

## Winter trunk injections of gibberellic acid altered the fate of 'Hass' avocado buds: Effects on inflorescence type, number and rate of development

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### SUMMARY

The objective of this study was to quantify the effects of high GA<sub>3</sub> concentrations applied through trunk injection on the developmental fate of buds of young (glasshouse study) and mature (field study) 'Hass' avocado (*Persea americana* Mill.) trees. The goal of this research was to determine whether a high dose of GA<sub>3</sub> could be used to promote vegetative growth, reduce flowering intensity and fruit set and to even out alternate bearing. In both studies, GA<sub>3</sub> injections were made at bud swell, prior to bud break. For young trees, injections of 25 or 50 mg GA<sub>3</sub> per tree caused precocious inflorescence development and anthesis three weeks earlier than in control trees. GA<sub>3</sub> injections did not affect the number of vegetative shoots produced but increased the number of indeterminate inflorescences, at the expense of determinate ones. Increased bud abscission resulting from the GA<sub>3</sub> treatments reduced total inflorescence number. Mature trees in a commercial orchard injected with GA<sub>3</sub> at 1.0 or 2.5 g per tree on 5 January (before bud break) started anthesis 3 and 23 d later than control trees, respectively. No determinate inflorescences were produced in any treatment. GA<sub>3</sub> injections increased the proportion of inactive (quiescent) buds, resulting in fewer indeterminate inflorescences, but did not affect vegetative shoot number. The results of this research are the first to demonstrate that a high concentration of GA<sub>3</sub> trunk-injected in the winter prior to bud break can, through increased bud abscission or inactivity, reduce inflorescence number, with no effect on vegetative shoot number. Yield reduction would be anticipated in response to trunk injection of 1.0 g GA<sub>3</sub> per tree, because this treatment reduced both inflorescence number and fruit set/inflorescence. This, or a lower concentration, may prove useful in evening-out alternate bearing.

The ability to manipulate flowering has been a goal of both researchers and growers. For the 'Hass' avocado, it is desirable to delay anthesis so that pollination and fruit set occur when climatic conditions are more favourable, to shorten the normally protracted flowering period so that fruit set would be completed before temperatures become too high, and to produce a sufficient number of inflorescences to set a good crop annually without causing alternate bearing. Inhibition of flowering and delayed anthesis have been reported consistently as responses of subtropical fruit trees, such as citrus (Guardiola *et al.*, 1982; Lord and Eckard, 1987) and mango (Kachru *et al.*, 1972; Nunez-Elisea and Davenport, 1991), to prebloom applications of GA<sub>3</sub>. For citrus, potential flowering buds are redirected to vegetative shoots when GA<sub>3</sub> is applied prior to bud break (Guardiola *et al.*, 1982; Lord and Eckard, 1987). In contrast, GA<sub>3</sub> applied when flowers were already differentiated caused precocious flower development of strawberry (Porlingis and Boynton, 1961) and coffee (Schuch *et al.*, 1990). This resulted in early and synchronized anthesis.

Recent results of a branch study conducted with mature 'Hass' avocado trees suggested that a high concentration of GA<sub>3</sub> applied prior to bud break might shift significantly the developmental fate of avocado

buds. A winter foliar application of 1 g GA<sub>3</sub> l<sup>-1</sup> decreased by 50% the number of inflorescences that developed and concomitantly increased by 50% the number of vegetative shoots produced (Salazar-García and Lovatt, 1998). In an earlier experiment, a delay in avocado flowering was achieved by GA<sub>3</sub> trunk injection (Dr Jonathan Cutting, pers. comm.).

The production of alternating heavy 'on' versus light 'off' 'Hass' avocado crops is a problem of economic significance to the global avocado industry. Alternate bearing results from the fact that spring flush shoots which set fruit do not produce a vegetative flush in the summer or autumn (Salazar-García *et al.*, 1998). Thus, when trees are carrying an 'on' crop, production of new shoots, which would bear inflorescences the following year, decreases significantly. This results in the 'off' crop year, with its concomitant increase in both summer and autumn vegetative shoot number, thus perpetuating the cycle. A strategy to produce uniform and sufficient flowering annually to even out alternate bearing would be of practical importance to the avocado industry.

