



'Hass' avocado tree growth on four rootstocks in California. II. Shoot and root growth

Michael V. Mickelbart^{a,b,*}, Paul W. Robinson^a, Guy Witney^a, Mary Lu Arpaia^a

^a Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124, United States

^b Department of Horticulture and Landscape Architecture, Purdue University, West Lafayette, IN 47907-2010, United States

ARTICLE INFO

Article history:

Received 17 February 2012

Received in revised form 6 June 2012

Accepted 12 June 2012

Keywords:

Rootstocks

Vegetative flushes

Alternate bearing

Phenology

ABSTRACT

We investigated the relationship between alternate cropping and shoot and root growth in mature 'Hass' avocado (*Persea americana* Mill.) trees growing on 'Thomas', 'Topa Topa', 'Duke 7', or 'D9' rootstocks over five years in Southern California. Shoot growth occurred during two distinct flushes each year: one in spring and one in late summer. Root growth occurred throughout the year, with higher rates during spring and summer but slower growth rates during shoot growth flushes. There was no effect of rootstock on shoot growth rate. There was no direct relationship between alternate bearing and shoot and root growth. It is possible that cropping affected shoot growth, with extensive shoot development occurring in a year with virtually no crop. The summer growth flush accounted for a greater proportion of the total shoot growth in years with light crop loads than in years with heavy crop loads. There were differences in root growth rate among rootstocks, but these relative differences varied among years. Root growth did not exhibit dormant periods as shoot growth did, but in general, root growth rate was greatest when soil temperatures were high and when shoots were not growing. This information gives us insight into the relative timing and relationships among growth events of avocado in Southern California and will help growers determine the optimal timing of cultural practices. Our results suggest that the best timing for fertilizing, spraying, and pruning is similar in trees growing on different rootstocks.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Fruit production in avocado (*P. americana* Mill.) depends on the accumulation and utilization of carbohydrates within the tree associated with shoot and root growth, flowering, and fruiting (Wolstenholme, 1986; Whiley and Wolstenholme, 1990). Rootstock can affect alternate bearing in avocado (Mickelbart et al., 2007), and understanding the relationship between vegetative and reproductive growth in trees on different rootstocks may help elucidate management strategies to minimize this phenomenon and improve grower returns.

Vegetative growth in avocado is cyclical, with one to six shoot flushes per year (Davenport, 1982; Gregoriou and Kumar, 1982; Thorp et al., 1995; Venning and Lincoln, 1958). In California, there are typically two flushes per year: one in spring and one in summer (Robinson et al., 1994). Root growth appears to be more continuous in other locations (Ploetz et al., 1993), including New Zealand

(Thorp et al., 1995), but has not been quantified in California. Floral buds develop during late summer and fall, concomitant with the summer shoot growth flush (Salazar-Garcia et al., 1998) and flowers appear in spring (Robinson et al., 1994). 'Hass' trees flower in February to May in Southern California and the fruit mature (based on commercially standardized measurements of dry matter percentage) within approximately six to eight months (Lee et al., 1983). The fruit may remain on the tree, however, for an additional 10 months.

In a previous trial that included the four rootstocks used in this study, trees on 'Duke 7' had higher yield than the other three rootstocks (Mickelbart et al., 2007). In this study, yields were more similar on the four rootstocks (part I of this study). In the first part of this study, heavy yields were associated with a higher number of fruit per tree, lower average fruit weight, and early and longer periods of flowering. Although yield varied among rootstocks, especially in heavy crop load years, trees growing on different rootstocks had similar cropping patterns. Here we provide further information on the relationship between fruit growth and the vegetative development of trees from the same experiment. With knowledge of the timing and relative intensity of various growth events, avocado growers can achieve more precise grove management using properly directed cultural practices, such as application of

* Corresponding author at: Department of Horticulture and Landscape Architecture, Purdue University, West Lafayette, IN 47907-2010, United States.
Tel.: +1 765 494 7902; fax: +1 765 499 0391.

E-mail address: mickelbart@purdue.edu (M.V. Mickelbart).

fertilizers and chemical sprays. Furthermore, identification of rootstock differences in growth will allow growers to more precisely manage trees on different rootstocks. The objectives of this study were to (1) determine the relative timing of root and shoot growth and shoot abscission, (2) identify differences in foliar nutrient concentration that might be related to shoot and/or root growth, (3) determine the effect of rootstock on any of these factors, and (4) use this information to develop a model of 'Hass' phenology in Southern California.

2. Materials and methods

2.1. Plant material and field environment

'Hass' avocado trees were grown on 'Thomas', 'Topa Topa', 'Duke 7', or 'D9' rootstocks (all Mexican race) at the University of California South Coast Research and Extension Center in Irvine, California (latitude, 33°44'N; longitude, 117°49'W) as described previously (Mickelbart et al., *this issue*). Trees were planted in randomized complete blocks. Rows (north–south orientation) acted as blocks, and each rootstock was represented once in each of 10 blocks. With the exception of trees on 'Thomas' rootstock, which were planted in 1987, all the other trees were planted in 1986. Ten trees per rootstock were used for all measurements, except shoot extension measurements, where five trees per rootstock were used.

