

Prohexadione-Calcium Affects Shoot Growth of Evergreen Subtropical Woody Perennials Differently than Deciduous Temperate Zone Woody Perennials - Is it a Case of Apples and Oranges?

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Abstract

Manipulation of vegetative shoot growth is an important factor in tree crop production. Results with apple demonstrated that a single application of the gibberellin (GA)-biosynthesis inhibitor Prohexadione-calcium (P-Ca) (250 mg L^{-1}) inhibited vegetative shoot growth for 4 weeks. Prohexadione-calcium was tested for its capacity to inhibit growth of vegetative shoots after spring pruning of citrus and spring shoot growth of avocado. 'Eureka' lemon (*Citrus limon* L.) and 'Washington' navel orange (*C. sinensis* L.) trees were topped and hedged in mid-May and P-Ca (250 or 500 mg L^{-1}) was applied 24 h later to the entire canopy to run off. Prohexadione-calcium (250 or 500 mg L^{-1}) reduced lemon shoot (elongation) growth by 30% for 5 weeks, but at 500 mg L^{-1} P-Ca reduced 2-year cumulative total yield and yield of commercially valuable large fruit ($\geq 6.1 \text{ cm}$ transverse diameter) (kg and number per tree) compared to the untreated control ($P \leq 0.05$). In contrast, P-Ca (250 and 500 mg L^{-1}) had no effect on navel orange shoot length and reduced 2-year cumulative total yield (kilograms and fruit number) per tree by reducing the yield of small fruit ($\leq 6.9 \text{ cm}$) ($P \leq 0.05$). The fruit-thinning effect of P-Ca (250 mg L^{-1}) increased the 2-year cumulative yield (kg/tree) of large fruit ($\geq 7.5 \text{ cm}$ transverse diameter) ($P \leq 0.05$). Three foliar-applications of P-Ca (250 mg L^{-1}) during bloom and fruit set of 'Hass' avocado (*Persea americana* Mill.) trees reduced the growth of the apical vegetative shoot of indeterminate floral shoots from May through June in the on-bloom year and April through July in the off-bloom year and increased fruit set from full bloom through August ($P \leq 0.05$). Prohexadione-calcium (125 mg L^{-1}) applied at the cauliflower stage of inflorescence development and again at full bloom significantly increased the 2-year cumulative yield of commercially valuable large fruit ($\geq 270 \text{ g/fruit}$) without reducing total yield (kilograms and number of fruit per tree) compared to the untreated control ($P \leq 0.05$).

INTRODUCTION

An ability to manipulate vegetative and reproductive shoot development of tree fruit crops is critical for maximizing production per hectare and, in some cases, is key to the sustainability of agricultural commodity-based industries. Currently, plant bioregulators (PBRs) are the most powerful tools available for manipulating tree growth and yield in an existing orchard in order to solve production problems and increase grower profit. The PBR prohexadione-calcium (P-Ca) inhibits vegetative shoot growth by inhibiting gibberellin (GA) biosynthesis. Specifically, P-Ca inhibits the conversion of GA_{20} to GA_1 by inhibiting GA_{20} 3 β -hydroxylase (Rademacher et al., 2006). As an analog of 2-oxoglutaric acid, the co-substrate of GA_{20} 3 β -hydroxylase, P-Ca is a competitive inhibitor of the enzyme. P-Ca has proven a cost-effective tool for inhibiting vegetative shoot extension of apple to increase yield and reduce pruning costs (Greene, 1999; Costa et al., 2006; Ramirez et al., 2006). Although different apple cultivars respond differently to P-Ca, in general, single or multiple low-dose foliar applications beginning at petal fall

(PF) to 10 days after PF reduce apple shoot extension by 20 to 70% (Greene, 1999; Norelli and Miller, 2004; Costa et al., 2006; Ramirez et al., 2006). Timing was more important than rate of application for significant early growth suppression. For example, the results of foliar applications of P-Ca at 0 (control), 125, 175 and 250 mg L⁻¹ when ‘Golden Delicious’ apple shoots reached 5 cm in length showed that P-Ca at any concentration reduced final shoot length (Ramirez et al., 2006). Leaf number per shoot was also reduced for all P-Ca treated trees. However, only P-Ca applications at 175 and 250 mg L⁻¹ increased total yield per tree. Harvested fruit from these two treatments had increased firmness but reduced total soluble solids.

