the PAM could be diverted to vegetative growth, but after which the PAM was irreversibly committed to flowering. Low temperature treatments ($10\text{ }^{\circ}\text{C}$ day/ $7\text{ }^{\circ}\text{C}$ night) were used to cause floral initiation and warm temperature ($25/20\text{ }^{\circ}\text{C}$) was used to stop or reverse the process.

In agreement with the results of Buttrose and Alexander (1978) and Nevin and Lovatt (1989), low temperature and short daylength (8- to 10-h day) effectively caused flowering of the 'Hass' avocado. The results showed that control trees and trees receiving one or two weeks of LT treatment did not become reproductive; all growth was vegetative (Salazar-García *et al.*, 1999). For the three-week LT treatment, 17 % of apical buds produced inflorescences, whereas 69 % produced vegetative shoots. Four weeks at $10/7\text{ }^{\circ}\text{C}$ (10-h day/14-h night) were sufficient for apical buds of the 'Hass' avocado to become fully committed to flowering as they produced 83 % inflorescences and no vegetative growth; the remaining buds remained inactive. Anatomical sections of the apical buds at time zero revealed a convex PAM that had produced a secondary axis inflorescence meristem in the axil of each of two inflorescence bracts. At this time the secondary axis inflorescence meristems did not have apical bracts. During the four weeks of exposure to low-temperature, no anatomical changes were observed in the primary axis meristem, despite the different effects of the length of the LT treatment on the developmental fate of the apical bud.

Macroscopic analysis of apical buds at the beginning and end of the LT treatments revealed that the buds had not visibly changed and remained pointed with closed scales (Salazar-García *et al.*, 1999). Thus, no anatomical differences were found between apical buds committed to flowering and those that were not. Axillary buds were less developed than the apical bud. At the start of the LT treatment, axillary buds bore no secondary axis inflorescence meristems in the axils of their inflorescence bracts, whereas apical buds had two (apical bracts were absent). After four weeks of LT treatment, axillary buds had produced one pair of secondary axis inflorescence meristems (with no apical bracts). Thus, after four weeks of LT treatment, axillary buds had caught up with apical buds both anatomically and developmentally since axillary buds were also committed to flowering at this time. Hence, based

on their anatomy, it is possible to distinguish axillary buds that are fully committed to flowering from those that are not by the presence or absence of a single pair of secondary axis inflorescence meristems (no apical bracts).

Partial senescence, abscission, and separation of the outermost bud scales of apical and axillary buds are the visual cue associated with the stage of inflorescence development when three or more secondary axis inflorescence meristems are formed. At this stage an apical or axillary bud is irreversibly committed to flowering (Salazar-García *et al.*, 1998). This visual cue can be used in a commercial avocado orchard to estimate the proportion of buds fully committed to flowering versus those that are not.

Inflorescence and flower development

After the transition from vegetative to reproductive growth and commitment to flowering has occurred in avocado buds, production of additional secondary axis meristems in the axils of bud bracts starts. This is the beginning of inflorescence bud initiation. With the goal of determining inflorescence bud development in the 'Hass' avocado, a visual scale of eleven macroscopic stages of external bud and subsequent inflorescence development was correlated with microscopic organogenesis for use in predicting specific stages of inflorescence development. This may be a valuable tool to schedule cultural practices in a commercial orchard (Salazar-García *et al.*, 1998). Stages 1 and 2 mark the transition from vegetative to reproductive growth. The main external feature of buds at these stages is that they have closed bud scales. It is at this stage when the highest vegetative response would be obtained if treatments that stimulate bud break were applied. When buds reached Stage 3 (by 30 August in California), their bud scales started to abscise; the primary axis meristem was convex and four secondary axis meristems were present in the axils of inflorescence bracts. The bud is fully committed to flowering. Buds at Stage 4 (approximately 15 November in California) were characterized by the separation of bud scales (often only scale bases remain), revealing the expanded inflorescence bracts. At this stage, the PAM had become flattened again and an average of 10 secondary axis inflorescence meristems was present, with the basal six having produced bracts. Presence of bracts on the basal meristems can result, if vegetative growth is stimulated, in the production of partially formed inflorescences, in which case the basal meristems with apical bracts develop into lateral panicles. Less developed meristems eventually are suppressed by the growth of the PAM. At Stage 5, (late January to early February in California), bud dimensions were larger, causing bud scales to be more separated. Elongation of secondary axis inflorescence meristems had occurred and tertiary axis meristems were apparent at this stage. It is in Stage 5 when the beginning of flower organ development (initiation of the perianth) was observed for terminal flowers of secondary and tertiary axes. Buds at Stage 6 (first observed by mid-