2.2. Measurements

Shoot growth was measured in the northeast quadrant of each tree. Individual tips were tagged in February before shoot growth commenced. Shoot extension was measured every two to four weeks. In year one (1992), 10 shoots on each of 10 trees per rootstock were measured, and in subsequent years twenty shoots on each of five trees (of the 10 total trees) per rootstock were measured. A single shoot was considered to be the primary shoot and any subsequent axillary shoots arising from a single dormant apical bud. Shoot growth rate was calculated as the amount of extension in the terminal and axillary buds.

Each primary, secondary, and tertiary (when present) shoot was designated as proleptic or sylleptic after shoot growth had ceased each November to December. Proleptic and sylleptic shoot types were identified by the presence or absence of bud scars, respectively, according to Tomlinson and Gill (1973). Shoot abscission was tracked on shoots tagged in 1995 and 1996 by recording the date on which the tagged shoots were recovered from the ground. Dates of shoot recovery were recorded from the time of tagging for up to 5 years.

Canopy volume was measured in the fall of each year, after the cessation of growth. The height and canopy width was recorded for individual trees. Two measurements for canopy width were taken 1.75 m from the ground: down row width and across row width. The average of these two values was used. Canopy volume was estimated by assuming that the tree was the shape of one half of a prolate spheroid, using the formula $V = 4/6\pi h(w/2)^2$, where V is canopy volume, h is tree height, and w is tree width (Turrell, 1946).

In early 1992, a vertical flat surface was exposed on the berm in the northeast quadrant approximately 1.5 m from the trunk of each tree for installation of a rhizotron. Microsprinklers were positioned on the rhizotron side at the base of each tree. The rhizotron consisted of a 34 cm × 38 cm plexiglass window mounted with a metal frame. A 5-cm wide foam pad glued to a sheet metal cover was placed on the window between measurements for insulation and to exclude light. Every 2–4 weeks, an acetate sheet was placed on the rhizotron and root growth against the window traced. Tracings were then scanned digitally and the number of roots and total

root length were determined with the NIH Image 1.43 computer program (National Institute of Health, Washington D.C.). Daily root growth rate was calculated as the total root length divided by the number of roots divided by the number of days between measurements.

Leaves were harvested each September for nutrient analyses, based on the recommendations of Goodall et al. (1981). Approximately 20 leaves from the spring flush were harvested from vegetative shoots on each tree within the quadrant used for shoot extension measurements. Leaves were washed in distilled water, dried in an oven at 60°C, and ground (40-mesh screen). Total N was determined by Kjeldahl analysis. Phosphorus and B were analyzed by colorimetric assays, Ca, Mg, Fe, and Mn analyzed by atomic absorption spectroscopy, and K analyzed by atomic emission spectroscopy. Sulfur was determined by automated combustion.

2.3. Statistical design and analysis

The trees were planted as a randomized complete block design. Analysis of variance and correlation analysis was conducted using the PROC GLM and PROC CORR procedures of SAS (SAS, 1990), respectively. Rootstock and block were considered fixed and random effects, respectively. When multiple measurements were made on an individual tree (e.g. shoot length), the experimental error (rootstock × block) was used to test rootstock effects. Mean separation was done with Fisher's protected least significant difference test. For graphical representation, data from heavy (1992 and 1994) or light crop load (1993, 1995, and 1996) years were pooled and the means presented. Where appropriate, analyses were conducted with transformed data. Growth rate (shoot and root) data were transformed as log to the base 10 of growth rate plus 1, and fruit volume measurements were log transformed prior to analysis.

3. Results

3.1. Shoot growth

The trees had two distinct shoot growth flushes each year: one in spring on days 60–160 and one in late summer on days 160–280 (Fig. 1). Whereas all trees exhibited two flushes, some individual shoots flushed only once. Shoots that flushed in spring and summer accounted for the bulk of the growth on individual trees. These shoots had higher growth rates and greater shoot extension in spring than shoots that flushed only in spring (data not shown). Rootstock had no significant ($P > 0.05$) effect on total shoot growth in a year, the timing of shoot growth (data not shown), or average shoot growth per flush (Table 1). Canopy volume did not differ significantly ($P > 0.05$) among rootstocks, except in 1992, when the trees on 'Thomas' rootstock, planted a year later than the other trees, were smaller.

The timing of shoot growth did not differ with cropping (Fig. 1). Cumulative shoot growth also did not differ between heavy and

Table 1

Rate of shoot growth in 'Hass' avocado trees at Irvine, California. Data are the means of 10 shoots on each of 40 trees (1992) or 20 shoots on each of 20 trees (1993–1996) pooled over four rootstocks. Rootstock did not significantly ($P > 0.05$) affect shoot growth.

Year	Shoot growth rate (mm day ⁻¹)	
	Spring	Summer
1992	0.64	0.27
1993	4.92	5.86
1994	1.80	0.50
1995	0.73	0.64
1996	1.22	0.29