Thus, the objective of this research was to quantify the effects of high concentrations of GA<sub>3</sub>, applied in the winter prior to bud break, on the developmental fate of 'Hass' avocado buds. Applications were made by trunk injection, rather than by spraying as winter rain would be likely to compromise foliar uptake and movement of spray equipment through an orchard at this time of the year. The possibility that trunk-injected GA<sub>3</sub> might evoke a uniform tree response was also evaluated.

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FIG. 1

Effect of GA<sub>3</sub> trunk injections to young 'Hass' avocado trees (glasshouse study) on inflorescence phenology. (A), Swollen buds at time of treatment. (B), Inflorescence development of control trees 70 d after treatment. (C), Inflorescence development 35 d after treatment with 25 mg GA<sub>3</sub>, per tree. Note that tertiary axes and immature flowers are still covered by a large bracteole. (D), Inflorescence size (at flower anthesis) and vegetative shoot development at the inflorescence apex of untreated control trees (left) and trees treated with GA<sub>3</sub> at 25 (centre) and 50 mg per tree (right). Abbreviations: b = bracteole. Bars = 20 mm (A-C) and 10 cm (D).

## MATERIALS AND METHODS

### Glasshouse study (young trees)

Twenty-one 'Hass' avocado trees on Duke 7 clonal rootstock, 33 months after grafting, were grown in 15 l of University of California Soil Mix III (Baker, 1957), amended with KNO<sub>3</sub>, K<sub>2</sub>SO<sub>4</sub>, dolomite limestone and oyster shell lime, in plastic containers and watered every other day with half-strength Hoagland's nutrient solution (Hoagland and Arnon, 1950). To obtain shoots of uniform age, all trees were pruned in March, nine months before the beginning of the study in December. From March through September, temperatures in the glasshouse were maintained between a maximum of 29°C and minimum of 18°C. Starting in October, and continuing until the end of the experiment in April,

temperatures in the glasshouse were maintained between a maximum of 25°C and minimum of 10°C. This temperature regime promotes inflorescence initiation and inflorescence development (Salazar-García *et al.*, 1998). At bud swell (17 December) (Figure 1A), prior to bud break, each tree was injected just above the bud union with 25 or 50 mg GA<sub>3</sub> using 1 ml syringes, each containing 0.5 ml of a 95% ethanolic solution of Proggibb (20% soluble powder, Abbott Laboratories, North Chicago, IL) adjusted to pH 5.5. Control trees were injected with ethanol only. Ten, five month old shoots with 12 ± 2 fully expanded leaves were selected for data collection per tree. The number of inflorescences (including determinate and indeterminate), vegetative shoots, and inactive (quiescent) and abscised buds was quantified for each shoot at the end of the study. The rate of inflorescence development was determined by quantifying the number of days from 17 December that each inflorescence bud required to reach the cauliflower stage of inflorescence development (Stage 8 in the scale developed by Salazar-García *et al.* (1998), which is characterized by elongation of secondary axes, with tertiary axes still covered by subtending bracts, and small visible flowers) and that the first flower buds in each inflorescence required to reach anthesis.

### Field study (mature trees)

Thirty, 12 year old 'Hass' avocado trees on a Mexican clonal rootstock in a commercial orchard in Corona, California, were used in this study. To test the effectiveness of high GA<sub>3</sub> concentrations to reduce flowering intensity, trees bearing no fruit were selected for the experiment to ensure an intense bloom. At bud swell (5 January), prior to bud break, each tree was injected just above the bud union with 1.0 or 2.5 g GA<sub>3</sub> using eight 30 ml syringes each of which contained a 25 ml aliquot (total 200 ml per tree) of aqueous Proggibb (20% soluble powder) solution adjusted to pH 5.5. Control trees were injected with distilled water only. For most trees, GA<sub>3</sub> uptake from the pressurized syringes was completed within 10 min to 3 h. Syringes that were not empty within this period were pressurized again and left overnight. Five 1 m long branches, 5–6 cm in diameter, were tagged at a height of 2.5 m from the ground around the canopy of each tree. For each branch, the number of inflorescences (including determinate and indeterminate), vegetative shoots, and inactive or abscised buds was recorded at the end of the flowering period. Time to anthesis for each tree was defined as the number of days after treatment required to produce 50 inflorescences with flowers at anthesis per tree. Fruit set on each branch was quantified in August after the 'June drop' period.