Here we report the efficacy of foliar-applied P-Ca to reduce vegetative shoot growth of three subtropical perennial fruit tree crops: ‘Eureka’ lemon; ‘Washington’ navel orange; and ‘Hass’ avocado. For citrus produced in California, pruning is an annual cultural practice and major expense. Trees are topped and hedged to improve light penetration for greater photosynthesis and increased yield and to facilitate pest management. Pruning is also necessary to maintain the drive-rows through the orchard for movement of vehicles and to maintain tree height within the limit specified for worker safety, as all citrus fruit are harvested by hand in California. For citrus, P-Ca was tested for its capacity to stop vegetative shoot elongation after pruning (regrowth) with the objective of extending the length of time between required pruning events and/or the amount of biomass to be removed and processed at pruning, without reducing the fruit number, size or quality of the harvested crop.

In contrast, for avocado the objective was to reduce vegetative shoot growth during spring bloom with the goal of increasing fruit set, fruit size and yield. Earlier research provided evidence that a mid-bloom foliar application of paclobutrazol inhibited spring vegetative shoot growth and increased fruit set, fruit size and annual or cumulative yield (Köhne and Kremer-Köhne, 1987; Kremer-Köhne and Köhne, 1998; Wolstenholme et al., 1990). It was of particular interest that removing or stopping the growth of the apical vegetative bud of indeterminate floral shoots increased their productivity (Cutting and Bower, 1992). In California, ‘Hass’ avocado trees produce predominantly indeterminate floral shoots (~90%) compared to determinate floral shoots (~10%) (Salazar-Garcia and Lovatt, 1998). Thus, the effect of P-Ca on spring vegetative shoot growth and the growth of the vegetative bud at the apex of indeterminate floral shoots was determined in relation to fruit set, fruit size and final yield of the ‘Hass’ avocado in California.

MATERIALS AND METHODS

Citrus

The research was conducted in commercial orchards of 16-year-old ‘Eureka’ lemon trees on *C. volkmariana* rootstock and 21-year-old ‘Washington’ navel orange trees on ‘Troyer Citrange’ rootstock (*C. sinensis* ‘Washington’ navel × *Poncirus trifoliata* L. Raf.) at the Citrus Research Center and Agricultural Experiment Station, University of California, Riverside (33.57° N, 117.23° W). Trees were topped and hedged in mid-May and P-Ca (250 or 500 mg L⁻¹) was applied 24 h later in 2337 L of water (containing 0.05% Silwet L77[®] surfactant) per ha to the entire canopy to run off using a 2758 KPa handgun sprayer. There were 16 individual tree replicates per treatment, including an untreated control, in a randomized complete block design. The number and length of shoots that developed within 12 cm of the pruning cut were determined weekly through July and every two weeks thereafter. Trees were harvested annually in January. Total yield (kg) per tree and fruit size distribution (pack out) as kilograms of fruit of each commercial packing size were determined at harvest for each data tree, using a portable, commercial in-field fruit sizer. The following packing carton sizes (based on fruit transverse diameter in mm) were used: lemon = 235 (47.75-51.05), 200 (51.06-54.10), 165 (54.11-56.90), 140 (56.91-61.20), and 115 (61.21-65.28), and for navel orange = <113 (<63.5), 113 (63.6-68.9), 88 (69.0-74.9), 72 (75.0-80.9), and 56 (81.0-88.0).

