FLOWERING OF AVOCADO (Persea americana Mill.): II. MANIPULATION WITH GA₃

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SUMMARY

The effects of GA₃ (25 or 100 mg·liter¹) canopy sprays applied to Hass avocado (*Persea americana* Mill.) trees in a commercial orchard in the months preceding an "off" or "on" bloom year on inflorescence and vegetative shoot number and yield were quantified. GA₃ (100 mg·liter⁻¹) applied in September (early stage of inflorescence initiation) reduced inflorescences number both years, but not yield. GA₃ (25 or 100 mg·liter⁻¹) applied in November (early stage of inflorescence development) before the "on" bloom reduced inflorescence number with a concomitant increase in vegetative shoot number and a 47 % yield reduction. GA₃ in January (initial development of the perianth of apical flowers) or March (cauliflower stage of inflorescence development) caused precocious development of the vegetative shoot apex of indeterminate inflorescences, but had no effect on inflorescence or shoot number either year. GA₃ (25 mg·liter⁻¹) applied in March of an "off" bloom year increased production (2-fold) of commercially valuable fruit (213-269 g per fruit) and delayed skin blackening. This paper provides basic information that can be used to develop strategies for manipulating yield and evening out alternate bearing in avocado.

ADDITIONAL KEY WORDS: alternate bearing, fruit set, gibberellic acid, inflorescence development, yield.

FLORACIÓN DEL AGUACATE (Persea americana Mill.): II. MANIPULACIÓN CON AG,

RESUMEN

Se cuantificó el efecto de la aspersión foliar de AG_3 (25 ó 100 mg·litro⁻¹) al aguacate 'Hass' (*Persea americana* Mill.) en los meses previos a un año de floración "escasa" o "abundante" sobre la producción de inflorescencias y brotes vegetativos. AG_3 (100 mg·litro⁻¹) aplicado en Septiembre (comienzo de la iniciación de la inflorescencia) redujo el número de inflorescencias en ambos años, pero no el rendimiento. La aplicación de AG_3 (25 ó 100 mg·litro⁻¹) en Noviembre (desarrollo inicial de la inflorescencia) previo al año de floración "abundante" redujo el número de inflorescencias, incrementó el número de brotes vegetativos y redujo 47 % el rendimiento. La aspersión con AG_3 en enero (desarrollo inicial del periantio de flores apicales) o marzo (inflorescencia en estado "coliflor") aceleró el desarrollo del brote vegetativo de las inflorescencias indeterminadas pero no afectó el número de inflorescencias o brotes vegetativos en ningún año. AG_3 (25 mg·litro⁻¹) aplicado en marzo del año de floración "escasa" incrementó la producción (al doble) de fruto de valor comercial (213 a 269 g por fruto) y retrasó el ennegrecimiento de su epidermis. Este trabajo presenta información básica que puede ser de utilidad para desarrollar estrategias para manipular el rendimiento y reducir la alternancia productiva del aguacate.

PALABRAS CLAVE ADICIONALES: alternancia productiva, amarre de fruto, ácido giberélico, desarrollo de la inflorescencia, rendimiento.

INTRODUCTION

Exogenous application of gibberellins (especially GA_3) has been reported to provide a tool to manipulate flowering. GA_3 application has been shown to inhibit or delay flower initiation in deciduous fruit crops (Seedgley, 1990). A similar response has been found in subtropical and tropical

perennial fruit crops such as lemon, mandarins, orange, and mango (Kachru *et al.*, 1972; Nir *et al.*, 1972; Guardiola *et al.*, 1977; Iwahory and Oohata, 1981; Nuñez-Elisea and Davenport, 1991). The inhibition of flowering caused by GA_3 treatment has been associated to the stimulation of vegetative growth, although this response may depend on the stage of bud development at the time of treatment. There exists evidence for a dual response to GA_3 treatment. For example, in strawberry, GA_3 accelerated the appearance of flowers that had differentiated at the time of application but inhibited the initiation of new flowers (Porlyngis and Boynton, 1961). With coffee, application of GA_3 stimulated early anthesis only when floral buds were 4 mm long at the time of treatment (Schuch *et al.*, 1990).