TABLE I  
Apical growth produced by shoots of young 'Hass' avocado trees in response to a winter prebud break trunk injection of GA<sub>3</sub> under glasshouse conditions

Treatment (mg GA <sub>3</sub> /tree)	Type of growth (% of total buds ± SE) <sup>1</sup>			
	Determinate inflorescence	Indeterminate inflorescence	Vegetative shoot	Abscised bud
0 (control)	90.0 ± 8.4 a <sup>2</sup>	8.6 ± 4.6 b	0.0 ± 0.0 a	1.4 ± 0.4 b
25	27.1 ± 8.1 b	52.9 ± 8.6 a	2.9 ± 1.8 a	17.1 ± 3.6 a
50	20.0 ± 12.9 b	54.3 ± 13.9 a	2.9 ± 1.8 a	22.8 ± 7.1 a

<sup>1</sup>Total number of buds averaged 70 per treatment.

<sup>2</sup>Mean separation in columns by Duncan's multiple range test, *P* = 0.05.

TABLE II

Development of inflorescences from apical buds of young 'Hass' avocado trees in response to a winter prebud break trunk injection of GA<sub>3</sub> under glasshouse conditions

Treatment (mg GA <sub>3</sub> /tree)	Average number of days ± SE from treatment to:		
	Cauliflower stage (C)	Anthesis (A)	Days from C to A
0 (control)	64.9 ± 1.6 a <sup>1</sup>	84.7 ± 1.0 a	19.7 ± 1.2 b
25	34.3 ± 2.2 b	65.8 ± 2.2 b	31.5 ± 1.3 a
50	31.5 ± 0.9 b	61.9 ± 0.8 b	30.3 ± 0.8 a

<sup>1</sup>Mean separation in columns by Duncan's multiple range test,  $P = 0.05$ .

### Experimental design and statistical analyses

A completely randomized design with seven and ten single-tree replicates was used in the glasshouse and field studies, respectively. Before analysis of variance, data expressed as percentages were transformed by arcsin of the square root (Steel and Torrie, 1980). Mean comparison was done using Duncan's multiple range test at  $P = 0.05$ .

## RESULTS

### Glasshouse study (young trees)

Determinate inflorescences were the most abundant type produced by control trees; trunk injections of GA<sub>3</sub> significantly increased the production of indeterminate inflorescences at the expense of determinate inflorescences (Table I). Inflorescences from both control and GA<sub>3</sub>-treated trees had ten secondary axes, the normal number for a fully formed inflorescence (Salazar-García *et al.*, 1998). However, GA<sub>3</sub>-treated trees produced inflorescences with longer secondary axes than control trees. Secondary axes of control inflorescences ranged from 5 to 20 cm in length, whereas those of GA<sub>3</sub>-treated trees were 30–50 cm long (Figure 1D). Growth of the vegetative shoot at the apex of indeterminate inflorescences of GA<sub>3</sub>-treated trees was precocious and vigorous relative to that of control trees (Figure 1D). The number of vegetative shoots produced was not affected significantly by GA<sub>3</sub> treatment (Table I). GA<sub>3</sub> injections significantly increased bud abscission, which greatly reduced total inflorescence number (Table I). No inactive buds were observed.