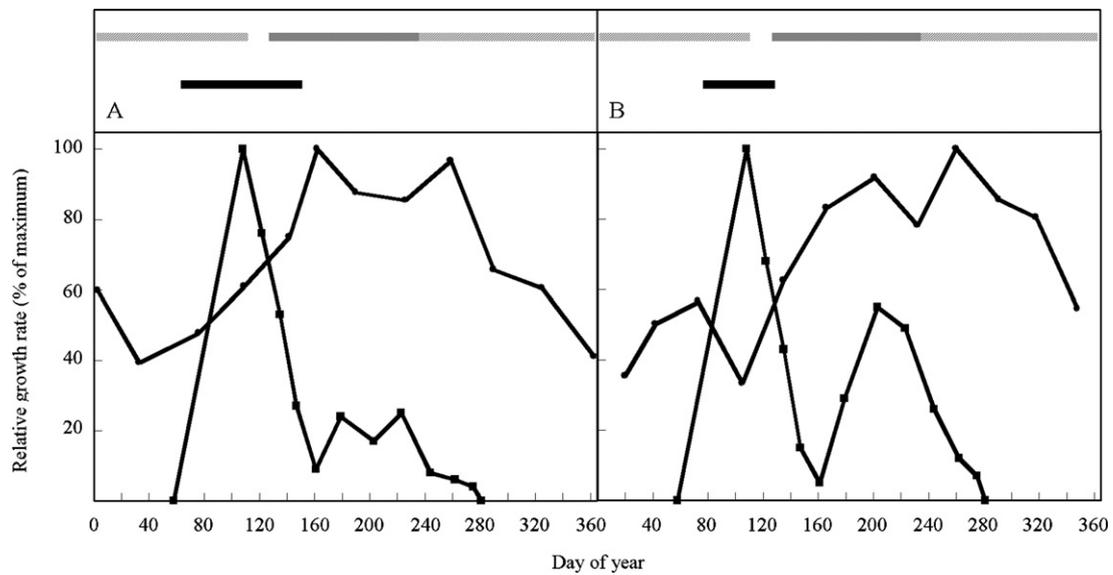


Fig. 1. Graphical model of relative timing of phenological events of 'Hass' avocado in Irvine, California. Relative shoot (■) and root (●) growth, flowering (solid line), and fruit growth (dark hatched line = period of maximum growth increase, light hatched line = continued growth period) in heavy crop load (A) and light crop load (B) years for 'Hass' on four clonal rootstocks. Shoot and root growth is expressed as the percent of the maximum growth rate observed. Fruit growth is for 'Hass' on 'Duke 7' rootstock only.

light crops except in 1993 ($P < 0.05$), when the yield was almost zero and shoot growth was nine times greater than in the other years. Higher than normal rainfall that winter may also have contributed to this growth.

When the crop was heavy in 1992 and 1994, the spring flush accounted for 60–80% of shoot growth. When the crop was light in 1993 and 1995, the growth of the summer flush was nearly equal to or higher than the spring flush, and accounted for 75% and 37% of total growth, respectively, in those years. The relationship between shoot growth and yield in 1996 was different to that of other years. There was a light crop on the trees in 1996 (average yield of $16.5 \text{ kg tree}^{-1}$), so it would be expected that the summer flush would account for a large proportion of the total growth, but instead, spring growth accounted for 80% of the total growth.

Crop load may also have an indirect effect on the type of shoots produced. The excessive growth observed in 1993 consisted of 46% sylleptic and 54% proleptic shoots compared with 2–0% sylleptic branches in the other years. Another feature of growth in 1993 was that all the measured shoots had tertiary branches, while the shoots in other years had almost no tertiary branches (data not shown).

In 1995 and 1996, some shoots abscised soon after tagging (Fig. 2). Abscission occurred mostly during the following September and October. By the fall of the third year, shoot retention for trees tagged in 1995 and 1996 was 47.7% and 62.4%, respectively. Only minimal abscission occurred after the third year. There were no significant differences ($P > 0.05$) in shoot abscission among rootstocks. Shoots that did not abscise within the first or second year were longer than those that did, in three out of four cases (Table 2), and these longer shoots subsequently became part of the tree's structure.

3.2. Root growth

Root growth was continuous, but slowed when shoot growth was strong in spring (Fig. 1). Overall, root growth rate tended to be highest after the spring and summer flushes and when soil temperatures were higher.

Root growth rate varied with rootstocks in different seasons and years (Table 3). In general, differences were only apparent in the fall of 1993, 1994, and 1995, and the winter of 1994 and 1996, when the shoots were not growing. Differences in yearly root growth

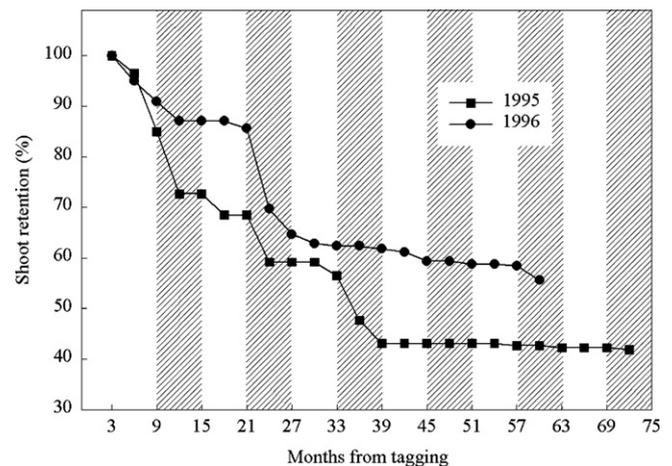


Fig. 2. The percentage of shoots retained in 'Hass' trees on four clonal rootstocks at Irvine, California. Data are means of the four rootstocks, since rootstock had no significant effect ($P > 0.05$) on growth. Shoots were tagged in February of 1995 (●) or 1996 (■), and shoot abscission monitored for up to 5 years. The first point for each year (with 100% retention) represents the date of tagging. Shaded areas represent fall and winter periods (September through February).