For the 'Hass' avocado in California, USA., it is desirable to delay anthesis so that pollination and fruit set occur when climatic conditions are more favorable, to shorten the normally protracted flowering period so that fruit set would be completed before high temperatures occur, and to produce a sufficient number of inflorescences to set a good crop annually without causing alternate bearing. Gibberellic acid₃ may provide to be useful to manipulate bloom for the mentioned purposes; however, information on the effect of endogenous application of GA₃ to avocados is limited. Thus, the objective of this paper is to present a complete report of several studies undertaken to assess the effect of GA₃ to regulate inflorescence phenology and intensity of flowering in order to increase yield and even out alternate bearing of the 'Hass' avocado.

GA₃ SPRAYS AFFECT THE TYPE OF GROWTH PRODUCED BY APICAL BUDS

The ability to manipulate flowering has been a goal of both researchers and growers, especially with regard to solving the problem of alternate bearing. Alternate bearing in the orchard under study resulted in higher production of vegetative shoots at the expense of inflorescence production for control trees carrying an "on" crop. The opposite occurred for the "off" crop year, resulting in greater production of inflorescences (Salazar-García and Lovatt, 2000). Our research was the first to use GA₃ to alter this relationship. GA₃ (100 mg·liter⁻¹) applied in September, before completion of the inflorescence bud initiation process (buds at Stage 3) (Figure 1) of any cropping year effectively reduced inflorescence production and increased vegetative shoot production. GA, (25 or 100 mg·liter⁻¹) applied in November (buds at Stage 4) prior to the "on" bloom year reduced inflorescence production and increased the production of vegetative shoots, compared to the control. GA, sprays in November, when buds had only one to three secondary axis inflorescence meristems without apical bracts, also resulted in production of partially formed inflorescences (with less than 10 secondary axes) (Salazar-García and Lovatt, 1998), which reduced flowering intensity. Stimulation of the growth of the vegetative primary axis meristem by GA₂ arrested the growth of secondary axis meristems adjacent to it, and the response was stronger at higher GA₃ concentrations. However, flowering was not fully inhibited, demonstrating that GA₃ did not revert secondary axis meristems into vegetative ones. Aborted meristems could be observed after inflorescence elongation

as scars with small inflorescence bracts (Salazar-García and Lovatt, 1998). GA₃ (25 mg·liter⁻¹) applied in November decreased yield (50 %) in the "on" bloom year. GA₃ treatment in January (buds at Stage 5) or in March (buds at the cauliflower stage; Stage 8) had no effect on the number of inflorescences produced in either the "on" or "off" bloom year, due to the high proportion of buds at an advanced stage of development at the time of treatment (Figure 2). Monthly applications of GA₃ (25 mg·liter⁻¹) during the process of inflorescence bud development (September to January) reduced production of inflorescences more than 65 % in both "off" and "on" bloom years; however, there was no related effect on yield.

GA₃ TREATMENTS ALTER FLORAL SHOOT PHENOLOGY

Inhibition of flowering and delayed anthesis are the most often reported response of subtropical and tropical fruit trees, such as citrus (Guardiola *et al.*, 1982; Lord and Eckard, 1987) and mango (Kachru *et al.*, 1972; Nuñez-Elisea and Davenport, 1991), to prebloom applications of GA₃. For citrus, potential flowering buds were diverted to vegetative shoots when GA₃ was applied prior to irreversible commitment to flowering (Guardiola *et al.*, 1982; Lord and Eckard, 1987). In contrast, GA₃ 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.

To test GA₃ spray dates and rates a series of studies were conducted by our lab in both greenhouse and commercial avocado orchards. Different to what has been reported for other fruit trees species, GA₃ sprays never delayed flowering, but hastened the floral shoot development of the 'Hass' avocado. Even at a low concentration (50 mg·liter⁻¹), when GA₃ was applied in December or January, 50 % of the inflorescences reached the cauliflower stage 23 days earlier than the non-GA₃-sprayed controls. Higher GA₃ concentrations applied to the foliage (100 or 1000 mg·liter⁻¹) and later application dates further accelerated the rate at which buds reached the cauliflower stage; however, the date of anthesis was not significantly affected (Salazar-García and Lovatt, 1998).

