HortScience 41(7):1541–1546. 2006.

Crop Load Affects Vegetative Growth Flushes and Shoot Age Influences Irreversible Commitment to Flowering of 'Hass' Avocado

Samuel Salazar-García[1]
Campo Experimental Santiago Ixcuintla, INIFAP, Apdo. Postal 100, Santiago Ixcuintla, NAY 63300, México

Luis E. Cossio-Vargas
Unidad Académica de Agricultura, Universidad Autónoma de Nayarit, Apdo. Postal 49, Xalisco, NAY 63780, México

Carol J. Lovatt
Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124

Isidro J.L. González-Durán and María H. Pérez-Barraza
Campo Experimental Santiago Ixcuintla, INIFAP, Apdo. Postal 100, Santiago Ixcuintla, NAY 63300, México

Additional index words. Persea americana, phenology, alternate bearing, floral development, girdling, floral determination

Abstract. **Several studies were undertaken in commercial nonirrigated 'Hass' avocado orchards under the subhumid semiwarm subtropical climate of the state of Nayarit, Mexico, with the following objectives: 1) to determine the frequency and intensity of vegetative shoot flushes and their contribution to the production of floral shoots, 2) to quantify the effect of tree fruit load on the occurrence of vegetative shoot flushes during the year and the relationship between vegetative and reproductive shoot number during flowering, and 3) to determine the time when apical buds borne on the major vegetative shoot flushes reached irreversible commitment to flowering (floral determination) through the use of shoot defoliation and girdling. Data trees were selected in two orchards based on their current crop load. Four to five branches per tree were tagged, and the number and intensity of vegetative flushes that developed during 2 years, as well as the type of growth produced by apical buds of shoots of different ages, were recorded at the end of the winter bloom periods for two separate years, 1999 and 2001. In a separate experiment using a different set of trees, winter and summer flush shoots were defoliated (year 1) or defoliated and girdled (year 2) at different stages of bud development from September to January in each case. Four vegetative flushes occurred each year. The winter flush that emerged in Feb. 1998 made the greatest contribution to the 1999 winter bloom—76.5% of the shoots produced floral shoots. Contributions of the summer 1 (late July 1998), summer 2 (early Aug. 1998), and summer 3 (late Aug. 1998) flushes to flowering were intermediate. A total of 30.6%, 36.4%, and 19% of the shoots produced floral shoots respectively. All four vegetative flushes produced a similar number of vegetative shoots during winter bloom. Evaluation of the 2001 winter bloom for trees with high (>95 kg fruit/tree) and low (<70 kg fruit/tree) crops showed no effect of tree fruit load on the production of vegetative or floral shoots by winter or summer vegetative flushes. Irrespective of time of treatment (shoot defoliation and girdling) or shoot age, irreversible commitment to flowering of apical buds occurred by 15 Oct., and this stage was associated with an average of 27.5 chilling days (temperature, ≤19 °C) for both years. Buds irreversibly committed to flowering were closed and pointed, with partial senescence of bud scales. Anatomically, the buds showed a convex primary axis meristem and four secondary axis floral shoot meristems.**

The state of Nayarit is the second highest avocado-producing state in Mexico, averaging 17,000 ton from almost 2000 ha (CONAPA, 2006). The 'Hass' avocado-producing area is located between 21°18′ and 21°32′ N latitude and from 850 to 1500 m above sea level (asl) in a subhumid warm climate (20 to 29 °C average annual temperatures) with 1300 mm of summer rain.

Bloom of the 'Hass' avocado in Nayarit occurs once a year and usually takes place during the winter (January to February), concomitantly with a flush of vegetative shoots. Other vegetative shoot growth flushes may occur during the summer and fall. Legal fruit maturity (21.5% mesocarp dry matter) is typically reached by October/November of the same year.

To remain competitive, Nayarit 'Hass' avocado growers need to increase the selling price of their crop and to maximize the effectiveness of orchard management practices, like fertilization, pruning, or application of plant bioregulators, in solving production problems. The low selling price of the crop is because peak harvest season for the 'Hass' avocado in Nayarit and Michoacán (the largest avocado-producing area) is from October to December, and thus coincides with that of Nayarit. To minimize this problem and to increase both the selling price of avocados and grower income, an ability to shift the time of maturity of the crop to before or after the period of maximum harvest is desired. A standard horticultural strategy for shifting the time of fruit maturity is to advance or delay flowering. However, an in-depth study of avocado reproductive physiology is a prerequisite to attempts to modify the time of bloom and, thus, change the date of harvest of the 'Hass' avocado (Salazar-García, 2000).

Knowledge of avocado flowering is critical to the development of orchard management strategies to increase floral intensity or, alternatively, to promote vegetative growth and decrease flowering. For such strategies to be successful, it is essential to know the time when shoot apical buds reach the irreversible commitment to flowering (ICF), or floral determination. To prevent an inadvertent increase in vegetative shoot growth at the expense of flowering, cultural practices that can prevent flowering, like nitrogen fertilization, light canopy pruning (hedging, topping), or application of some plant bioregulators, must be carried out after ICF.

A 2-year study in California showed that apical buds of summer shoots of 'Hass' avocado transitioned from vegetative to reproductive growth from 30 Aug. to 15 Oct. (Salazar–García et al., 1998). Latitudinal differences between California and Nayarit may influence tree phenology and may affect the time and stage of development when apical buds become committed to reproductive growth.