(Table 3) generally reflected these seasonal differences. Yield was not related to daily, seasonal, or yearly root growth.

Although root growth tended to be higher during summer and fall when soil temperatures were higher (Fig. 1), there were no

Table 2

Effect of shoot type (present or abscised) on the length of primary shoots of 'Hass' avocado Trees 1 or 2 years after tagging in Irvine, California. Data are the means of 40 trees pooled over four rootstocks.

	Shoot length (cm)			
	Tagged in 1995		Tagged in 1996	
	After 1 year	After 2 years	After 1 year	After 2 years
Present	107.7	117.2	121.0	133.5
Abscised	50.2	68.6	85.4	87.7
Sig. of F^a	***	*	n.s.	***

^a ns, *, *** are non-significant, or significant at $P \leq 0.05$, or $P \leq 0.001$, respectively. Statistical analysis performed using log transformed data.

Table 3
Effect of rootstock on mean annual root growth rate of 'Hass' avocado trees at Irvine, California. Data are the means of 10 trees per rootstock.

Rootstock	1992	1993	1994	1995	1996
	Root growth rate (mm day ⁻¹)				
Thomas	0.75ab ^a	0.72	0.67a	0.52a	0.38a
Topa Topa	0.84a	0.97	0.75a	0.32bc	0.25b
Duke 7	0.60c	0.69	0.47b	0.18c	0.23b
D9	0.67bc	0.72	0.75a	0.38ab	0.24b
Sig. of F ^b	*	n.s.	*	**	*

^a Means within a column with different letters are significantly ($P=0.05$) different based on Fisher's Protected Least Significant Difference test at $P=0.05$.

^b ns, *, **, are non-significant, or significant at $P \leq 0.05$, or $P \leq 0.01$, respectively. The data were transformed [$\log_{10}(\text{rate} + 1)$], before analysis with backtransformed data presented.

significant correlations between average high or low temperatures within a measurement period (*i.e.*, the time between root growth data collection) and root growth.

3.3. Nutrient analyses

Leaf N and P were lowest on 'Thomas' and 'Topa Topa', respectively, only in 1992 (Table 4). Leaf Fe varied among rootstocks only in 1993. The only leaf nutrient that did not differ among rootstocks in any year was B. Leaves of trees on 'Thomas' had higher S concentrations in 1993 and 1994, trees on 'Topa Topa' had high Mg and low K in 1992 and 1994, and trees on 'D9' had low Mn concentrations from 1993 to 1995. Leaf concentrations of P, Ca, and S were all lower in years preceding low yields.

4. Discussion

In the first part of this study, we observed the typical alternate bearing pattern of avocado trees in California (Mickelbart et al., this issue). Heavy yields consisted of a higher number of fruit per tree and a lower average fruit weight. These heavy yields coincided with a lighter, shorter return bloom that preceded a lighter crop in the following year. Rootstock did not affect the timing or magnitude of these events. Here we report on the vegetative growth of the same trees in relation to alternate bearing. Shoot growth consisted of two flushes: one in spring and one in summer. In years in which a small crop was on the tree, the summer flush accounted for a greater proportion of the total shoot growth for the year. Shoot abscission was monitored in two years and was as high as 60% in 1995. Unlike shoot growth, root growth occurred throughout the year, but was slightly reduced during the shoot flush periods. Leaf nutrient concentrations varied among rootstocks in different years, but concentrations of P, Ca, and S were all lower in years following a heavy crop. As noted for reproductive aspects of avocado phenology in California, rootstock did not affect the vegetative phenology of these trees.

Davenport (1982), Ploetz et al. (1993), and Whiley and Wolstenholme (1990) studied avocado phenology using visual observations rather than quantitative growth measurements. Our study is also the first quantitative assessment of vegetative and reproductive avocado phenology in Southern California, a state that accounts for approximately 90% of avocado production in the U.S., and nearly 100% of the 'Hass' production in the U.S. (Anonymous, 2000).

4.1. Shoot growth

Two shoot flushes (Fig. 1) occurred during the warmest periods of the year, spring and summer (Table 1). However, the number of flushes did not vary with year, rootstock, or crop load. In subtropical Southern Australia, New Zealand, Florida, Mexico, and Southern California, avocado trees typically have two to three flushes per

year (Cossio-Vargas et al., 2008; Davenport, 1982; Ploetz et al., 1993; Rocha-Arroyo et al., 2011; Thorp et al., 1995; Whiley and Wolstenholme, 1990; Venning and Lincoln, 1958). In tropical climates such as Trinidad, trees can flush up to six times a year (Gregoriou and Kumar, 1982).

Shoot growth rates (Table 1) were similar to those recorded in Florida (Ploetz et al., 1993), and shoot growth was typically greater in spring than in summer, as previously reported (Thorp et al., 1993; Venning and Lincoln, 1958). Within a given tree, some shoots remained dormant while others flushed, as previously demonstrated (Salazar-Garcia et al., 2006; Venning and Lincoln, 1958), and this perhaps contributed to the difficulty in identifying significant rootstock effects. Rootstock can affect shoot growth (Thorp and Sedgley, 1993). In our study there was sometimes an almost two-fold difference in mean total shoot growth among rootstocks, but a large variation among replicates. There are several classes of shoots within an avocado tree (Gregoriou and Kumar, 1982), and these can exhibit different rates of shoot extension. In 1993, individual shoot extension was as low as 10 cm and as high as 1775 cm. Overall, rootstock did not influence shoot extension or canopy volume.