A popular hypothesis to explain low fruit set in avocado is that there may be a competition between the vegetative shoot and the flowers of indeterminate inflorescences at the time of fruit set (Zilkah *et al.*, 1987; Cutting and Bower, 1990; Whiley, 1990; Bower and Cutting, 1992). Under the climatic conditions of California, vegetative growth and leaf expansion of indeterminate inflorescences of the 'Hass' avocado is usually delayed relative to the elongation of the secondary axes of the inflorescence. GA₃ sprays dramatically increased the rate of development of the vegetative shoot at the apex of indeterminate inflorescences (Salazar-García and Lovatt, 1998; Salazar-García and Lovatt, 2000). The precocious vegetative shoot development in indeterminate inflorescences caused by GA_3 treatments might result in more successful inflorescences in terms of fruit set and yield by eliminating the competition between reproductive and vegetative growth. Leaves of the precocious vegetative shoot of indeterminate inflorescences treated with GA_3 were sufficiently mature to be sources (based on net CO_2 assimilation rates) at the time of fruit set (Blanke and Lovatt, 1998).

GA₃ TREATMENT DETERMINES INFLORESCENCE MORPHOLOGY

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 the primary axis meristem continues the growth of the shoot (Reece, 1942). With few exceptions, the indeterminate type of inflorescence is more abundantly produced (Schroeder, 1944; Thorp *et al.*, 1994; Salazar-García and Lovatt, 1998). 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 indeterminate inflorescence was the predominant type produced by 'Hass' avocado trees during both "on" and an "off" bloom years in California (Salazar-García and Lovatt, 2000). No GA₃ treatment affected the percentage of determinate inflorescences in either year. GA₃ (100 mg·liter¹) sprayed in September or monthly at 25 mg·liter¹ from September to January prior to the "off" bloom resulted in fewer indeterminate inflorescences and more vegetative shoots. For the "on" bloom year, the highest production of indeterminate inflorescences was by the control trees (42 % of the total shoots). All applications of GA₃ made prior to the "on" bloom significantly reduced the percentage of indeterminate inflorescences and increased the number of vegetative shoots, with the exception of the January treatments.

It was confirmed that determinate inflorescences have a much higher percentage of fruit set per flower (0.17 %) than indeterminate (0.05 %) inflorescences (Salazar-García and Lovatt, 1998). The percentage of fruit set was close to the range previously reported for avocado (0.02 % to 0.1 %) (Chandler, 1958; Bergh, 1967). Given the predominance of indeterminate inflorescences and their low percent fruit set, eliminating the competition between vegetative and reproductive growth in these inflorescences by foliar application of GA₃ might provide a management strategy to increase yield.

TRUNK INJECTED GA₃ ALTERS FLORAL SHOOT PHENOLOGY AND MORPHOLOGY

Trunk injections of GA₃ to young (25 or 50 mg GA₃ per tree) or mature (1.0 or 2.5 g GA, per tree) 'Hass' avocado trees were made before bud break (Stage 5) in a glasshouse and a commercial orchard, respectively. The results showed a lack of difference in the number of days after treatment that apical buds required to reach the cauliflower stage (Stage 8) (Salazar-García and Lovatt, 1999). Inflorescences of young GA₂-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 revealed 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 injected with 1.0 g GA₂ per tree reached the cauliflower stage earlier than control trees did. However, subsequent flower bud development was slow, resulting in anthesis at 3 and 23 days later than control trees for GA, at 1.0 and 2.5 g-tree-1, respectively (Salazar-García and Lovatt, 1999). Injection of mature trees with 2.5 g GA, per tree resulted in a 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.