Depending on environmental conditions, 'Hass' avocado trees can produce two or more flushes of vegetative growth every year (Salazar-García, 2000). The magnitude of

---

Received for publication 20 June 2005. Accepted for publication 14 July 2006.

Major funding for this work was obtained from the University of California Institute for Mexico and the United States, The Consejo Nacional de Ciencia y Tecnología, and the Fondo Mixto de Fomento a la Investigación Científica y Tecnológica de Nayarit. Additional support was provided by the INIFAP, the USPR Aguacate Hass de Nayarit, and by the Fundación Produce Nayarit, A.C.

We thank Alberto Ante and Bernabé Sánchez for use of their avocado orchards.

[1] To whom reprint requests should be addressed; e-mail samuelsalazar@prodigy.net.mx.

each flush is variable and usually one of them is the main producer of floral shoots. For the 'Hass' avocado in Nayarit, the relative importance of each vegetative flush to flowering has not been quantified.

The avocado produces two types of floral shoots: 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 (Reece, 1942). With few exceptions, the indeterminate type of inflorescence is more abundantly produced (Salazar-García et al., 1998; Schroeder, 1944). Both types of floral shoots consist of secondary axes (lateral panicles), producing tertiary axes (cymes) that bear a terminal flower and two lateral flowers (Reece, 1942; Salazar-García et al., 1998). Development of the secondary axes within the bud proceeded in an acropetal fashion, so a developmental range occurs in a single floral shoot, 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 (Salazar-García et al., 1998). However, on an individual secondary axis, development is basipetal, with the terminal flowers (lacking subtending bracts) differentiating and maturing first, as is typical in a cyme (Salazar-García et al., 1998). The fate of the apex of the primary axis meristem of the floral shoot becomes determined after the secondary and tertiary axes reached the ICF (Salazar-García and Lovatt, 1999).

Several techniques have been used to study early development of avocado floral buds, such as warm (≥20 °C) or low (<20 °C) temperatures to inhibit or promote flowering respectively (Buttrose and Alexander, 1978; Nevin and Lovatt, 1989; Salazar-García et al., 1999), as well as exogenous applications of gibberellins (GA_3) (Salazar-García et al., 1999). Shoot defoliation, alone or in combination with girdling, has also been used to achieve this goal in other plant species. Leaves maintain buds in a paradormant condition. Defoliation removes this growth-inhibiting factor, forcing rapid bud growth—hence its usefulness as a tool for imposing timed responses. The main effect of girdling is to prevent the influx of phloem-translocated, floral-stimulating signals (Bernier, 1988; Bernier et al., 1981) produced in other portions of the tree into experimental branches, as it has been demonstrated for mango (Nunez-Elisea and Davenport, 1992; Nunez-Elisea et al., 1996). In a branch that has been both defoliated and girdled, buds are forced to grow and express their developmental state without the influence of incoming developmental signals and can serve as a convenient tool to determine the time of ICF in avocado under field conditions. If flowering occurs, buds are said to have been irreversibly committed to flowering—that is, capable of initiating floral morphogenesis using their own "developmental program." In avocado, girdling has been studied only on woody branches to elucidate its effect in augmenting bloom and fruitfulness (Coit, 1920–21; Lahav et al., 1971–72), as well as to control alternate bearing (Davie and Stassen, 1997).

Thus, the study of early floral development of the 'Hass' avocado in Nayarit will provide the basic information essential to developing management strategies to solve several production problems. Therefore, the objectives of this is research were 1) to determine the frequency and intensity of vegetative shoot flushes and their contribution to the production of floral shoots, 2) to quantify the effect of tree fruit load on the occurrence of vegetative shoot flushes during the year and the relationship between vegetative and reproductive shoot number during flowering, and 3) to determine the time when apical buds borne on the major vegetative shoot flushes reached irreversible commitment to flowering through the use of shoot defoliation and girdling.

Materials and Methods

Research was conducted at several intervals from 1997 to 2003 in two 14-year-old commercial 'Hass' avocado orchards in the state of Nayarit, Mexico. The Alberto orchard was located in Venustiano Carranza (21°32′ N, 104°59′ W; 900 m asl; 1300 mm annual rain; 21 °C annual average temperature). The second orchard, Bernabé, was situated in Xalisco (21°26′ N, 104°55′ W; 1100 m asl; 1185 mm annual rain; 21.7 °C annual average temperature). Trees were grafted on local seedling rootstocks (natural hybrids of West Indian × Guatemalan races), spaced at 8 × 8 m and cultivated under rain-fed conditions with no supplemental irrigation.

Effect of vegetative shoot age and crop load on production of inflorescences

Identification of flushes of vegetative and reproductive growth. In Oct. 1997 (2 weeks before harvest), 20 'Hass' avocado trees were selected in the Alberto orchard with an estimated yield greater than 100 kg fruit/tree. Five 1-m-long fruiting branches of similar diameter (5 cm) and with at least 20 vegetative shoots each were tagged around the canopy of each tree. Starting on 10 Feb. 1998 (winter bloom), all vegetative shoots produced by each flush were tagged to determine the contribution of each vegetative shoot flush to the 1999 return winter bloom. At the end of the bloom period (Feb. 1999), the production of determinate and indeterminate floral shoots as well as the number of vegetative shoots and inactive buds (those that did not show any type of growth) produced by apical buds of the primary axis of the shoot was quantified for each tagged shoot. Total yield of fruit from the 1998 winter bloom was obtained for each selected tree in October of the same year. A randomized design with 20 single-tree replications was used.