The negative relationship between crop load and vegetative growth in temperate fruit tree species is well established (Boynton and Anderson, 1956; Webster and Brown, 1980). However, this relationship has not been extensively studied in tropical or subtropical fruit tree crops. Furthermore, in the few species that have been examined, the relationship is unclear (Menzel et al., 1993). The lack of vegetative growth in heavy cropping years has been noted in avocado (Venning and Lincoln, 1958), and avocado shoots that bear fruit are on average shorter than those that do not (Wolstenholme et al., 1990).

In this study, the relationship between yield and shoot growth was not clear. In 1993, the crop was almost zero and shoot growth was nine times the average of all the other years. However, from 1994 to 1996, yield was not related to cumulative shoot growth. This suggests that crop load *per se* does not affect vegetative growth in avocado, but the lack of a crop results in excessive vegetative growth. It is important that growers control excessive vegetative growth in years with little or no yield. Crop load did affect the relative growth occurring in summer and spring. This is an important finding in that it may help to elucidate strategies for timing of pruning or spraying. In years with light crops, it may be more important to prune the summer flush to control tree size.

A heavy crop followed years with a longer summer flush, especially in 1993. There were also more tertiary shoots and more sylleptic growth in that year. Tomlinson and Gill (1973) define proleptic shoots as developing after a period of dormancy, whereas sylleptic shoots develop without dormancy. In most cases, sylleptic growth is related to increased shoot extension (Tomlinson and Gill, 1973; Kurian and Reddy, 1999). It is therefore not surprising that the extensive shoot growth in 1993 was mainly sylleptic.

Tomlinson (1978) noted that some tropical tree species have continual and sylleptic growth as opposed to less vigorous species that exhibit primarily proleptic growth. This in turn affected the shape of the tree. Seasonal differences in shoot growth may, therefore, influence tree architecture and more vigorous and spreading trees require more pruning than less vigorous and compact trees.

Shoot abscission plays a major role in determining the architecture of the tree in different environments (Addicott, 1978). Most abscission occurred in fall or winter before the spring flush (Fig. 2). Abscission data were collected in the final two years of shoot growth measurements, so the relationship between growth and abscission cannot be determined. It has been suggested that short photoperiods induce shoot abscission (Wareing, 1954; Downs, 1958). While shoot abscission occurred throughout the year, most shoot abscission occurred during those times of the year when photoperiod was below 12 h (Fig. 2).

Table 4

Effect of rootstock leaf nutrient concentrations in 'Hass' avocado trees in Irvine, California. Data are the means of ten trees per rootstock.

Rootstock	N (mg g ⁻¹ DW)					P (mg g ⁻¹ DW)					K (mg g ⁻¹ DW)				
	1991	1992	1993	1994	1995	1991	1992	1993	1994	1995	1991	1992	1993	1994	1995
Thomas	2.59	2.60a ^c	2.40	2.27	2.18	0.12	0.19a	0.16	0.18	0.15	1.31	1.11a	1.32a	1.61a	1.56a
Topa Topa	2.41	2.30b	2.33	2.09	2.36	0.11	0.16b	0.16	0.17	0.15	1.21	0.98b	1.11b	1.13c	1.34b
Duke 7	2.47	2.40b	2.36	2.14	2.12	0.10	0.18a	0.15	0.18	0.14	1.35	1.08a	1.31a	1.37b	1.43ab
D9	2.38	2.40b	2.44	2.18	2.24	0.12	0.18a	0.16	0.18	0.15	1.36	1.08a	1.33a	1.69a	1.54a
Sig. ^b	n.s.	***	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	*	**	***	*
Average ^a	2.46a	2.42a	2.38a	2.17b	2.23b	0.11d	0.18a	0.16b	0.18a	0.15c	1.31b	1.06c	1.27b	1.45a	1.47a
Rootstock	Mg (mg g ⁻¹ DW)					Ca (mg g ⁻¹ DW)					S (mg g ⁻¹ DW)				
	1991	1992	1993	1994	1995	1991	1992	1993	1994	1995	1991	1992	1993	1994	1995
Thomas	0.46c	0.54d	0.58b	0.63b	0.41c	1.51	1.94b	1.58	1.85b	1.32	–	0.46a	0.43a	0.55a	–
Topa Topa	0.68a	0.79a	0.75a	0.84a	0.51a	1.63	2.28a	1.70	2.23a	1.30	–	0.40b	0.35b	0.41bc	–
Duke 7	0.65a	0.73b	0.73a	0.66b	0.48ab	1.65	2.35a	1.77	1.83b	1.44	–	0.46a	0.37b	0.45b	–
D9	0.55b	0.65c	0.63b	0.57b	0.44bc	1.53	2.27a	1.60	1.76b	1.33	–	0.41b	0.31c	0.37c	–
Sig.	***	***	***	***	*	n.s.	***	n.s.	**	n.s.		**	***	***	***
Average	0.58b	0.68a	0.67a	0.68a	0.46c	1.58c	2.21a	1.66c	1.92b	1.34d		0.43a	0.36b	0.44a	0.58b
Rootstock	B (μg g ⁻¹ DW)					Fe (μg g ⁻¹ DW)					Mn (μg g ⁻¹ DW)				
	1991	1992	1993	1994	1995	1991	1992	1993	1994	1995	1991	1992	1993	1994	1995
Thomas	23.9	26.0	30.6	44.4	50.2	45	56	57b	58	70	331a	228a	126a	101a	103a
Topa Topa	23.9	28.2	27.0	39.6	48.7	49	52	62ab	52	70	300a	186b	119a	94a	91a
Duke 7	22.9	29.6	26.8	42.5	47.4	48	52	58b	65	67	266ab	274a	120a	110a	100a
D9	22.9	29.3	28.4	40.6	48.0	42	53	67a	53	60	222b	153b	78b	62b	63b
Sig.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	*	***	**	***	***
Average	23.4d	28.3c	28.2c	41.7b	48.6a	46d	53c	61ab	57bc	67a	280a	208b	110c	91d	89d