February in California) had rounded shape and inflorescence bracts, enclosing secondary axes of the inflorescence, were evident. The secondary axes of the inflorescence were completely formed, with each bearing several cymes of flowers, equivalent to the tertiary axis. 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. At Stage 7, the inflorescence had started to emerge from the bud, the flowers were more developed (i.e., the ovule was initiated) and pollen mother cells and a tapetum were visible in the anthers. Stage 8, also known as "cauliflower stage" (Lovatt, 1994), was observed by 15 March and corresponded to an obvious elongation of the secondary axes of the inflorescence. Meiosis had occurred in the anther locules and microspores were evident. Integuments were forming on the ovule. This is a particularly important stage. Foliar sprays of boron made at the cauliflower stage but prior to full inflorescence expansion and anthesis increased the number of pollen tubes that reached the ovule and also increased ovule viability (Jaganath and Lovatt, 1998). Stage 9 was designated as the point when elongation of the tertiary axes (cymes) was observed. Microspores with well developed exine layers and ovules in the anatropous position with megaspore present were characteristic of Stage 9. At this stage, the vegetative bud emerging above the inflorescence (which will produce the spring vegetative flush) was visible, but bud break did not occur until Stage 11 (anthesis). At Stage 10, flowers were fully differentiated but unopened. Microspore mitosis had given rise to the two-celled pollen grains; sexual organs were mature and ready for anthesis. Stage 11 was reached in April and corresponded to the flower at anthesis where the stigma is receptive and pollen may be shed. At this stage, bud break at the apex of indeterminate inflorescences initiated the spring vegetative flush.

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 California and other avocado producing regions (Reece, 1942; Schroeder, 1951; Alexander, 1975; Davenport, 1982; Inohue and Takahashi, 1989). The earlier onset of inflorescence initiation for the 'Hass' avocado protracted the period required to reach anthesis (seven and a half months) and was much longer than the two to four months previously reported (Reece, 1942; Schroeder, 1951). Misappropriated use of the term "floral initiation" may be the cause of this discrepancy as it has been used to designate both the presence of secondary axis meristems of the inflorescence and the presence of flower meristems.

The eleven visual stages of inflorescence and flower development distinguished by Salazar-García *et al.* (1998) 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 reduce inflorescence initiation to even-out alternate bearing should be done before buds reach Stage 3. This stage is also important to the timing of treatments designed to increase inflorescence number. However, if the goal is to influence flower organ development (e.g., to improve pollen or ovule viability), treatments at Stage 5 to 9 would be more appropriate.

EFFECTS OF FRUIT LOAD ON FLOWERING

Inflorescence bud development is not affected by tree fruit load

In a two-year study performed in California, USA during an "on" and "off" crop year (average yield was 66 and 18 kg per tree for the "on" and "off" crop year, respectively), the average length of time from the initiation of an inflorescence bud (August) through end of Stage 4 was approximately the same for the 'Hass' avocado in both cropping years (Salazar-García *et al.*, 1998). After this period, an increased rate of inflorescence development was observed for trees in the "off" crop year which reached the cauliflower stage (Stage 8) earlier. However, no difference was detected for the time of anthesis (Stage 11), which was reached by the second week of April in both years. Differences in bud or inflorescence development were not attributable to temperature, because there was no significant difference in the number of days with temperatures $\leq 15^{\circ}\text{C}$ between the two cropping years from 1 August to 15 March. Thus under California conditions, anthesis (full bloom) was not affected by fruit load.

High fruit load decreases intensity of flowering

High yield during an "on" crop year (average of 66 kg per tree) significantly reduced flowering intensity for the next year's crop (Salazar-García *et al.*, 1998). This reduction was associated with a decreased production of inflorescences (13 % of the total shoots/branch), which was accompanied by a higher production of vegetative shoots (72 % of the total shoots/branch). 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 were a reduced number of shoots that could produce inflorescences because of the "on" crop. During the "on" crop year, 20 % of the trees produced less than 50 inflorescences or had no flowering at all. Tree flowering intensity (percentage canopy covered with inflorescences) was slightly higher than 25 % per tree.

The opposite was found for trees carrying the "off" crop (average of 18 kg per tree). Inflorescences were produced on 46 % of the total shoots and vegetative shoots on only 38 %. For the "off" crop year, all trees had a flowering intensity >75 %. The proportion of inactive apical buds was not affected by yield.

Lahav and Kalmar (1977) and Schaffer *et al.* (1991) have reported a similar reduction in the number and intensity of vegetative flushes caused by a heavy crop. 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 (GA₃) has been hypothesized to prevent the formation of floral buds during the "on" crop year in other fruit trees (Jonkers, 1979; Ebert and Bangerth, 1981; Garcia-Luis *et al.*, 1988). In addition, 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 contributing to alternate bearing in avocado but this hypothesis has not yet been tested.

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