Avocado

The research was conducted in commercial orchards of 7-year-old (experiment 1) and 8-year-old (experiment 2) ‘Hass’ avocado trees on Mexican race rootstocks (*P. americana* var. *drymifolia*) located in Irvine, California (33.40° N, 117.49° W). In experiment 1, P-Ca (250 mg L⁻¹) was applied as three consecutive treatments at the cauliflower stage of inflorescence development (March), full bloom (April) and early fruit abscission (May). The length of 10 developing spring flush vegetative shoots and the apical vegetative shoot of 10 indeterminate floral shoots was measured monthly from April through July for all data trees. To determine percent fruit set, flowers or fruit were counted for tagged indeterminate floral shoots just prior to treatment applications in April and May and then monthly. In experiment 2, P-Ca (125 mg L⁻¹) was applied at the cauliflower stage of inflorescence development (March) and again at full bloom (April). For both experiments P-Ca was applied in 1869 L water (containing 0.05% Silwet L77[®] surfactant) per ha using a 2758 KPa handgun sprayer to give full canopy coverage. In each experiment, there were 25 individual tree replications per treatment, including an untreated control, in a randomized complete block design. At harvest, total yield was determined as kilograms fruit per tree. A randomly selected subsample of 100 to 150 fruits/tree, representing approximately 20 to 100% of the fruit per tree, was collected for each data tree. The weight of each fruit in the subsample was determined. These data were used to determine pack out, i.e., kilograms of fruit of each commercial packing carton size per tree, and to estimate the total number of fruit per tree. The following packing carton fruit sizes (g per fruit) were used: 84 (99-134); 70 (135-177); 60 (178-212); 48 (213-269); 40 (270-325); 36 (326-354); and 32 (355-397). In addition, at harvest, two fruit were selected randomly per tree and allowed to ripen at 22±2°C. The number of days from harvest to “eating ripe” was recorded. When ripe, fruit internal mesocarp quality was evaluated for discoloration, vascularization (presence of vascular bundles and associated fibers), seed germination and stem-end decay. Fruit quality parameters were rated on a scale from 0 (normal) to 4 (high incidence of discoloration, vascularization and stem-end decay). In addition, fruit length, fruit width, seed diameter, and mesocarp width were measured.

Alternate bearing index (ABI) was calculated for the avocado trees in experiments 1 and 2 to assess the severity of alternate bearing in each orchard. When ABI is 1, alternate bearing is 100% and when ABI is 0, there is no alternate bearing (Pearce and Dobersek-Urbanc, 1967). ABI was calculated according to the equation below, in which a_i is yield in the *i*th year, with a_1 being the year 1 harvest and n is number of years for which the alternate bearing index is calculated:

$$ABI = \frac{\sum \frac{|a_{i+1} - a_i|}{a_{i+1} + a_i}}{n - 1}$$

Statistical Analyses

The data were analyzed using the General Linear Model procedure of the SAS 9.2 statistical program (SAS Inst., Inc., Cary, N.C.). Analysis of variance was used to test for treatment effects on total yield in kilograms and number of fruit per tree, kilograms and number of fruit in each size category per tree, fruit quality parameters and shoot growth. Means were separated using Fisher’s Protected LSD or Dunnett’s test at $P=0.05$.

RESULTS

Effect of Prohexadione-Calcium on Citrus

Prohexadione-Ca successfully reduced the growth (length) of lemon shoots 30 days after application up to 15% through mid-July or 20% through the end August for

trees treated with 500 or 250 mg L⁻¹, respectively, for the two years of the study (Fig. 1A). However, final shoot length for the untreated control over this period was low (<8 cm). Neither P-Ca treatment significantly reduced the number of shoots that developed after pruning. P-Ca (500 mg L⁻¹) significantly reduced both the total number and kilograms of fruit per tree as 2-year cumulative yield compared to trees treated with 250 mg L⁻¹ but not the untreated control trees (Table 1). Treating trees with 500 mg L⁻¹ P-Ca significantly reduced the 2-year cumulative yield of commercially valuable large fruit (packing carton size 115) as both kilograms (Table 1) and number of fruit per tree (Data not shown) compared to trees treated with 250 mg L⁻¹ P-Ca and untreated control trees. P-Ca at 250 mg L⁻¹ had no effect on lemon or fruit size.

In contrast, for navel orange, P-Ca (250 and 500 mg L⁻¹) had no effect on shoot length (Fig. 1B), but significantly reduced the number of shoots that developed in response to pruning from early June (2 weeks after treatment) through the end of July ($P<0.05$). Prohexadione-calcium (250 and 500 mg L⁻¹) significantly reduced 2-year cumulative total yield (kilograms and number of fruit) per tree compared to the untreated control (Table 2). In addition, P-Ca (250 and 500 mg L⁻¹) significantly reduced the kilograms of small fruit, i.e., fruit of packing carton size 113 that have commercial value and packing carton sizes <113 that have no commercial value. The fruit-thinning effect of P-Ca at 250 mg L⁻¹, but not 500 mg L⁻¹, resulted in a significant increase in the 2-year cumulative yield of commercially valuable large fruit of packing carton size 72 as kilograms per tree compared to the untreated control ($P=0.0846$) (Table 2).

