



Dynamics of shoot and fruit growth following fruit thinning in olive trees: Same season and subsequent season responses



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ABSTRACT

The need to understand how the balance between vegetative and reproductive growth in olive trees is modified by different crop loads has become more important over the last 20 years due to increasing planting densities and the greater use of irrigation. The objectives of this study conducted in a well-irrigated olive orchard were to: (1) evaluate shoot and fruit growth dynamics following fruit thinning during the same growing season in which thinning was applied and during the next growing season; and to (2) determine crop load effects on bloom, fruit set, and fruit yield over three growing seasons. Hand-thinning of fruit 35 days after full bloom on 9-year-old cv. 'Arauco' trees in an "on" year led to thinning treatments of 24, 48, and 87% with respect to an unthinned control. Apical and lateral shoot elongation were measured every two weeks throughout the growing season, and fruit were sampled to determine fruit weight at the same interval. Apical shoot elongation occurred only early in the season when crop load was medium or high, while apical elongation continued for most of the season when crop load was low. Elongation of laterals contributed significantly to total shoot elongation on fruit-bearing branches in trees with low crop loads after thinning the first season. Individual fruit dry weight was reduced about 40% by high crop loads in both seasons. Differences in relative growth rates of both the shoots and the fruit due to crop load suggest fruit growth was limited by photoassimilate availability early in the season, but shoot growth was limited most of the season under medium and high crop loads. Inflorescence number per shoot was reduced by crop load in the two seasons following the thinning event. Fresh fruit yield was only reduced in one of the two biennia (i.e., periods of 2 years) in the trees that were heavily thinned (87%) the first season. The trees in which about one-half (48%) of the fruit were thinned the first season did not show biennial yield reductions and maintained a low alternate bearing index over three seasons. Thus, chemical thinning could be applied in growing seasons with high flowering. Further studies are needed to better assess competition for resources between shoots and fruit with the ultimate goal of reducing alternate bearing.

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1. Introduction

Similar to the Mediterranean region, the expansion of large, intensively-managed olive orchards (>100 ha) with greater planting densities than traditional orchards has resulted in profound changes in olive growing in South America over the past 20 years. Such intensive orchards use high levels of irrigation and fertiliz-

ers to improve yields and are often located at warm, subtropical latitudes with long growing seasons (Ayerza and Sibbett, 2001; Gómez del Campo et al., 2010; Searles et al., 2011). Alternate bearing (i.e., "off" versus "on" production years) is fairly common in warm regions when an event such as a hot desert wind or a frost in some mountainous areas eliminates flowering structures, which can lead to vigorous vegetative growth the current season and high yield the next season (Lavee et al., 2007). Once an alternate bearing cycle is initiated, it may continue throughout the life of the tree unless fruit thinning or other management options are explored (Monselise and Goldschmidt, 1982; Lavee, 2006).

In olive, bloom and subsequently fruit number depend on the number of axillary buds formed by shoot growth in the previous season, the induction of these potentially reproductive buds, and

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the accumulation of sufficient winter chilling to break endodormancy (Rallo et al., 1994; Smith and Samach, 2013). Floral induction occurs during the fruit growth period and high crop load may facilitate a hormonal signal that inhibits induction (Fernández-Escobar et al., 1992; Samach and Smith, 2013). Thus, early fruit thinning in an 'on' year can play an important role in increasing return bloom the following season and in reducing alternate bearing (e.g., Dag et al., 2009, 2010). The thinning of flowers or fruit also improves fruit quality in many fruit tree species (Forshey and Elfving, 1989; Guardiola and García-Luis, 2000). In olive, chemical fruit thinning is commercially practiced in table varieties in California (USA) and Israel to increase fruit size (Krueger et al., 2002; Birger et al., 2008). However, it is still quite uncommon in the newer commercial growing regions of South America.

Shoot and fruit growth in olive are largely a function of the crop load in a given season (Rallo et al., 1994; Lavee, 2007). For example, both apical and lateral shoot elongation have been reported to be greater on five year-old, non-fruit bearing branches than on similar fruit-bearing branches (Castillo-Llanque and Rapoport, 2011). When partial fruit thinning is practiced, shoot length is also most often greater at the end of the season (Proietti and Tombesi, 1996). Shoot elongation has been found to have the capacity to increase even when fruit are removed up to 120 days after full bloom (i.e., mid-summer) (Dag et al., 2010). In terms of reproductive growth, both individual fruit weight and pulp-to-pit ratio are consistently greater in olive when crop load is low (Barone et al., 1994; Proietti et al., 2006; Gucci et al., 2007; Trentacoste et al., 2010).