^a Rootstock means for a given nutrient and year within a column with no letter(s) in common are significantly different based on Fisher's protected least significant difference test at $P=0.05$.

^b Significance of F value, ns, *, **, *** are non-significant, or significant at $P \leq 0.05$, $P \leq 0.01$, or $P \leq 0.001$, respectively.

^c Year means for a given nutrient within a row with no letter(s) in common are significantly different based on Fisher's protected least significant difference test at $P=0.05$.

4.2. Root growth

There was no consistent effect of rootstock on root growth (Table 3). Total root growth is difficult to quantify in mature avocado trees when only a small portion of the root zone is monitored. Variations in the distribution of roots in the soil from tree to tree (Durand and Claassens, 1987) make it difficult to determine the effect of rootstock. However, we observed consistent patterns from year to year in terms of total root growth per tree, number of roots per tree, and individual root growth rate.

Roots grew throughout the year as in Florida (Ploetz et al., 1993) and New Zealand (Thorp et al., 1995). Growth was highest during warm months (Fig. 1). Root growth rates per day were lower than those reported for 'Lula' or 'Simmonds' growing on seedling rootstocks in Florida (Ploetz et al., 1993). The trees in that study were grown in containers on West Indian rather than Mexican rootstocks. Mean seasonal temperatures during summer are also lower in California than in Florida. Root growth did not exhibit distinct flushes as described by Cull (1986), and also did not follow the model of Whiley and Wolstenholme (1990), which showed two distinct flushes and the cessation of growth during winter in subtropical Queensland, Australia. Thorp et al. (1995) showed that in one location in New Zealand, root growth coincided with shoot growth, however, other authors indicate that shoot and root growth flushes alternate (Ploetz et al., 1993). Our data also suggests that root growth is highest when the shoots are not actively growing (Fig. 1). This would suggest that growers in California should use soil-applied fertilizers or root rot fungicides any time it is warm and when the shoots are not growing.

4.3. Leaf nutrient concentrations

Conflicting data exist in the literature regarding the effect of crop load or alternate bearing on leaf nutrient concentrations in fruit and

nut trees (Picchioni et al., 1997). In heavy-yield years, leaf P, Ca, and S concentrations were higher than in low-yield years (Table 4). The increase in leaf P in years with heavy crops contrasts reports on olive (Fernandez-Escobar et al., 1999), pistachio (Rosecrance et al., 1998), and citrus (Golomb and Goldschmidt, 1987). The patterns of Ca accumulation reflect those of all other reports in the literature (see Picchioni et al., 1997 for a review). Calcium may need to be applied in years with light crop loads, as the low Ca concentrations observed may lead to Ca-related fruit disorders (Ferguson and Watkins, 1992). As far as we are aware, this is the first report of fluctuating concentrations of leaf S with crop load.

Leaf N concentrations in avocado may be lower during periods of very active shoot growth (Cull, 1986). Leaves and new shoots account for the majority of the N stored within an avocado tree (Lovatt, 1996). Therefore, it would be expected that N might be limiting in a year in which the tree is flushing heavily. Leaf N decreased in 1994 after excessive vegetative growth in 1993. Overall, however, leaf N concentration did not correlate with vegetative growth. Leaf N concentrations in trees on each of the rootstocks in our study were within the recommended values for avocado (Embleton and Jones, 1966), presumably because N uptake by the roots matches N demand by the tree. Overall, differences in nutrient concentrations among rootstocks were not correlated with growth or yield.

4.4. Conclusions

We did not measure carbohydrates in this study, so we can only speculate on the possible role of the production, storage, and/or use of carbohydrates related to phenology. Monerri et al. (2011) found no relationship between carbohydrate concentrations and yield in orange trees, whereas Scholefield et al. (1985) measured high carbohydrate concentrations preceding a high-yield year and lower concentrations in the following year. In general, the relationship between avocado yields and carbohydrates is weak (Whiley et al.,

1996). The relationship between yield and shoot growth was weak in this study. However, in 1993, when yields were very low, shoot growth was approximately nine times that of other years. This may be due to the availability of carbohydrates that in a high-yield year would have been utilized during fruit growth.

Phenology is asynchronous in most species (Alvim and Alvim, 1978), making comparisons among species or rootstocks difficult. Overall, trees grown on different rootstocks have similar patterns of shoot and root growth, indicating the major commercial rootstocks used by the California avocado industry today exhibited similar phenological patterns over a five-year period. Therefore, any recommendations made with respect to cultural practices can be made with confidence that rootstock does not alter the timing or intensity of phenological events. Yield was not directly related to the pattern of vegetative growth, suggesting that other factors, such as carbohydrate reserves, may be important for productivity in avocado. Undoubtedly, weather, water availability, and nutrient status of the tree also affected the timing and rate of the observed phenological events.