Effect of Prohexadione-Calcium on Avocado

In experiment 1, growth of spring flush vegetative shoots and the apical vegetative shoot of indeterminate floral shoots was related to differences in crop load and its effect on floral intensity related to alternate bearing, the cyclic production of a heavy on-crop followed by a light off-crop. The ABI for the 'Hass' avocado orchard in experiment 1 was 0.68. Elongation of spring flush vegetative shoots of trees carrying a light off-crop and producing an intense on-crop spring bloom (on-bloom trees) was delayed relative to trees carrying a heavy on-crop and producing a light off-crop bloom (off-bloom trees). However, by July spring flush vegetative shoots of on-bloom trees were significantly longer than those of off-bloom trees by 1.8 cm ($P<0.001$) (Fig. 1C and D). For on-bloom trees, P-Ca (250 mg L⁻¹) applied in March, April and May only reduced spring flush vegetative shoot elongation in May (Fig. 1C). For off-bloom trees, P-Ca reduced elongation of spring flush vegetative shoots through June (Fig. 1D). The length of the apical vegetative shoot of indeterminate floral shoots was also longer (2.5 cm) by July for on-bloom trees than off-bloom trees ($P<0.001$) (Fig. 1E and F). Application of P-Ca significantly reduced the length of the apical vegetative shoot of indeterminate floral shoots in May and June for on-bloom trees and in May, June and July for off-bloom trees. The reduction in shoot length was not accompanied by a decrease in the number of leaves (nodes) per shoot, consistent with a shortening of the internodes characteristic of low GA biosynthesis. For off-bloom trees, P-Ca significantly increased fruit set by indeterminate floral shoots through July: compare 3.7% for P-Ca-treated trees to 2.3% for untreated control trees ($P=0.05$), but did not result in a significant increase in yield. P-Ca reduced fruit length to width ratio, resulting in less elongated fruit for both on-and off-bloom trees ($P=0.05$), but produced no significant physiological effects on any internal fruit quality parameters evaluated.

In experiment 2, application P-Ca (125 mg L⁻¹) at the cauliflower stage of inflorescence development and again at full bloom had no significant effect on 2-year cumulative total yield (kilograms or number of fruit) per tree, but significantly increased the 2-year cumulative yield of commercially valuable large fruit of packing carton sizes ≥ 40 (≥ 270 g/fruit) (Table 3). In addition, P-Ca significantly increased the combined pool of fruit of packing carton sizes 36, 32 and 28 (≥ 326 g/fruit) more than two-fold compared to the untreated control trees as both kilograms and number per tree for the two years of the study ($P=0.03$) (data not shown). Fruit of this size are not commercially valuable to all

growers. Thus, the effect of P-Ca on avocado yield was a positive effect on fruit growth with a numerical, but not significant, increase in fruit retention compared to the untreated control trees. In the light off-crop year, P-Ca increased fruit length ($P=0.05$), fruit width ($P=0.01$), and seed diameter ($P=0.01$), but had no effect on mesocarp width. These parameters were not affected by P-Ca treatment during the heavy on-crop year. Prohexadione-calcium treatment had no effect on the number of days to ripen, mesocarp discoloration, vascularization, stem-end decay, or seed germination for either on- or off-crop trees. Prohexadione-calcium had no effect on the severity of alternate bearing in the 'Hass' avocado orchard in experiment 2 (ABI = 0.59).

DISCUSSION

The responses of lemon, navel orange and avocado trees to P-Ca were uniquely different. A single application of P-Ca (250 mg L^{-1}) 24 h after pruning reduced the length of lemon shoots from mid-June through end of August with no effect on yield or fruit size. However, P-Ca at 500 mg L^{-1} reduced vegetative shoot growth only until July and significantly reduced total yield and fruit size. In contrast, P-Ca (250 and 500 mg L^{-1}) had no effect on the length of vegetative shoots that developed after navel orange trees were pruned, but reduced the number of shoots that developed in response to pruning during June and July and increased fruit size by reducing total yield. For avocado, P-Ca (250 mg L^{-1}) applied three times during spring bloom reduced elongation of the apical vegetative shoot of indeterminate floral shoots at least through June with a concomitant increase in percent fruit set. In a second experiment, P-Ca (125 mg L^{-1}) applied twice during bloom increased the yield of large size fruit without reducing total yield.