Because bloom occurs early in the season, vegetative and reproductive growth in fruit trees occur simultaneously for several months during the season, which can lead to competition for resources among the various plant organs (Forshey and Elfving, 1989; DeJong, 1999; Wünsche and Ferguson, 2005). In peach, analysis of growth dynamics indicates that both shoot elongation and fruit growth may be limited by resources (i.e., photoassimilates) during some periods (Grossman and DeJong, 1994). For example, shoot elongation in peach was often limited by resources for a short period early in the season likely due to the re-establishment of leaf area in this deciduous species, while fruit growth was limited for a longer period early in the season and again just before harvest (Pavel and DeJong, 1993; Grossman and DeJong, 1995a,b,c). Resource limitations have also been observed in other deciduous fruit trees such as apple as reviewed by Wünsche and Ferguson (2005).

In evergreen olive trees, less knowledge is available concerning how the seasonal dynamics of shoot and fruit growth are modified by different crop loads and when source-limited periods may occur. Rallo and Suárez (1989) observed that leaf length, number, and area as well as the dry weight of fruit-bearing branches increased rapidly in the spring with a plateau being reached approximately 60–100 days after bloom and little or no growth the rest of the season. Trunk growth may also slow sharply at about the same time (Cuevas et al., 2010), probably due to competition for assimilates with the fruit, which may be strong sinks after pit hardening (50–60 d after bloom). In contrast, Connor and Fereres (2005) have suggested that shoot elongation and leaf expansion may be maintained from spring to autumn if sufficient irrigation is provided. Studies with different crop loads could provide much needed information to more explicitly assess the observations and assumptions mentioned above.

The objectives of this study conducted in an intensive, well-irrigated olive orchard in Northwest Argentina (La Rioja) were to: 1) evaluate shoot and fruit growth dynamics in cv. 'Arauco' olive trees following fruit thinning during the same growing season in which thinning was applied and during the next growing season; and to 2) determine crop load effects on bloom, fruit set, and fruit yield over three growing seasons. It should be noted that fruit thin-

ning was only performed the first season, and that many of the fruit and shoot growth responses in subsequent seasons were thus considered to be indirect responses to the single thinning event.

2. Materials and methods

2.1. Experimental orchard

The study was conducted in a commercial olive orchard (*Olea europaea* cv. 'Arauco') located near Bañado de Los Pantanos in the Province of La Rioja, Argentina (28.4°S, 66.8°W, 805 m above sea level) over three growing seasons. The cv. 'Arauco' has large fruits, high vegetative vigor, and is considered to be unique to Argentina (International Olive Oil Council, 2000). The trees were 9 years-old at the start of the experiment with a spacing of 6 m within rows × 8 m between rows (208 trees ha⁻¹) and an east-west row orientation. Tree canopy volume was initially 13 ± 3 m³ and was approximately spherical in shape due to its being trained as a free-vase with little branch thinning in the internal part of the canopy (Gucci and Cantini, 2000). The trees were not pruned during the experiment in order to better assess responses to crop load.

The soil was gravelly sand in texture, deep (>1 m), and classified as typical Torripsamenes using the USDA soil classification system. Main annual rainfall in the area is approximately 900 mm with most rainfall occurring between November and March (i.e., late spring – summer). Due to the coarse soil texture and low rainfall, crop evapotranspiration requirements (100% ETC) were covered by irrigating 3–4 times weekly over the entire year using a drip irrigation system. A crop coefficient (Kc) of 0.7 was employed most of the year based on previous results in a neighboring orchard (Correa-Tedesco et al., 2010), and a reduction factor (Kr) was used to correct for crop ground cover. Fertilization with N, P, K and Mg was provided through the drip system based on periodic foliar nutrient analyses at a commercial laboratory (La Buena Tierra, Catamarca ARG). If any deficiencies were detected, supplemental fertilization was provided to the experimental trees.