Determinate inflorescence was the most abundant type produced by young 'Hass' avocado trees growing in a glasshouse. Trunk injections of GA₃ (25 or 50 mg·tree) at Stage 5 of inflorescence development significantly increased the production of indeterminate inflorescences at the expense of determinate inflorescences (Salazar-García and Lovatt, 1999). Inflorescences from both control and GA₃-treated trees had 10 secondary axes, the normal number for a fully formed inflorescence (Salazar-García et al., 1998). However, GA₃-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 GA₃-treated trees were 30 to 50 cm long. GA, injected at Stage 5 of inflorescence development in this study caused precocious development of the vegetative shoot apex of indeterminate floral shoots that developed successfully. Stimulating vegetative growth at the inflorescence apex did not inhibit inflorescence development. Whereas the full number of secondary axis meristems of the inflorescence is already formed at Stage 5, tertiary axes are still being initiated (Salazar-García et al., 1998). The results provided additional evidence that secondary and tertiary axes are committed to flowering at this stage, consistent with the presence of the perianth on these axes, but that the final fate of the floral shoot apex is determined much later. Thus, potentially determinate inflorescences were redirected to indeterminate floral shoots by the GA₃ treatments.

ABSENCE OF GA, PHYTOTOXICITY

Interestingly, no visual signs of toxicity have been observed for any GA₃ spray concentration evaluated in avocado. GA₃ at 50 and 100 mg·liter⁻¹ had no negative morphological effects. However, GA₃ at 1000 mg·liter⁻¹ applied for all treatment dates caused a remarkable elongation of inflorescence axes, which in general appeared too weak to support setting fruit. Despite this axis elongation, individual flowers produced with GA₃ at mg·liter⁻¹ were not elongated but rather they were smaller than control flowers. A similar response, but with much greater vigor, was found for young and mature trees injected with GA₃ (Salazar-García and Lovatt, 1999).

EFFECT OF GA₃ TREATMENTS ON YIELD, FRUIT SIZE, AND FRUIT QUALITY

'Hass' avocado trees bearing a heavy crop produce a light "off" bloom the next spring. This results in a light crop and a subsequent intense "on" bloom the year after. The effects of GA₃ canopy sprays applied to 'Hass' avocado trees during the months proceeding an "off" or "on" bloom were evaluated in California by Salazar-García and Lovatt (2000). GA₃ (25 or 100 mg·liter⁻¹) was applied to separate sets of trees in September (early stage of inflorescence initiation), November (early stage of inflorescence development), January (initial development of the perianth of terminal flowers), March (cauliflower stage of inflorescence development; only 25 mg·liter⁻¹) (Figure 1), or monthly from September through January (only 25 mg·liter⁻¹). Control trees did not receive any treatment. GA₃ sprays at 25 mg·liter⁻¹ in November prior to an "off" bloom year increased fruit set (avg. = 0.5 fruit/1 m long branch) compared to the control and all other GA₃ treatments, except 25 mg·liter⁻¹ GA₃ applied in January (0.3 fruit per branch). Fruit set for the control was higher for the "on" bloom than for the "off" bloom. GA₃ (25 mg·liter⁻¹) applied in November prior to the "on" bloom significantly reduced fruit set compared to the control; other GA₃ treatments did not affect fruit set that year.

In the first year of the research GA₃ treatments were made prior to the "off" bloom, thus the yield data was for an expected "off" crop year. Control trees had an average yield of 18 kg-tree⁻¹. GA₃ applications did not affect kg-fruit⁻¹-tree⁻¹, compared to control. The March (cauliflower stage) GA₃ (25 mg-liter⁻¹) application doubled the production of commercially valuable fruit of size 48 (213 to 269 g) compared to the control (Figure 2).

The second year GA₃ treatments were made prior to an anticipated "on" bloom; yield data corresponded to an "on" crop year. Control trees yielded 80 kg·fruit⁻¹·tree⁻¹. Except for the November prebloom GA₃ (25 mg·liter⁻¹) treatment, which significantly reduced yield (42 kg·tree⁻¹), no treatment differed significantly from the control. GA₃ treatments did not significantly affect fruit size compared to the control.