Crop load and production of vegetative and floral shoots. In June 2000, 20 avocado trees were selected in each avocado orchard (Alberto and Bernabé) based on their current estimated fruit load: 10 trees with a low off-year crop (<70 kg fruit/tree) and 10 trees with higher on-year crop (>95 kg fruit/tree). In each tree, four 1-m-long branches with similar diameter (≈5 cm) and having at least 10 winter flush vegetative shoots each were randomly selected around the canopy of the tree and all their shoots tagged. Vegetative shoots produced during the summer 2000 flush also were tagged to determine the type of apical growth (floral shoots, vegetative shoots, or inactive buds) that would be produced by the main axis of both winter and summer flush shoots during the 2001 winter bloom period. A randomized design with 10 single-tree replications per each crop load was used.

Effect of shoot age on ICF of apical buds

Shoot defoliation. Ten trees with previously recorded yields greater than 100 kg fruit/tree were selected in the Alberto orchard. In each tree, 20 vegetative shoots produced by indeterminate inflorescences during the 2001 winter bloom were tagged and numbered at the beginning of shoot elongation (10 Feb.). Similarly, 20 shoots per tree that were produced during the 2001 summer vegetative flush were selected, tagged, and numbered on 30 July. Shoot defoliation was performed at biweekly intervals, starting on 1 Sept. 2001 through 15 Jan. 2002. On each date, 10 shoots of the winter vegetative flush and 10 shoots of the summer flush were randomly selected in each tree and defoliated by hand. Control shoots were left intact. The type of growth produced by apical buds (floral shoots, vegetative shoots, or inactive buds) on the shoot primary axis was recorded for individual shoots at the end of the 2002 winter bloom period (27 Feb.).

Stage of bud development at the time of treatment. To determine the stage of inflorescence bud development on each defoliation date, three apical buds from the winter or summer vegetative shoot flushes were collected. Buds were immediately fixed in 5 formalin: 5 acetic acid: 90 ethanol, by volume, examined under a dissecting microscope (Stereomaster FW99–25–1217, Fisher Scientific, Pittsburgh) and graded according to the visual scale designed by Salazar-García et al. (1998).

Accumulation of chilling. Air temperature was recorded every hour at each avocado orchard with a battery-operated HOBO H8 (Onset Computer, Bourne, Mass.). Chilling days accumulated for each treatment date were calculated using daily occurrence of temperatures equal to or lower than 15, 16, 17, 18, 19, and 20 °C. Zero time was the date on which shoot elongation was initiated for the winter (10 Feb.) or summer (30 July) vegetative shoot flushes.

Shoot defoliation and girdling. During the second year of this study, defoliation was combined with girdling to strengthen the effect of treatments and to confirm the results of year 1. A second set of 10 trees was selected in the Alberto orchard using the same criteria. Ten shoots of the winter and 10 shoots of the summer vegetative shoot flushes were tagged and numbered on 10 Feb. and 30 July 2002 respectively. Shoot defoliation and girdling was performed at biweekly intervals from 1 Sept. 2002 through 15 Jan. 2003. To avoid healing, girdling consisted of the removal of a 2-cm-wide strip of bark at the base of the shoot using a budding knife. On each date, 10 shoots of the winter vegetative shoot flush and 10 shoots of the summer flush were randomly selected in each tree and treated. Control shoots were left untreated. The type of growth produced by apical buds was recorded for individual shoots of both vegetative flushes at the end of the 2003 winter bloom period (14 Feb.). Inflorescence bud development and calculation of chilling days were assessed as described earlier.

Table 1. Vegetative shoot flushes that developed in 1988 and their contribution to the 1999 winter bloom of 'Hass' avocado trees in the Alberto orchard (evaluation date, 10 Feb. 1999).

Vegetative shoot flushes (date shoot flush initiated)	Type of growth and % total shoots at winter bloom 1999[z] Floral shoot	Vegetative shoot	Inactive bud
Winter (10 Feb. 98)	76.5 a[y]	4.3 b	19.2 b
Summer 1 (25 July 98)	30.6 b	8.8 a	60.6 a
Summer 2 (2 Aug. 98)	36.4 b	3.9 b	59.7 a
Summer 3 (21 Aug. 98)	19.0 c	7.6 a	73.4 a

[z] Means were obtained from five 1-m-long branches/tree for 20 tree replications.

[y] Means within columns followed by different letters are significantly different by Duncan's multiple range test, $P = 0.05$.

Statistical analysis. Data from the type of growth produced by tagged shoots expressed as percentages were transformed by arcsine of the square root (Steel and Torrie, 1980) and then a normal analysis of variance was performed. Means comparison was performed using Duncan's multiple range test at $P = 0.05$.