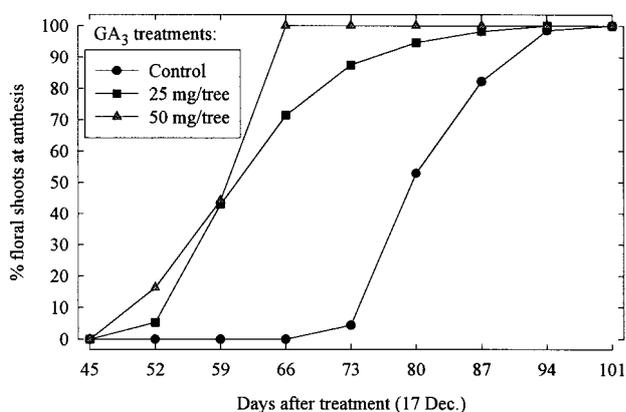


FIG. 2

Effect of GA<sub>3</sub> trunk injections to young 'Hass' avocado trees (glasshouse study) on the number of days after treatment that inflorescence buds required to bear flowers at anthesis. Each data point is an average of 9.9, 8.0, and 7.4 floral shoots per tree for control trees and trees injected with GA<sub>3</sub> at 25 or 50 mg per tree, respectively.

The average number of days after treatment required for inflorescence buds to reach the cauliflower stage, or for the first flower buds of an inflorescence to reach anthesis was significantly less for GA<sub>3</sub>-treated trees than for control trees (Table II; Figure 1B and 1C). Whereas the total time required for the first flower bud to reach anthesis was shorter for GA<sub>3</sub>-treated trees, the time from the cauliflower stage to flower anthesis was approximately 10 d longer than for the control trees. The first flowers to reach anthesis were located at the base of the inflorescence. The difference between the developmental stage of flowers at the base and at the apex of the inflorescence was greater for GA<sub>3</sub>-treated trees than for control trees. Anthesis was observed 52 d after GA<sub>3</sub> treatment, compared with 73 d for control trees (Figure 2). Trees injected with 50 mg GA<sub>3</sub> per tree had 100% inflorescences with flowers at anthesis 28 and 35 d in advance of trees treated with GA<sub>3</sub> at 25 mg per tree and control trees, respectively.

### Field study (mature trees)

Mature 'Hass' avocado trees were characterized by the production of exclusively indeterminate inflorescences (Table III). Large inflorescences with precocious vegetative shoot development at the inflorescence apex were produced in response to GA<sub>3</sub> injections (Figure 3). Only injections of GA<sub>3</sub> at 2.5 g per tree significantly reduced flowering intensity compared with that of control trees. The decrease in inflorescence number was associated with an increase in the proportion of inactive buds (Table III). No buds abscised. The number of vegetative shoots produced was not affected by GA<sub>3</sub> injections (Table III).

Inflorescence development was precocious only for trees injected with 1.0 g GA<sub>3</sub> per tree. Thirty-five days after treatment, eight-fold more inflorescences on these trees had reached the cauliflower stage than trees injected with 2.5 g GA<sub>3</sub> per tree or untreated control trees (Figure 4). The total population of inflorescences on these trees remained advanced in their development compared with trees injected with 2.5 g GA<sub>3</sub> per tree and untreated control trees until 56 d after treatment (Figure 4). Thirty-five days after treatment, 10% of the control trees and 10% of those injected with 1.0 g GA<sub>3</sub> per tree had 50 inflorescences with flowers at anthesis (Figure 5). Anthesis was delayed in trees injected with 2.5 g GA<sub>3</sub> (Figure 5). Even 56 d after treatment, none of these trees had attained 50 inflorescences with flowers at anthesis. However, 7 d later, 70% of the trees injected with 2.5 g GA<sub>3</sub> per tree had 50 inflorescences with flowers at anthesis. The delay in anthesis resulting from the highest GA<sub>3</sub> concentration synchronized anthesis with the shortest period of open-flowers.