Temperature data were obtained from an automatic weather station (Davis Instruments, CA USA) located in a neighboring orchard at the same height above sea level. Daily maximum and minimum temperatures indicated a wide range of temperature conditions during the experimental period (Fig. 1). Freezing temperatures (<0 °C) were recorded on an average of 35 days during the winters of 2008–2010, while maximum daily temperatures were often above 35 °C during the summer.

2.2. Fruit thinning treatments

Twenty-four trees were selected in early October 2007 at full bloom. Thinning was performed on 18 of the trees approximately five weeks after full bloom on November 13–14, 2007 by manually removing different percentages (33, 66, or 95%) of fruit from the entire tree canopy. The remaining 6 trees were used as controls and were not thinned. The experimental design was a randomized complete block design with one tree from each of the experimental four groups assigned to a given block and there were 6 blocks (i.e., 4 trees per block × 6 blocks = 24 trees).

The various thinning treatments were applied to the entire tree canopy by removing from each branch one of every three fruit (33%), two of every three fruit (66%), or 19 of every 20 fruit (95%). The number of thinned fruit was quantitatively assessed by dividing the fresh weight of all thinned fruit per tree by the weight of a sub-sample of 50 thinned fruits. After the final harvest, the percentage of thinned fruits could then be calculated as the number of thinned fruits divided by total fruit number. Total fruit number included the thinned fruit, fruit sampled during the course of the

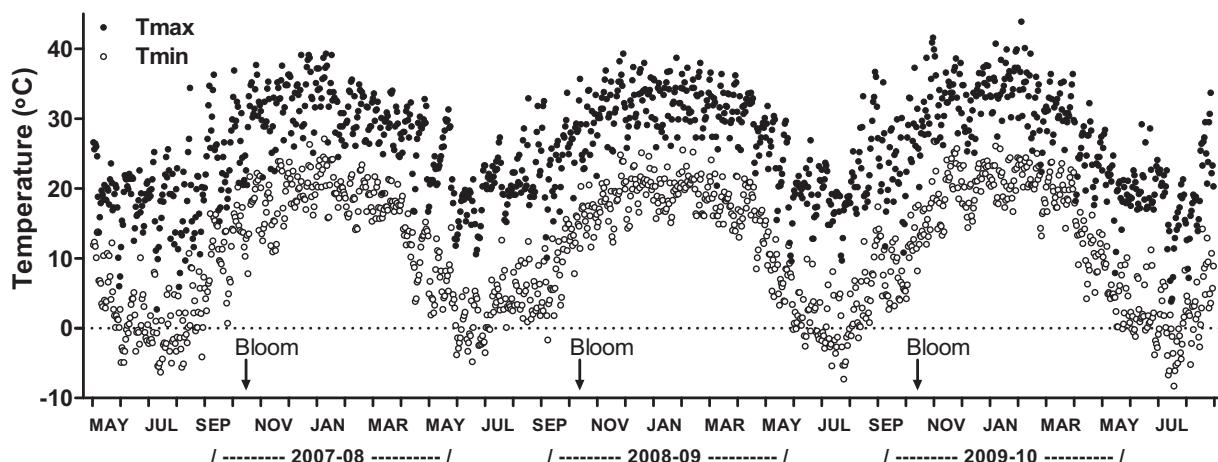


Fig. 1. Daily maximum and minimum air temperatures over three growing seasons (2007–08, 2008–09, 2009–10). A growing season is considered to be from approximately September through May for our Southern Hemisphere location with full bloom occurring in early- to mid-October.

season, and the fruit at final harvest. The number of fruits sampled during the season represented only 1–2% of the total fruit number per tree with the exception of the heavily thinned experimental trees the first growing season where the percentage was slightly higher (7%).

2.3. Shoot, trunk, and canopy growth

Apical shoot elongation was measured every 15 days from early spring until the winter rest period on vegetative and reproductive shoots during the 2007–08 and 2008–09 seasons. The term vegetative shoot refers to young shoots with no fruits that were formed late in the previous growing season or at the start of the current growing season. Reproductive shoots were one-year-old shoots with fruit load representative of each experimental group. Four vegetative and four reproductive shoots were measured per tree including one for each cardinal direction. The vegetative and reproductive shoots were about 5 cm and 20 cm long at the beginning of the season, respectively. The vegetative shoots used the first growing season were re-categorized as reproductive the second season, while new vegetative shoots were selected for the second season. Additionally, the number and length of lateral shoots formed on the vegetative and reproductive shoots were measured every 15 days, although these measurements were not initiated until at least 45 days after full bloom (DAFB) the first growing season because their potential importance for determining total shoot growth was not anticipated. Total shoot growth was calculated by summing apical and lateral shoot elongation for each measurement date.