Results

Effect of vegetative shoot age and crop load on production of inflorescences

Vegetative shoot flushes and their contribution to flowering. A portion of the vegetative shoots that were initiated in the 1998 winter flush (10 Feb.) gave rise to three flushes during the 1998 summer. The first flush was initiated on 25 July (summer 1) and originated on 7.7% of the winter vegetative shoots. The second flush (summer 2) started on 2 Aug. and had a similar intensity to the previous one (7.4%). A third vegetative flush (summer 3) was recorded on 21 Aug. and had the least intensity, because it only occurred on 1.8% of the winter shoots. These four vegetative shoot flushes for 1998 winter and summer contributed disproportionately to the 1999 winter bloom. In all cases, data on the type of growth produced corresponded to that produced by the apical bud on the tagged shoots' primary axis. Winter shoots contributed more to flowering, as 76.5% of them produced floral shoots in the 1999 bloom—a value directly proportional to the number of winter vegetative shoots that did not produce vegetative shoots during the summer (Table 1). The summer 1 and summer 2 shoots contributed a similar proportion of floral shoots (30.6–36.4%) to the 1999 winter bloom. The summer 3 flush had the lowest contribution to flowering, because only 19% of these shoots produced floral shoots (Table 1). Floral shoots observed were of the indeterminate type with no determinate floral shoots observed during the bloom period.

From all the vegetative shoot flushes that occurred in 1998, only a small proportion of them (3.9% to 8.8%) produced vegetative shoots in the 1999 winter bloom (Table 1). On the other hand, the proportion of shoots for which apical buds remained inactive was much higher for the three summer flushes (59.7% to 73.4%) than for the winter flush (19.2%).

Crop load and production of vegetative and floral shoots. Fruit mesocarp dry matter was determined by packinghouse people, and harvest was carried out when the dry matter content of fruit mesocarp was 22% to 23%. In the Alberto orchard, harvest was on 26 Oct. 2000, and the average yield ± SE for on- and off-crop trees was 170 ± 19 kg fruit/tree and 70 ± 10 kg fruit/tree respectively. The Bernabé orchard was harvested on 15 Oct. 2000 and yield was 95 ± 6 kg fruit/tree and 34 ± 4 kg fruit/tree for on- and off-crop trees respectively.

Tagged branches of both orchards showed two major vegetative shoot flushes: the winter flush, which started in Feb., was the more intense with 11.5 to 31.5 shoots produced per tagged branch. The summer flush was of lower intensity (1.4–4.3 shoots/tagged branch) and was composed of several small flushes that were initiated in July through Aug. (Table 2).

Tree crop load did not affect the proportion of winter or summer shoots that produced floral or vegetative shoots at the end of the 2001 winter bloom period (Table 2). Moreover, irrespective of tree crop load and shoot age, a greater proportion of floral than vegetative shoots developed. The proportion of floral shoots produced by winter and summer shoots ranged from 66% to 85% and 56% to 94% respectively (Table 2). The proportion of shoots with inactive apical buds was very low (≤1.2%).

Taking into account the sum of winter and summer flush shoots present on labeled branches, it was observed that, independent of orchard and tree crop load, there was always a higher proportion of floral shoots produced by winter flush shoots compared with the summer ones (Table 3). The proportion of floral shoots produced by winter flush shoots in the Alberto orchard was three- to fivefold greater than that of summer shoots. This proportion increased to 8- to 29-fold in the Bernabé orchard.

Effect of shoot age on ICF of apical buds

Effect of the date of defoliation or defoliation and girdling on the type of growth produced by winter and summer flush shoots. The type of growth produced by apical buds from both winter and summer flush shoots was affected by the date of treatment in both years of the study. Winter and summer flush shoots treated during September never produced floral shoots, and, in fact, 50% to 87.5% of them only produced vegetative shoot growth (Table 4).

Production of floral shoots by winter and summer flush shoots that received defoliation or defoliation and girdling was first observed

Table 2. Effect of tree crop load on the type of growth produced by apical buds of 2000 winter and summer slush shoots of 'Hass' avocado (evaluation date, 18 Feb. 2001).

Orchard, vegetative shoot flush, and tree crop load	Shoots per branch[y]	Type of growth and % total tagged shoots at winter bloom 2001[z] Floral shoot	Vegetative shoot	Inactive bud
Alberto orchard (900 m asl)				
Winter (Feb. 2000)				
On crop	11.6	84.8 a[x]	14.9 a	0.3 a
Off crop	11.5	79.4 a	19.4 a	1.2 a
Summer (July to Aug. 2000)				
On crop	2.7	60.9 a	39.1 a	0 a
Off crop	4.3	56.8 a	43.2 a	0 a
Bernabé orchard (1125 m asl)				
Winter (Feb. 2000)				
On crop	31.5	66.1 a	33.0 a	0.9 a
Off crop	24.7	80.8 a	18.5 a	0.7 a
Summer (July to Aug. 2000)				
On crop	1.4	65.8 a	34.0 a	0.2 a
Off crop	2.4	94.3 a	5.7 a	0.0 a

[z] Percentage of the number of shoots per branch. Means were obtained from four 1-m-long branches/tree for 10 tree replications for each crop load.

[y] Average number of vegetative shoots tagged per branch.

[x] For each type of shoot, means within columns followed by different letters are significantly different by Duncan's multiple range test, $P = 0.05$.

Table 3. Effect of shoot age (winter or summer flush) on the type of growth produced by on- and off-crop trees on the 2001 winter bloom of 'Hass' avocado (evaluation date, 18 Feb. 2001).