TABLE III

Apical growth produced by shoots of mature 'Hass' avocado trees in response to a winter prebud break trunk injection of GA<sub>3</sub> under field conditions

Treatment (g GA <sub>3</sub> /tree)	Type of growth (% of total shoots ± SE) <sup>1</sup>			
	Determinate inflorescence	Indeterminate inflorescence	Vegetative shoot	Inactive bud
0 (control)	0.0 a <sup>2</sup>	66.6 ± 6.9 a	21.2 ± 5.5 a	12.2 ± 3.9 b
1.0	0.0 a	47.3 ± 7.9 ab	16.9 ± 4.5 a	35.8 ± 5.1 a
2.5	0.0 a	24.8 ± 5.8 b	28.2 ± 5.5 a	47.0 ± 5.7 a

<sup>1</sup>Average total number of shoots per tree ± SE was 86 ± 10, 75 ± 5, and 70 ± 5 for control, 1.0 and 2.5 g GA<sub>3</sub> per tree, respectively.<sup>2</sup>Mean separation in columns by Duncan's multiple range test, *P* = 0.05.

Fruit set was quantified on 23 August, after the normal period of fruit thinning due to 'June drop'. Mature 'Hass' avocado trees injected with GA<sub>3</sub> at 1.0 or 2.5 g per tree set significantly fewer fruit: compare 0.003 and 0.0008 fruit per inflorescence, respectively, to 0.128 fruit per inflorescence for untreated control trees.

## DISCUSSION

Buds of both young trees (glasshouse study) and mature trees (field study) were swollen, but bud break had not occurred, at the time of the trees were injected with high concentrations of GA<sub>3</sub>. At this stage of development the GA<sub>3</sub> treatments produced very similar responses in young and mature 'Hass' avocado trees despite the differences in environmental conditions during the course of the two experiments. According to the scale developed by Salazar-García *et al.* (1998), the buds in both studies were at Stage 5. By this stage of inflorescence bud development, all ten secondary axis inflorescence meristems have formed. The most basal two (oldest) secondary axes of the inflorescence have begun to elongate. The perianth has been initiated only for the terminal flower of the tertiary axis borne on these secondary axes. For both the young and mature trees, trunk injections of high concentrations of GA<sub>3</sub> increased the proportion of either abscised or inactive buds and decreased inflorescence number with no effect on vegetative shoot number. These results indicate that inflorescence buds were more sensitive to growth inhibition by high GA<sub>3</sub> concentrations than vegetative

shoot buds. In contrast, the results suggest that growth of vegetative shoot apices associated with indeterminate inflorescences were sensitive to high concentrations of GA<sub>3</sub> because the number of indeterminate inflorescences was reduced by high GA<sub>3</sub> concentrations without an accompanying increase in vegetative shoot number.

GA<sub>3</sub> applied at Stage 5 of inflorescence development in these two studies caused precocious development of the vegetative shoot apex of indeterminate inflorescences that developed successfully. Stimulating vegetative growth at the inflorescence apex did not inhibit inflorescence development. Whereas the full number of secondary axes meristems of the inflorescence are already formed at Stage 5, tertiary axes are still being initiated (Salazar-García *et al.*, 1998). The results provide additional evidence that secondary and tertiary axes are committed to flowering at this stage, consistent with perianth formation on these axes, but that the final fate of the inflorescence apex is determined much later. Thus, determinate inflorescences in the glasshouse study were redirected to indeterminate inflorescences by the GA<sub>3</sub> treatments.

The number of days after treatment required for buds to reach the cauliflower stage of inflorescence development was similar for both young and mature trees injected with GA<sub>3</sub>, approximately 33 d for young trees and 35 d for mature trees. Inflorescences of young GA<sub>3</sub>-treated trees needed a longer time to develop from the cauliflower stage to flower anthesis, but still had inflorescence flowers that reached anthesis earlier than control trees. The results suggest that the earlier bud break yielded less developed inflorescences, which required a longer time to form fully mature flowers. As with the young trees, inflorescences of mature trees



FIG. 3

Effect of GA<sub>3</sub> trunk injections to mature 'Hass' avocado trees (field study) on inflorescence size and development of the vegetative shoot at the inflorescence apex at the beginning of flower anthesis. (A), Branch of a control tree. (B), Branch of a tree treated with 1.0 g GA<sub>3</sub> per tree. Bars = 10 cm (A and B).