Trunk cross-sectional area (TCSA) was calculated by measuring trunk circumference with a tape measure 30 cm above the soil surface every 15 days during the 2007–08 and 2008–09 growing seasons. The tree canopy volume (V) was determined as a spherical cap using the formula, $V = \pi d^2 h/6$, where d is the average of canopy diameter in the east-west and north-south directions and h is canopy height (i.e., tree height minus the distance between the soil surface and the tree skirt). Volume measurements were performed at the beginning and end of three consecutive growing seasons (2007–08, 2008–09, and 2009–10).

2.4. Fruit growth

Fresh and dry fruit weight were determined every 15 days from mid-spring (15–30 DAFB) until final harvest during the 2007–08 and 2008–09 seasons by sampling 20 fruit per tree from the outer portion of the tree canopy. The fruit were stored in airtight plastic

cups in the field and weighed in the laboratory using an analytic balance to obtain fresh weight. The fruit were then dried in a drying-oven at 75 °C for several days until a constant weight was reached.

2.5. Harvest

Total fresh fruit yield (kg) per tree was obtained by harvesting each tree individually by hand in late-summer (i.e., mid-March) for green table olives as is most common in our region for the cv. 'Arauco'. To avoid any sampling bias between treatments due to the earlier fruit samples, the weight of the sampled fruits over the course of the season (0.8–1.2 kg tree⁻¹) was added to the yield of each tree for all four experimental groups. Although fruit growth dynamics were not evaluated during the third season (2009–10), the trees were harvested to further assess the indirect, subsequent season responses to the earlier thinning event. The number of fruits per tree at harvest was calculated as total yield per tree divided by the fresh weight of 50 fruits. Number of fruit was then used to express crop load as the number of fruit per cubic meter of canopy volume (# fruits m⁻³).

2.6. Return bloom and fruit set

The trees selected for the experiment the first growing season (2007–08) were considered to have potentially high crop loads based on the number of inflorescences counted just prior to full bloom on four, one-year-old reproductive shoots of each tree. On average, 66% of the axillary bud positions had inflorescences, which equated to 0.73 inflorescences per cm of shoot. In the following two seasons (2008–09, 2009–10), the number of inflorescences were determined on the vegetative branches marked the previous season. The number of fruit were counted on the same branches 40 DAFB in 2008–09 and 2009–10 to estimate fruit set as the number of fruit per inflorescence. The number of flowers on each inflorescence was not determined due to their small size, which makes counting them difficult under field conditions.

2.7. Shoot and fruit growth rates

Either relative or absolute elongation rates of the apical, lateral, and total shoot growth were determined on the marked vegetative and reproductive shoots. Similar to Solari et al. (2006), relative elongation rates (RER) of apical shoot growth were calculated every 15 days for the entire first two growing seasons as $[\ln(L_2) - \ln(L_1)] / (T_2 - T_1)$ where L_2 and L_1 represent length at times T_2 and T_1 and the

units are $\text{mm m}^{-1} \text{d}^{-1}$. When data for both apical and lateral shoots were available from the middle of the first season until the end of the second season, the RER of total growth were similarly calculated. In the case of lateral shoots, absolute elongation rates rather than relative rates were determined because some vegetative and reproductive shoots did not produce laterals, and the natural log of zero is undefined. The absolute rates were calculated as $(L_2 - L_1) / (T_2 - T_1)$ in mm d^{-1} . Relative fruit growth rates (RFGR) were obtained using the dry weights of the fruit samples collected every 15 days over the first two growing seasons with the units being $\text{mg g}^{-1} \text{d}^{-1}$.