The decrease in lemon shoot length and yield were dependant on P-Ca concentration and consistent with reduced GA biosynthesis. The reduction in navel orange yield caused by P-Ca is also consistent with low GA, but the resulting shift in fruit size distribution towards larger fruit is likely due to reduced crop load not to stimulation of navel orange fruit growth. The results suggest that lemon shoot elongation is more sensitive to P-Ca or reduced GA₁ availability than lemon fruit, but that the reverse is the case for navel orange, for which P-Ca had no effect on the length of vegetative shoots developed in response to pruning. The results obtained with the use of P-Ca on citrus are not consistent with the inhibition of ethylene biosynthesis, an effect of P-Ca (Rademacher et al., 2006); inhibition of ethylene biosynthesis with aminoethoxyvinylglycine (AVG) has been shown to increase fruit set of navel orange (Gonzalez and Lovatt, 2007). P-Ca applied during avocado bloom reduced vegetative shoot growth (length), especially of the apical vegetative shoot of indeterminate floral shoots, consistent with inhibition of GA₁ biosynthesis, but also increased fruit set and fruit size with out reducing total yield, which could be the result of inhibition of ethylene biosynthesis. Application of AVG to 'Hass' avocado trees at bloom has been shown to significantly increased the 3-year cumulative yield of commercially valuable large avocado fruit without reducing total yield (Lovatt, unpublished). For apple, P-Ca applied at concentrations similar to those used in the present research (175 to 250 mg L^{-1}) significantly reduced shoot growth and increased total yield, which was not achieved with the use of P-Ca on citrus or avocado. For apple P-Ca is also a valuable tool for mitigating fire blight and scab damage through its effect on the synthesis of 3-deoxyflavonoids (Norelli and Miller, 2002; Rademacher et al., 2006; Costa et al., 2006). Whether P-Ca reduces the incidence or severity of any subtropical tree crop diseases remains unknown.

CONCLUSIONS

For lemon, P-Ca (250 mg L^{-1}) reduced the length of shoots that developed in response to pruning with no negative effect on total yield or yield of commercially valuable large size fruit (61.21-65.28 mm in diameter). Thus, this PBR strategy should be tested further. Since P-Ca concentrations having no impact on the length of vegetative shoots after pruning significantly reduced total yield and fruit size of navel orange, further research is not warranted. The effect of P-Ca (125 mg L^{-1}) on avocado yield was positive

for all fruit size categories, with the increase in yield of commercially valuable large fruit (≥ 270 g/fruit) being statistically significant. This PBR strategy has significant economic potential and should be developed further.

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Tables

Table 1. Effect of prohexadione-calcium applied to the canopy of ‘Eureka’ lemon trees 24 h after topping and hedging (mid-May) on 2-year cumulative yield and fruit size.

Treatment	Concentration (mg L ⁻¹)	Total no.	Packing carton size based on fruit transverse diameter (mm)					
			Total wt.	235 (47.75- 51.05)	200 (51.06- 54.10)	165 (54.11- 56.90)	140 (56.91- 61.20)	115 (61.21- 65.28)
		no./tree	kg/tree					
Prohexadione- Ca	250	4499a	521.1a	18.3	31.7	95.3	102.2	143.5a
Prohexadione- Ca	500	399b	462.6b	17.3	28.8	84.4	92.8	115.1b
Control		4246ab	493.7ab	19.0	32.0	85.7	96.0	139.6a
<i>P</i> -value		0.025	0.071	0.717	0.565	0.112	0.405	0.0391

No.: Number means followed by different letters are significantly different by Fisher’s protected LSD test at $P \leq 0.05$. NS: Not significant.

Table 2. Effect of prohexadione-calcium applied to the canopy of ‘Washington’ navel orange trees 24 h after topping and hedging (mid-May) on 2-year cumulative yield and fruit size.

Treatment	Concentration (mg L ⁻¹)	Total no.	Packing carton size based on fruit transverse diameter (mm)					
			Total wt.	<113 (<63.5)	113 (63.6- 68.9)	88 (69.0- 74.9)	72 (75.0- 80.9)	56 (81.0- 88.0)
		no./tree	kg/tree					
Prohexadione- Ca	250	534b	138.2b	7.7b	19.4b	50.0	24.3a	24.8
Prohexadione- Ca	500	534b	134.8b	12.8b	22.3b	40.9	19.3ab	27.4
Control		684a	164.8a	24.8a	38.0a	46.8	18.2b	24.8
<i>P</i> -value		0.012	0.053	0.005	0.001	0.438	0.085	0.642

No.: Number. Means followed by different letters are significantly different by Fisher’s protected LSD test at $P \leq 0.05$. NS: Not significant.