Acknowledgements

The authors thank Eric Focht, Michelle Gottlieb (deceased), William Manor, Stacey Ontai, Christine Reints, David Stottlemyer, and Angela Wang for assistance in the data collection, and Carol Adams (deceased) for data analysis. The research reported was funded in part by a grant-in-aid from the California Avocado Commission.

References

- Addicott, F.T., 1978. Abscission strategies in the behavior of tropical trees. In: Tomlinson, P.B., Zimmermann, M.H. (Eds.), *Tropical Trees as Living Systems*. Cambridge University Press, Cambridge, pp. 381–397.
- Alvim, P.D.T., Alvim, R., 1978. Relation of climate to growth periodicity in tropical trees. In: Tomlinson, P.B., Zimmermann, M.H. (Eds.), *Tropical Trees as Living Systems*. Cambridge University Press, Cambridge, pp. 445–464.
- Anonymous, 2000. Calif. Avocado Comm. Annu. Rpt. 1999–2000, 8 pp.
- Boynnton, D., Anderson, L.C., 1956. Some effects of mulching, nitrogen fertilization, and liming on McIntosh apple trees, and the soil under them. *Proc. Amer. Soc. Hortic. Sci.* 67, 26–36.
- Cossio-Vargas, L.E., Salazar-García, S., González-Durán, I.J.L., Medina-Torres, R., 2008. Fenología del aguacate 'Hass' en el clima semicálido de Nayarit. Mexico. *Revista Chapingo Serie Hortic.* 14, 325–330.
- Cull, B.W., 1986. A phenological cycling approach to tree crop productivity research. *Acta Hortic.* 175, 151–156.
- Davenport, T.L., 1982. Avocado growth and development. *Proc. Fla. State Hortic. Soc.* 95, 92–96.
- Downs, R.J., 1958. Photoperiodic control of growth and dormancy in woody plants. In: Thimann, K.V. (Ed.), *The Physiology of Forest Trees*. Ronald Press, New York, pp. 529–537.
- Durand, B.J., Claassens, N.J.F., 1987. Root distribution of avocado trees in different soil types. *S. Afr. Avocado Growers' Assn. Yrbk.* 10, 15–19.
- Embleton, T.W., Jones, W.W., 1966. Avocado and mango nutrition. In: Childers, N.F. (Ed.), *Fruit Nutrition*. Horticultural Publications, Rutgers, New Jersey, pp. 51–76.
- Ferguson, I.B., Watkins, C.B., 1992. Crop load affects mineral concentrations and incidence of bitter pit in 'Cox's Orange Pippin' apple fruit. *J. Amer. Soc. Hortic. Sci.* 117, 373–376.
- Fernandez-Escobar, R., Moreno, R., Garcia-Creus, M., 1999. Seasonal changes of mineral nutrients in olive leaves during the alternate-bearing cycle. *Sci. Hortic.* 82, 25–45.
- Golomb, A., Goldschmidt, E.E., 1987. Mineral nutrient balance and impairment of the nitrate-reducing system in alternate-bearing 'Wilking' mandarin trees. *J. Amer. Soc. Hortic. Sci.* 112, 397–401.
- Goodall, G.E., Embleton, T.W., Platt, R.G., 1981. Avocado fertilization. Univ. of Calif. Div. of Agric. Sci., Oakland, California, Leaflet, 2024.
- Gregoriou, C., Kumar, D.R., 1982. Some aspects of shoot and root growth of avocado under lowland tropical conditions. *Calif. Avocado Soc. Yrbk.* 66, 127–144.
- Kurian, R.M., Reddy, Y.N., 1999. Pattern of shoot growth in *Zizyphus mauritiana* and *Z. oenoplia*. *Ann. Bot.* 84, 289–295.
- Lee, S.K., Young, R.E., Schiffman, P.M., Coggins Jr., C.W., 1983. Maturity studies of avocado fruit based on picking dates and dry weight. *J. Amer. Soc. Hortic. Sci.* 108, 390–394.
- Lovatt, C.J., 1996. Nitrogen allocation within the 'Hass' avocado. *Calif. Avocado Soc. Yrbk.* 80, 75–83.
- Menzel, C.M., Haydon, G.F., Doogan, V.J., Simpson, D.R., 1993. New standard leaf nutrient concentrations for passionfruit based on seasonal phenology and leaf composition. *J. Hortic. Sci.* 68, 215–229.
- Mickelbart, M.V., Bender, G.S., Witney, G.W., Adams, C., Arpaia, M.L., 2007. Effects of clonal rootstocks on 'Hass' avocado yield components, alternate bearing, and nutrition. *J. Hortic. Sci. Biotech.* 82, 460–466.
- Mickelbart, M.V., Robinson, P.W., Witney, G., Arpaia, M.L., 2012. 'Hass' avocado tree growth on four rootstocks in California. I. Yield and flowering. *Sci. Hortic.* 143, 184–188.
- Monerri, C., Fortunato-Almeida, A., Molina, R.V., Nebauer, S.G., Garcia-Luis, A., Guardiola, J.L., 2011. Relation of carbohydrate reserves with the forthcoming crop, flower formation and photosynthetic rate in the alternate bearing 'Salustiana' sweet orange (*Citrus sinensis* L.). *Sci. Hortic.* 129, 71–78.