During the first year of the experiment, fruit from the previous spring bloom were present on the trees. This provided the opportunity to evaluate the effect of GA_3

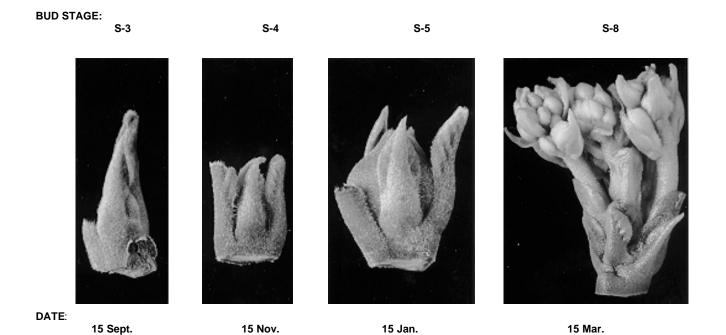


Figure 1. Stage of bud and inflorescence development of avocado 'Hass' at the time of GA, sprays.



Figure 2. A single spray of gibberellic acid at the cauliflower stage increased fruit set and yield, decreased alternate bearing, and increased production of fruit size 48 (213-269 g) in the 'Hass' avocado in California. Note the young developing fruitlets on the indeterminate inflorescence (right).

treatments on fruit retention and fruit size of the existing crop, an effect that is independent of altering bloom or inflorescence morphology. For the existing fruit, GA_3 (25 mg·liter⁻¹) applied in September (10 months before harvest) increased the amount of size 40 fruit (270 to 325 g) relative to the control (6.2 *vs* 2.7 kg·tree⁻¹). In addition, GA_3 (25 mg·liter⁻¹) applied in September increased the kg·tree⁻¹ of size 48 fruit (213-269 g) relative to other GA_3 treatments, and had no effect on the quantity of smaller fruit per tree (sizes 84 to 60).

GA₃ applications tended to delay color break, thus increasing the proportion of green fruit at harvest. GA₃ applied during the "on" bloom year (harvest date: 30 June) reduced the proportion of black fruit at harvest. GA₃ (25 mg·liter⁻¹) in September and GA₃ (100 mg×liter⁻¹) in November or January reduced by 10 % the proportion of fruit with black peel compared to the control. Internal fruit quality was not significantly affected by GA₃ treatments in any of the years evaluated. Even GA₃ 100 mg·liter⁻¹ all fruit sampled ripened normally and had excellent quality.

GA, EFFECTS ON ALTERNATE BEARING

GA₃ applications affected the two-year cumulative yield, although no treatment differed significantly from the control (Salazar-García and Lovatt, 2000). Treatments with GA₃ (25 mg·liter⁻¹) had higher cumulative yields when applied in September (121 kg·tree⁻¹) or March (123 kg·tree⁻¹) than in November (77 kg·tree⁻¹) or January (87 kg·tree⁻¹). The alternate bearing index (ABI) was not affected by GA₃ treatments. Controls trees had an average cumulative yield of 98 kg·tree⁻¹, with an ABI = 56.8 %.

Tree yield variation made it difficult to detect significant differences between treatments. However, the results indicate that some treatments deserve further research. GA_{a}

applied in September or November may have the potential to break the alternate bearing cycle by reducing production of inflorescences in an expected "on' bloom year to reduce yield that year in order to achieve a higher yield during an expected "off" crop year. GA₃ spray at the cauliflower stage (March) appears to be a promising strategy to reduce alternate bearing. The March spray had no effect on the production of inflorescences; instead it caused precocious development of the vegetative shoot of indeterminate inflorescences (Figure 2) and resulted in numerically higher fruit set and yield when applied either during an "off" or "on" bloom year, with no loss in the yield of large size fruit.

Our results support the hypothesis that, under California conditions, low fruit set in avocado may be caused, at least in part, by competition between growth of the vegetative shoot of indeterminate floral shoot and setting fruit (Blanke and Lovatt, 1998). The metabolic changes caused by GA_3 -induced precocious leaf development and their effect(s) on fruit set and development remain to be quantified.

The effects of GA_3 treatments (time of application and concentration) were different when made prior to an "off" versus "on" bloom year, despite the fact that the buds were on average at the same stage of development when the treatments were made in two separate years. Using GA_3 sprays during an "off" or "on" bloom year to increase yield or to even out alternate bearing will require careful attention to GA_3 concentration, stage of inflorescence development at the time of treatment, and tree fruit load.

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