Orchard, tree crop load, and vegetative shoot flush	Shoots per branch[y]	Type of growth and % total tagged shoots at bloom 2001[z]		
		Floral shoot	Vegetative shoot	Inactive bud
Alberto orchard (900 m asl)				
On crop	14.3			
Winter (Feb. 2000)		68.5 a[x]	11.3 a	0.2 a
Summer (July to Aug. 2000)		12.2 b	7.8 a	0.0 a
Off crop	15.8			
Winter (Feb. 2000)		58.3 a	12.1 a	0.8 a
Summer (July to Aug. 2000)		17.0 b	11.8 a	0.0 b
Bernabé orchard (1125 m asl)				
On crop	32.9			
Winter (Feb. 2000)		63.7 a	31.2 a	0.9 a
Summer (July to Aug. 2000)		2.2 b	2.0 b	0.0 b
Off crop	27.1			
Winter (Feb. 2000)		72.9 a	17.1 a	0.7 a
Summer (July to Aug. 2000)		8.7 b	0.6 b	0.0 b

[z] Percentage of the total number of shoots per branch. Means were obtained from four 1-m-long branches/tree for 10 tree replications for each fruit load.

[y] Pool (average) of winter and summer vegetative shoots tagged per branch, which were considered as 100%.

[x] For each tree crop load, means within columns followed by different letters are significantly different by Duncan's multiple range test, $P = 0.05$.

Table 4. Type of growth produced by apical buds from winter and summer vegetative shoot flushes of 'Hass' avocado trees defoliated or defoliated and girdled at different dates. (Evaluations were done at full bloom on 25 Feb. 2002 and 2003).

Date of treatment	Vegetative shoot flush and type of growth produced (%)					
	Winter shoots			Summer shoots		
	Floral shoot	Veget. shoot	Inactive bud	Floral shoot	Veget. shoot	Inactive bud
	Shoot defoliation					
01 Sept. 2001	0 g[z]	66.7 a	33.3 b	0 e	66.7 c	33.3 b
15 Sept.	0 g	66.7 a	33.3 b	0 e	87.5 a	12.5 d
30 Sept.	0 g	50.0 b	50.0 a	0 e	57.2 e	42.8 a
15 Oct.	28.6 f	42.8 c	28.6 c	22.2 c	55.6 e	22.2 c
30 Oct.	37.5 d	37.5 d	25.0 c	25.0 c	62.5 d	12.5 d
15 Nov.	33.3 e	50.0 b	16.7 d	12.5 d	75.0 b	12.5 d
30 Nov.	37.5 d	50.0 b	12.5 ef	12.5 d	62.5 d	25.0 c
15 Dec.	33.3 e	50.0 b	16.7 d	50.0 a	50.0 f	0 e
30 Dec.	44.4 b	44.4 c	11.2 ef	44.4 b	55.6 e	0 e
15 Jan. 2002	42.9 c	42.9 c	14.2 de	50.0 a	25.0 h	25.0 c
Control	53.7 a	37.4 d	8.9 f	48.6 a	40.3 g	11.1 d
	Shoot defoliation and girdling					
01 Sept. 2002	0 h[y]	75.0 b	25.0 c	0 f	83.3 a	16.7 d
15 Sept.	0 h	83.3 a	16.7 d	0 f	83.3 a	16.7 d
30 Sept.	0 h	50.0 c	50.0 a	0 f	75.0 b	25.0 b
15 Oct.	33.3 g	33.4 h	33.3 b	40.0 d	40.0 de	20.0 c
30 Oct.	44.4 f	44.4 d	11.2 g	50.0 b	50.0 c	0 g
15 Nov.	60.0 b	40.0 f	0 i	37.5 e	37.5 e	25.0 b
30 Nov.	57.2 c	42.8 e	0 i	42.8 c	28.6 g	28.6 a
15 Dec.	50.0 e	50.0 c	0 i	50.0 b	33.3 f	16.7 d
30 Dec.	62.5 a	25.0 j	12.5 f	57.2 a	42.8 d	0 g
15 Jan. 2003	57.2 c	28.5 i	14.3 e	42.8 c	42.8 d	14.4 e
Control	55.9 d	35.6 g	8.5 h	50.0 b	41.5 d	8.5 f

[z] For each shoot treatment, means within columns followed by different letters are significantly different by Duncan's multiple range test, $P = 0.05$.

on shoots treated on 15 Oct. During the first year, the proportion of shoots that produced floral shoots when treated on this date was 28.6% and 22.2% for winter and summer vegetative shoot flushes respectively (Table 4). For the second year, these values were 33.3% and 40% respectively. Production of floral shoots by untreated (control) winter and summer flush shoots varied from 48.6% to 55.9% for the 2 years evaluated. The type of growth produced by shoots treated after 15 Oct. for both years was variable. However, there was always a proportion of winter and summer flush shoots that produced floral shoots ($\geq$12.5%) during both years of the study (Table 4). At the time of bloom, production of vegetative shoots by control shoots of both ages ranged from 35.6% to 41.5%. In general, the proportion of shoots that remained inactive was much higher for treated shoots than for the control ones (Table 4).

Stage of bud development at the time of ICF. At the time that shoots of the winter (10 Feb.) and summer (30 July) vegetative flushes were initiated and tagged during both years of the study, development of apical buds was at S-1 (data not shown). According to the scale developed by Salazar-García et al. (1998), this developmental stage corresponded to a closed, pointed bud within the two most distal nonexpanded leaves of the vegetative shoot. By the first treatment date of both years (1 Sept.) average bud development (n = 3) was 1.6 to 2.6 for winter and summer shoots (Table 5). Winter apical buds showed a slightly faster rate of development compared with the ones on the summer flush shoots. However, there was no difference in the date of anthesis (25 Feb.) in both years of the study (data not shown).