In all rate calculations, time was principally expressed as DAFB rather than thermal time because the information available concerning the lower and upper temperature thresholds for olive shoot and fruit growth is scarce (Pérez-López et al., 2008; García-Inza et al., 2014). Nevertheless, thermal time, which was calculated as degree days ($^{\circ}\text{C d}^{-1}$) using the single sine, horizontal cut-off method (<http://www.ipm.ucdavis.edu>), is indicated in the figure captions when appropriate using the threshold temperatures of 7 and 40°C proposed by Cherbiy-Hoffmann et al. (2013).

2.8. Alternate bearing index

Fluctuations in fresh fruit yield between growing seasons were evaluated for each experimental group using the alternate bearing index (ABI), $(Y_n - Y_{n+1}) / (Y_n + Y_{n+1})$, where Y_n and Y_{n+1} are the fresh fruit yield in a given year and in the following year, respectively. The ABI was calculated for two biennia (2007–08 + 2008–09; 2008–09 + 2009–10), and total yield for each biennium was also determined.

2.9. Statistical analysis

The responses of shoot elongation, fruit weight, and the growth rates to crop load over the course of each growing season were analyzed with general linear mixed models of ANOVA for repeated measurements over time (InfoStat Version 2011, Universidad Nacional de Córdoba, Argentina). When statistically significant interactions ($P < 0.05$) were detected between crop load and time in these analyses, the Fisher LSD post-test was used to assess treatment differences between crop loads for each date during the growing season. Similar to Pavel and DeJong (1993), a significant difference in relative growth rate between crop loads at a specific date was considered to indicate a source (i.e., photoassimilate) limitation. Canopy volume, trunk parameters, and yield were evaluated using ANOVA at end of each season.

3. Results

3.1. Fruit thinning

The estimated fruit thinning percentages were slightly lower (24, 48, 87%) than the proposed target percentages (33, 66, 95%) when thinning was applied the first growing season. This likely occurred due to difficulty in seeing the small fruit within the dense tree canopy. Nevertheless, statistically significant differences in crop load were observed between treatments during the first season and in the subsequent two seasons when thinning was not applied (Table 1; $P < 0.05$). Unthinned, control trees and lightly thinned trees (i.e., 24% thinning) showed relatively high crop loads in the first and third growing seasons and a low crop load in the second season. As would be expected, the heavily thinned trees (87%) demonstrated an opposite pattern with only a high crop load in the second season. In contrast, the moderately thinned trees (48%)

Table 1

Crop load for the season in which fruit thinning was applied (2007–08) and for subsequent seasons (2008–09, 2009–10).

	Fruit thinning (%)	Crop load (# m^{-3} canopy)		
		Seasons 2007–08	2008–09	2009–10
Control	1061 ± 103a	480 ± 94c	825 ± 58a	
24%	818 ± 85b	483 ± 33c	803 ± 50a	
48%	539 ± 33c	759 ± 77b	571 ± 53b	
87%	132 ± 15d	1338 ± 60a	114 ± 13c	

Values with different letters indicate significant differences between crop loads in the same season using the Fisher LSD post-test ($P < 0.05$). $n = 6 \pm$ standard error.

trees showed only minor fluctuations in crop load over the three seasons.

3.2. Apical shoot elongation

The apical elongation of non-bearing, vegetative shoots occurred mainly in the first 45 DAFB on unthinned trees with high crop load ($1061 \text{ fruit m}^{-3}$) during the first growing season based on repeated measures analysis (Fig. 2a, $P < 0.05$). The duration of apical elongation of vegetative shoots for trees with moderate crop loads was similar to that of high crop load trees, while elongation occurred over a longer period (90–120 DAFB) in heavily thinned trees with low crop load (87% thinning; 132 fruit m^{-3}). This longer duration led to nearly twice the apical elongation of vegetative shoots on trees with low crop load compared to that of the other treatments at the end of the season. Lastly, elongation of fruit-bearing, reproductive shoots during the first season (Fig. 2c) was much lower than that of vegetative shoots (Fig. 2a), but the response to crop load did not differ between the two shoot types.