Table 3. Effect of prohexadione-calcium (125 mg L^{-1}) applied to the canopy of ‘Hass’ avocado trees at the cauli-flower stage of inflorescence development and full bloom on 2-year-cumulative yield and fruit size.

Treatment	Total no.	Total wt. no./tree	Packing carton size based on individual fruit mass (g)				
			84 + 70 (99-177)	60 (178-212)	48 (213-269)	40 (270-325)	>40 (>325)
Prohexadione-Ca	192	42.3	5.7	10.1	17.1	7.1 a	9.3 a
Control	143	30.3	5.7	7.9	10.9	4.6 b	5.9 b
<i>P</i> -value	0.200	0.147	0.815	0.332	0.201	0.072	0.040

No.: Number. Means followed by different letters are significantly different by Fisher’s protected LSD test at $P \leq 0.05$. NS: Not significant.

Figures

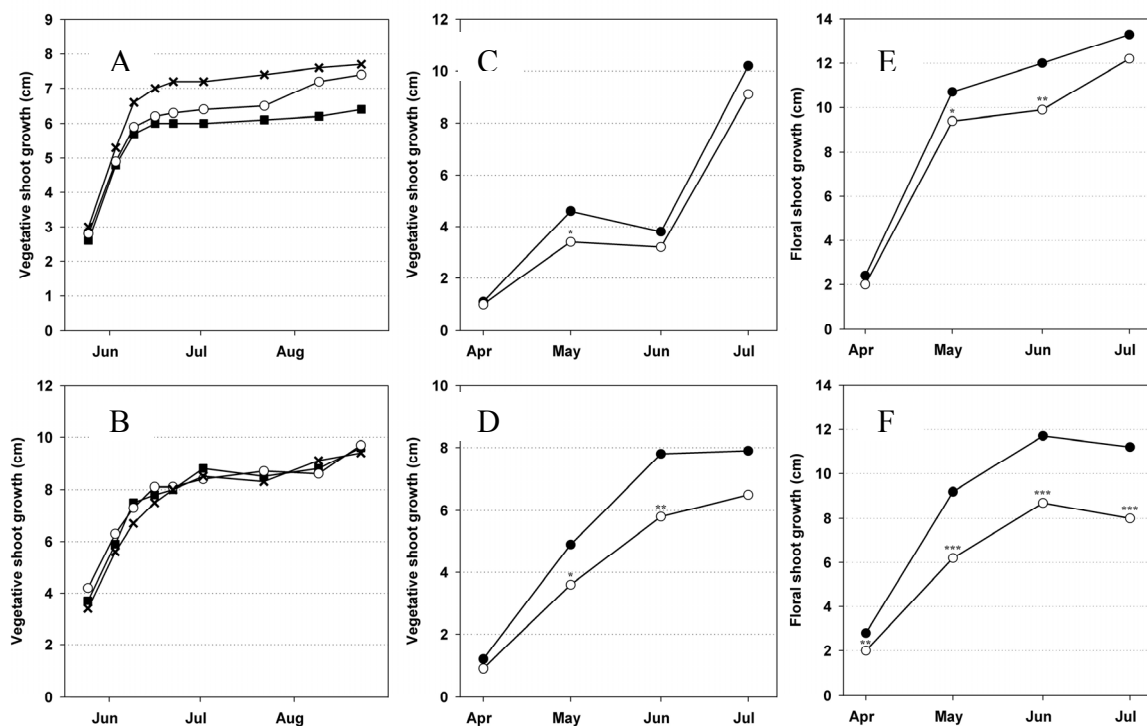


Fig. 1. ‘Eureka’ lemon (A) and ‘Washington’ navel orange (B) - effect of prohexadione-calcium (P-Ca) at 250 mg L^{-1} (■) or 500 mg L^{-1} (○) compared to the untreated control (x) on vegetative shoot growth (average shoots length) after topping and hedging (mid-May). Avocado - effect of P-Ca (250 mg L^{-1}) applied at the cauliflower stage of inflorescence development (March), full bloom (April) and during fruit set (May) (○) compared to the untreated control (●) on growth of spring flush vegetative shoots of heavy on-bloom trees (C) and light off-bloom trees (D) and on the growth of the apical vegetative shoot of indeterminate floral shoots of on-bloom trees (E) and off-bloom trees (F). ***, **, * Significantly different by Dunnett’s test at $\alpha \leq 0.001$, 0.01, or 0.05, respectively.