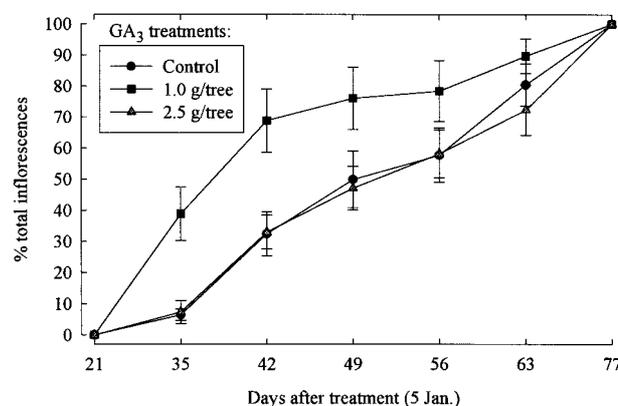


FIG. 4

Effect of GA<sub>3</sub> trunk injections to mature 'Hass' avocado trees (field study) on the proportion of inflorescences (% ± SE) that reached the cauliflower stage of inflorescence development as a function of time after treatment.

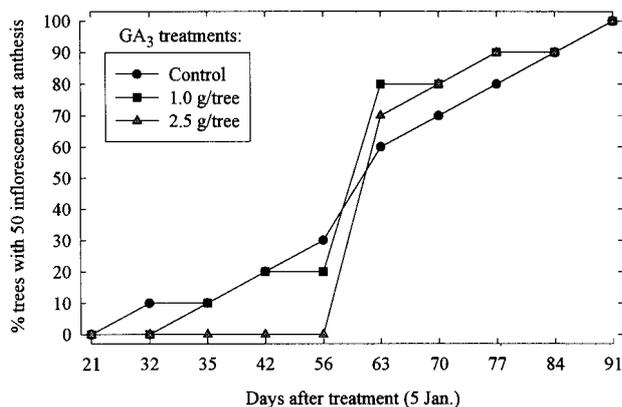


FIG. 5

Effect of GA<sub>3</sub> trunk injections to mature 'Hass' avocado trees (field study) on the number of days required to produce 50 inflorescences with flowers at anthesis per tree.

injected with 1.0 g GA<sub>3</sub> per tree reached the cauliflower stage earlier than did control trees, but subsequent flower bud development was slow. In this case the trees had inflorescences with flowers at anthesis at the same time as the control trees. Injection of mature trees with 2.5 g GA<sub>3</sub> per tree resulted in the most desirable flowering response. Inflorescence and flower bud development was delayed, resulting in a short synchronized period of anthesis, which occurred at the time of maximum anthesis for the untreated control trees.

Comparison of the results obtained in this study with those obtained in an earlier preliminary study in which 1.0 g GA<sub>3</sub> l<sup>-1</sup> was sprayed on the buds and foliage of a branch of mature 'Hass' avocado trees (Salazar-García and Lovatt, 1998) indicates that trunk injections produce a more uniform and stronger response to GA<sub>3</sub>. This could prove beneficial in reducing the amount of plant growth regulator required to achieve a desired response.

In the current study, mature 'Hass' avocado trees receiving winter GA<sub>3</sub> trunk injections had more inactive buds, resulting in fewer inflorescences. However, this was not accompanied by an increase in vegetative shoot number as occurred in the branch study. Whereas trunk injections of 2.5 g GA<sub>3</sub> per tree delayed anthesis and contracted and synchronized the period of flower-opening, both highly desired goals for avocado growers, the combined reductions in inflorescence number and fruit set/inflorescence may reduce yield too much for this concentration to be a useful remedy for alternate bearing. The effectiveness of trunk injections of 1.0 g GA<sub>3</sub> per tree or a lower concentration of GA<sub>3</sub> to achieve this goal, or GA<sub>3</sub> injections at other times in the phenology of the 'Hass' avocado tree, to increase vegetative shoot production and even out alternate bearing remains to be determined. To our knowledge this study is the first to report the effect of a trunk-injected plant growth regulator on avocado flowering phenology.

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