Based on the response of winter and summer flush shoots to the treatments applied, 15 Oct. was identified as the point in time when most apical buds of the 'Hass' avocado became ICF. By that date, average bud development (n = 3) on winter shoots was 3.3 (two buds in S-3 and one in S-4) in both years studied (Table 5). In the case of summer shoots, apical buds were graded as 2.6 (two buds in S-3 and one in S-2) for both years. According to Salazar-García et al. (1998), buds at S-2 are closed and pointed within the two most distal mature expanded leaves of the shoot. Anatomically, these buds have a flat primary axis meristem with separated bracts and one to three secondary axis meristems in the axils of bracts. Buds at S-3 correspond to closed, pointed buds with partial senescence of bud scales. Microscopically, they present a convex primary axis meristem and four secondary axis meristems. Further stages (up to S-11, anthesis) include the production and elongation of additional secondary and tertiary axes of the floral shoot and development of flower parts.

Commitment to flowering and chilling. Temperatures $\geq$20 °C are known to prevent flowering in avocados and were not considered as effective chilling. Chilling days for temperatures $\leq$19 °C were accumulated from 30 July through 15 Oct. both years (when more than 60% of apical buds from winter and summer shoot flushes were ICF; Table 5). The chilling requirement for buds to reach ICF was unaffected by shoot age, and variation between years was restricted to the 2-week sampling interval. For year 1, winter and summer shoots reached when they had accumulated 31 chilling days with threshold temperatures $\leq$19 °C (Table 5). Using the same temperature threshold for year 2, chilling accumulated for winter and summer shoots was 24 chilling days. Winter flush shoots started to grow on 10 Feb. of each year, when low temperatures were still present and thus they had accumulated a significant amount of chilling by the time treatments were first applied (1 Sept.). However, low temperatures recorded from 10 Feb. to 30 July did not contribute to meeting the chilling requirement.

Discussion

In Nayarit, the 'Hass' avocado produced four flushes of vegetative shoot growth. The first vegetative flush occurred in the winter,

Table 5. Apical bud development and chilling days accumulated at different temperature thresholds from 30 July through 15 Oct., the date when winter and summer shoots of 'Hass' avocado reached irreversible commitment to flowering.

Date of treatment	Stage of apical bud development^z		Chilling days accumulated per temp. threshold (°C)					
	Winter shoots	Summer shoots	≤15	≤16	≤17	≤18	≤19	≤20
Shoot defoliation								
01 Sept. 2001	2.6	1.6	0	0	0	4	11	24
15 Sept.	2.6	2.0	0	0	0	4	15	33
30 Sept.	2.6	2.3	0	0	0	5	20	45
15 Oct.	3.3	2.6	2	3	6	15	31	58
30 Oct.	3.6	3.0	8	9	16	27	44	73
Shoot defoliation and girdling								
01 Sept. 2002	1.7	1.7	0	0	0	5	14	25
15 Sept.	2.4	1.7	0	0	0	5	14	29
30 Sept.	2.4	2.0	0	0	0	7	17	35
15 Oct.	3.3	2.6	0	0	0	7	24	48
30 Oct.	3.7	3.0	0	0	0	16	36	63

^{z}According to the visual scale developed by Salazar-García et al. (1998).

during the bloom period, and contributed 76.5% of the floral shoots produced in the next year's bloom. Three more vegetative shoot flushes of low magnitude took place later during the summer, and no fall vegetative flush was observed. Production of floral shoots by the different vegetative shoot flushes decreased as they grew closer to the time of bloom (January–February). Thus, only 19% of the summer 3 (late August) vegetative flush shoots resulted in floral shoots. Similar results were obtained in southern California, where the majority of floral shoots comprising the spring bloom of the 'Hass' avocado was produced by old shoots initiated during the previous year's summer flush of vegetative shoots (Salazar-García et al., 1998).

Apical buds of 'Hass' avocado growing in the subtropical climate of California did not require a clear period of dormancy before initiation of reproductive growth (Salazar-García et al., 1998). Although both mature (spring or summer vegetative flush) and young (fall flush) shoots were capable of flowering, they differed in the total number of floral shoots produced. Fall flush vegetative shoots typically produced floral shoots at the shoot apex, in contrast to mature spring or summer shoots, which produced lateral floral shoots (borne in axillary buds) in addition to the apical floral shoot. A similar situation was observed in the current study for winter (oldest) and summer (youngest) flush shoots, although no data were collected.

A heavy "on" crop can suppress the number and intensity of vegetative flushes, as well as reduce bloom intensity (Lahav and Kalmar, 1977; Salazar-García et al., 1998). Preliminary results suggest that the heavy "on" crop inhibits the development of the summer vegetative shoot flush of 'Hass' avocado trees in California, and thus indirectly causes reduced return bloom because of the lack of "wood" on which to bear the floral shoots the following year (Paz-Vega, 1997). A study in California with on- (66 kg/tree) and off-crop (18 kg/tree) 'Hass' avocado trees showed that only 13% of the total shoots produced floral shoots when trees were carrying the "on" crop, but 46% of the total shoots produced floral shoots the following off-crop year (Salazar-García et al., 1998). In California, bloom occurs from mid March to mid May and mature fruit are typically still on the tree (Robinson et al., 2002).