- Picchioni, G.A., Brown, P.H., Weinbaum, S.A., Muraoka, T.T., 1997. Macronutrient allocation to leaves and fruit of mature, alternate-bearing pistachio trees: magnitude and seasonal patterns at the whole-canopy level. *J. Amer. Soc. Hortic. Sci.* 122, 267–274.
- Ploetz, R.C., Ramos, J.L., Parrado, J.L., 1993. Periodicity of shoot and root growth in grafted avocado. *Trop. Agric.* 70, 248–251.
- Robinson, P.W., Mickelbart, M.V., Arpaia, M.L., 1994. 'Hass' avocado phenology in California—preliminary results. *HortScience* 29, 517.
- Rocha-Arroyo, J.L., Salazar-García, S., Bárceñas-Ortega, A.E., González-Durán, I.J.L., Cossio-Vargas, L.E., 2011. Phenology of 'Hass' avocado in Michoacán. *Rev. Mexicana Cienc. Agric.* 2, 303–316.
- Rosecrance, R.C., Weinbaum, S.A., Brown, P.H., 1998. Alternate bearing affects nitrogen, phosphorus, potassium and starch storage pools in mature pistachio trees. *Ann. Bot.* 82, 463–470.
- Salazar-García, S., Lord, E.M., Lovatt, C.J., 1998. Inflorescence and flower development of the 'Hass' avocado (*Persea americana* Mill.) during on and off crop years. *J. Amer. Soc. Hortic. Sci.* 123, 537–544.
- Salazar-García, S., Cossio-Vargas, L.E., Lovatt, C.J., Gonzalez-Durán, I.J.L., Pérez-Barraza, M.H., 2006. Crop load affects vegetative growth flushes and shoot age influences irreversible commitment to flowering of 'Hass' avocado. *Hortic. Sci.* 41, 1541–1546.
- Scholefield, P.B., Sedgley, M., Alexander, D.McE., 1985. Carbohydrate cycling in relation to shoot growth, floral initiation and development and yield in the avocado. *Sci. Hortic.* 25, 99–110.
- SAS Institute, INC., 1990. *SAS User's Guide: Statistics*, Sixth ed. SAS Inst., Inc., Cary, N.C.
- Thorp, T.G., Aspinall, D., Sedgley, M., 1993. Influence of shoot age on floral development and early fruit set in avocado (*Persea americana* Mill.) cv. Hass. *J. Hortic. Sci.* 68, 645–651.
- Thorp, T.G., Sedgley, M., 1993. Manipulation of shoot growth patterns in relation to early fruit set in 'Hass' avocado (*Persea americana* Mill.). *Sci. Hortic.* 56, 147–156.
- Thorp, T.G., Anderson, P., Camilleri, M.J., 1995. A New Zealand model of avocado tree growth cycles. *Avocado Res. Rep.* 1994/95, A report to the New Zealand Avocado Growers' Association. 8 pp.
- Tomlinson, P.B., 1978. Branching and axis differentiation in tropical trees. In: Tomlinson, P.B., Zimmermann, M.H. (Eds.), *Tropical Trees as Living Systems*. Cambridge University Press, Cambridge, pp. 445–464.
- Tomlinson, P.B., Gill, A.M., 1973. Growth habits of tropical trees: some guiding principles. In: Meggers, B.J., Ayensu, E.S., Duckworth, W.D. (Eds.), *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*. Smithsonian Institution Press, Washington, D.C, pp. 129–143.
- Turrell, F.M., 1946. Tables of Surfaces and Volumes of Spheres and of Prolate and Oblate Spheroidal and Spheroidal Coefficients. Univ. of Calif. Press, Oakland, California, p. 153.
- Venning, F.D., Lincoln, F.B., 1958. Developmental morphology of the vegetative axis of avocado (*Persea americana* L.) and its significance to spacing, pruning practices, and yields of the grove. *Proc. Fla. State Hortic. Soc.* 71, 350–356.
- Wareing, P.F., 1954. Growth studies of woody species: VI. The locus of photoperiodic perception in relation to dormancy. *Physiol. Plant.* 7, 191–214.
- Webster, D.H., Brown, G.L., 1980. Trunk growth of apple tree as affected by crop load. *Can. J. Plant Sci.* 60, 1383–1391.
- Whiley, A.W., Rasmussen, T.S., Saranah, J.B., Wolstenholme, B.N., 1996. Delayed harvest effects on yield, fruit size and starch cycling in avocado (*Persea americana* Mill.) in subtropical environments. I. The early-maturing cv. Fuerte. *Sci. Hortic.* 66, 23–34.
- Whiley, A.W., Wolstenholme, B.N., 1990. Carbohydrate management in avocado trees for increased production. *S. Afr. Avocado Growers' Assn. Yrbk.* 13, 25–27.
- Wolstenholme, B.N., 1986. Energy costs of fruiting as a yield-limiting factor with special reference to avocado. *Acta Hortic.* 175, 121–126.
- Wolstenholme, B.N., Whiley, A.W., Saranah, J.B., 1990. Manipulating vegetative:reproductive growth in avocado (*Persea americana* Mill.) with paclobutrazol foliar sprays. *Sci. Hortic.* 41, 315–327.