Our results provided evidence that tree crop load or differences in altitude between the two 'Hass' avocado orchards (900 m asl vs. 1125 m asl) included in this research, which explored the most common altitude variation for commercial orchards, did not affect the number of vegetative flushes produced during the year nor their intensity of flowering. In addition, it was documented that winter bloom was composed mainly of floral shoots borne on the previous year's winter shoots rather than on summer flush shoots. Regardless of tree fruit load, production of floral shoots varied from 56% to 94%. However, different to many 'Hass' avocado-producing areas, in Nayarit, harvest is usually done 2 to 4 months before the full bloom period. Late harvest has been reported to reduce bloom intensity of the 'Hass' avocado in Australia (Whiley et al., 1996).

Production of inflorescences by apical buds despite having received defoliation or defoliation and girdling was considered evidence of ICF. In this study, girdling was found not to be essential to modify shoot flowering response; defoliation alone was sufficient. However, a trend for a more profuse bloom was observed when shoots were girdled and defoliated (Table 4). Reports on mango (Nunez-Elisea and Davenport, 1992; Reece et al., 1946, 1949) also have shown that shoot defoliation interrupted the process of floral shoot development, presumably only when floral buds were not ICF.

Most work done on girdling in avocados has been done on mature woody branches (not shoots) to elucidate the mode of action of girdling in augmenting bloom and fruitfulness of avocado (Lahav et al., 1971–72; Tomer, 1977), therefore both defoliation and stage of bud development at the time of girdling was not considered. Our working hypothesis was the use of timed shoot defoliation to prevent the onset of the flowering process in avocado.

Winter flush shoots were more than 5 calendar months older than summer flush shoots. However, by 15 Oct., shoots of both ages had attained a similar reproductive competence because they were both ICF and had a similar date of anthesis. A similar behavior was observed for summer and fall shoots of the 'Hass' avocado in Australia (Thorp et al., 1993). According to the macro- and microscopic stages of avocado bud and inflorescence development proposed by Salazar-García et al. (1998), S-3 was the stage at which apical buds were fully committed to reproductive growth. This developmental stage was also demonstrated to be related to the transition from vegetative to reproductive development of apical buds of summer shoots of 'Hass' avocado trees in California (Salazar-García and Lovatt, 1998; Salazar-García et al., 1998), although no information is available for fall flush shoots.

In the current research, buds of mature 'Hass' avocado trees that were ICF showed a more advanced stage of development than previously reported by Salazar-García et al. (1999) for young 'Hass' avocado trees subjected to floral-inductive low-temperature treatments (10 °C/7 °C day/night with a 10-h photoperiod for 1 to 4 weeks to promote flowering followed by warm temperature, 25 °C/20 °C day/night, at the same photoperiod in growth chambers to stop the process). This difference can be attributed to a longer exposure of shoots to inconsistent floral-promoting conditions in the field, and consequently more time for bud growth and development to occur. Additionally, root activity would not be entirely suppressed under field conditions, in contrast to the controlled environmental conditions imposed earlier.

In this study, the threshold temperatures ≤17 °C or ≤18 °C were not related to commitment to flowering because their accumulation was not significant before buds reached that developmental stage. Temperatures at 20 °C also were discarded because they have been shown not to promote flowering (Nevin and Lovatt, 1989; Salazar-García et al., 1999). Based on this, 24 to 31 chilling days at ≤19 °C were required for apical buds on winter and summer flush shoots to become ICF. Using the 2-year average of 27.5 chilling days, it can be deduced that there were at least 28 d with temperatures ≤19 °C before buds were ICF. This amount of chilling was equivalent to the 4-week low-temperature treatment previously reported to cause flowering of the 'Hass' avocado under controlled environmental conditions in a growth chamber (Nevin and Lovatt, 1989; Salazar-García et al., 1999).

The current research results revealed three physiological advantages derived from the phenology of the 'Hass' avocado growing in a subhumid (summer rain) semiwarm and subtropical climate of Nayarit. The first advantage was that the primary source of floral shoots at bloom was the vegetative shoots that developed from the indeterminate floral shoots of the previous year's bloom. Because 66.1% to 84.8% of these shoots produced inflorescences the following year, floral intensity can be anticipated to remain reasonably stable from year to year. The second advantage was derived from the high percentage of vegetative shoots from the several summer flushes that produced inflorescences (56.8% to 94.3%). Although fewer vegetative shoots were produced during the summer flushes than during the single winter vegetative flush, the contributions of the summer flush shoots to flowering further stabilizes floral intensity of the 'Hass' avocado from year to year and, hence, yield. These flushes also renewed the foliage and provided a pool of temporally inactive buds with the potential to develop into either floral or vegetative shoots in the subsequent year. The third advantage was that tree fruit load had no effect on either vegetative or floral shoot development. It is likely that these three factors interact to maintain the good balance between vegetative and reproductive growth that provides for high yields and new "wood" for return bloom and cropping of the 'Hass' avocado in Nayarit.

The results of this research provide new insight into the relative importance of each vegetative flush to flowering of the 'Hass' avocado in Nayarit. Because in two separate orchards with distinctly environmental conditions, crop load was documented to have no effect on either the number or intensity of vegetative shoot flushes or the relative number of vegetative and reproductive shoots produced at bloom, strategies to alter the time of harvest should be minimally compromised by this factor. An understanding of the relative importance of each vegetative flush to flowering is also basic to decisions related to pruning, pest management, and use of growth-promoting and growth-inhibiting plant bioregulators.

Our results indicate that even in warm environments, cool temperature was an important factor that stimulated the transition of avocado buds to the reproductive state by repressing vegetative growth. Cumulative evidence shows that in avocado, buds that are ICF are at the same developmental stage, irrespective of variation in latitude and climatic conditions.

Literature Cited

Bernier, G. 1988. The control of floral evocation and morphogenesis. Ann. Rev. Plant Physiol. Plant Mol. Biol. 39:175–219.

Bernier, G., J.-M. Kinet, and R.M. Sachs. 1981. The physiology of flowering, p. 232–257, Vol. 2. CRC Press, Boca Raton, Fla.

Buttrose, M.S. and D.M. Alexander. 1978. Promotion of floral initiation in 'Fuerte' avocado by low temperature and short daylength. Sci. Hort. 8:213–217.

Coit, J.E. 1920–21. The effect of girdling the avocado. Calif. Avocado Soc. Yrbk. 7:69–71.

CONAPA. 2006. Resultados del padrón de productores de aguacate. Consejo Nacional de Productores de Aguacate, A.C. Uruapan, Michoacán, México. http://www.conapa-ac.com/. Accessed 14 July 2006.

Davie, S.J. and P.J.C. Stassen. 1997. Avocado tree girdling and fruit thinning. South Afr. Avocado Growers' Assn. Yrbk. 20:55–58.

Lahav, E., B. Gefen, and D. Zamet. 1971–72. The effect of girdling on fruit quality, phenology and mineral analysis of the avocado tree. Calif. Avocado Soc. Yrbk. 55:162–169.

Lahav, E. and D. Kalmar. 1977. Water requirement of avocado in Israel. II. Influence on yield, fruit growth and oil content. Aust. J. Agr. Res. 28:869–877.

Nevin, J.M. and C.J. Lovatt. 1989. Changes in starch and ammonia metabolism during low temperature stress-induced flowering in 'Hass' avocado: A preliminary report. S. Afr. Avocado Growers' Assn. Yrbk. 12:21–25.

Nunez-Elisea, R. and T.L. Davenport. 1992. Requirement for mature leaves during floral induction and floral transition in developing shoots of mango. Acta Hort. 296:33–37.

Nunez-Elisea, R., T.L. Davenport, and M.L. Caldeira. 1996. Control of bud morphogenesis in mango (*Mangifera indica* L.) by girdling, defoliation and temperature modification. J. Hort. Sci. 71:25–39.

Paz-Vega, S. 1997. Alternate bearing in the avocado. Calif. Avocado Soc. Yrbk. 81:117–148.

Reece, P.C. 1942. Differentiation of avocado blossom buds in Florida. Bot. Gaz. 104:458–476.

Reece, P.C., J.R. Furr, and W.C. Cooper. 1946. The inhibiting effect of the terminal bud on flower formation in the axillary buds of the 'Haden' mango. Amer. J. Bot. 33:209–210.

Reece, P.C., J.R. Furr, and W.C. Cooper. 1949. Further studies of floral induction in the 'Haden' mango (*Mangifera indica* L.). Amer. J. Bot. 36:734–740.

Robinson, P.W., M.V. Mickelbart, X. Liu, C. Adams, G. Whitney, and M.L. Arpaia. 2002. Development of a phenological model of avocado tree growth in California. Acta Hort. 575:859–864.

Salazar-García, S. 2000. Fisiología reproductiva del aguacate, p. 57–83. In: D. Téliz–Ortíz (coord.). El Aguacate y su Manejo Integrado. Ediciones Mundi–Prensa, México.

Salazar-García, S., E.M. Lord, and C.J. Lovatt. 1998. Inflorescence and flower development of the 'Hass' avocado (*Persea americana* Mill.) during "on" and "off" crop years. J. Amer. Soc. Hort. Sci. 123:537–544.

Salazar-García, S., E.M. Lord, and C.J. Lovatt. 1999. Inflorescence development of the 'Hass' avocado: Commitment to flowering. J. Amer. Soc. Hort. Sci. 124:478–482.

Salazar-García, S. and C.J. Lovatt. 1998. GA_3 application alters flowering phenology of the 'Hass' avocado. J. Amer. Soc. Hort. Sci. 123:791–797.

Salazar-García, S. and C.J. Lovatt. 1999. Winter trunk injections of gibberellic $acid_3$ altered the fate of 'Hass' avocado buds: Effects on inflorescence type, number and rate of development. J. Hort. Sci. Biotechnol. 74:69–73.

Schroeder, C.A. 1944. The avocado inflorescence. Calif. Avocado Soc. Yrbk. 28:39–40.

Steel, R.G.D. and J.H. Torrie. 1980. Principles and procedures of statistics: A biometrical approach. 2nd ed. McGraw-Hill, Tokyo.

Thorp, T.G., D. Aspinall, and M. Sedgley. 1993. Influence of shoot age on floral development and early fruit set in avocado (*Persea americana* Mill.) cv. 'Hass'. J. Hort. Sci. 68: 645–651.

Tomer, E. 1977. The effect of girdling on flowering, fruit setting and abscission in avocado trees. The Hebrew Univ. of Jerusalem, Israel, unpublished PhD thesis.

Whiley, A.W., T.S. Rasmussen, J.B. Saranah, and B.N. Wolstenholme. 1996. Delayed harvest effects on yield, fruit size and starch cycling in avocado (*Persea americana* Mill.) in subtropical environments. II. The late-maturing cv. Hass. Sci. Hort. 66:35–49.