In the second season (2008–09), indirect effects of fruit thinning the previous season on apical shoot elongation were observed. Heavily thinned trees with the lowest crop load (132 fruit m^{-3}) and the greatest apical elongation the first season had the highest crop load ($1338 \text{ fruit m}^{-3}$) and the lowest vegetative shoot elongation the second season (Fig. 2b). In a similar manner, the unthinned control the first season ($1061 \text{ fruit m}^{-3}$) had the lowest crop load (480 fruit m^{-3}) and the greatest apical elongation of vegetative shoots the second season. In contrast to the first season, apical shoot elongation of vegetative shoots continued up to 160–190 DAFB with the exception of the highest crop load (Fig. 2b). In reproductive shoots, although statistically significant differences ($P < 0.05$) in apical elongation were detected between crop levels the second season, apical elongation was generally very low (<20 mm; Fig. 2d).

3.3. Relative elongation rates

The apical RER of non-bearing, vegetative shoots decreased markedly from full bloom to 75 DAFB the first season in trees with moderate and high crop loads, but decreased to a lesser degree in the lowest crop load treatment (132 fruit m^{-3}) (Fig. 3a). The apical RER was greater in this treatment than the others from approximately 25 days after thinning (60 DAFB) until about three weeks before harvest (135 DAFB). At the end of the season (180–210 DAFB), trees with fairly high crop loads prior to harvest (818 , $1061 \text{ fruits m}^{-3}$) showed slightly greater apical RER in vegetative shoots compared to trees with lower crop loads before harvest (132 , 539 fruit m^{-3}). For reproductive shoots, the apical RER response to fruit thinning was pronounced with apical RER increasing after thinning in the lowest crop load treatment and being greater than that of the other treatments from 60 to 120 DAFB (Fig. 3c).

In the second season (2008–09), the apical RER of vegetative and reproductive shoots decreased until about 90 DAFB and remained

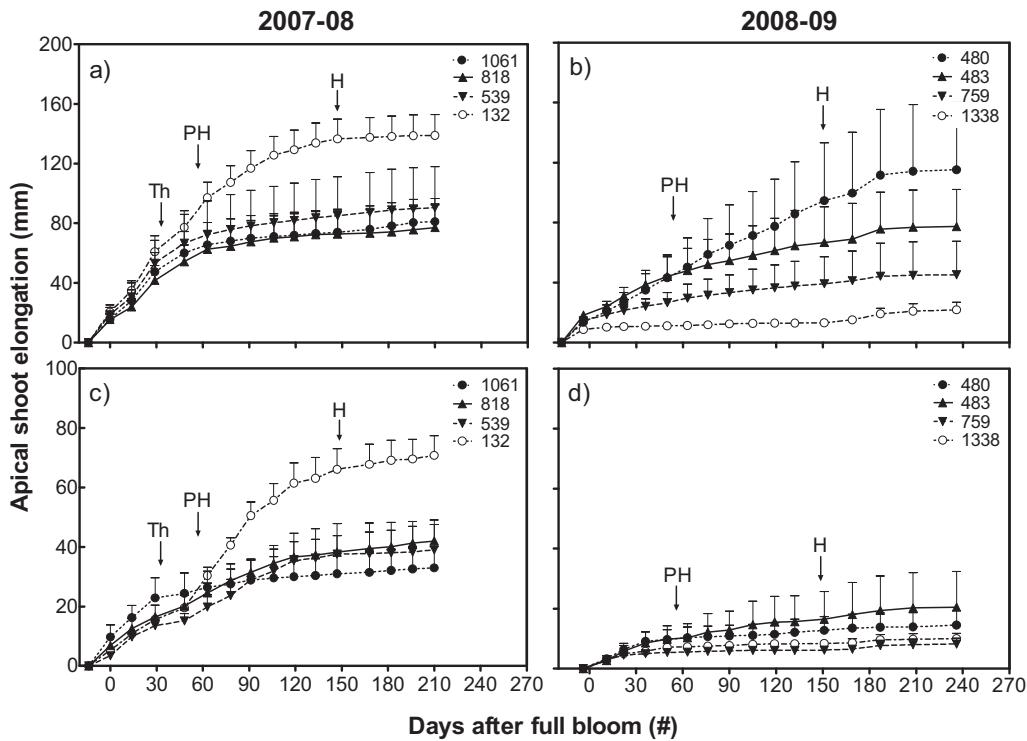


Fig. 2. Apical elongation of vegetative (a, b) and reproductive (c, d) shoots under different tree crop loads ($\# \text{ m}^{-3}$) in the same season as fruit thinning (2007–08) and in the subsequent season (2008–09). All vegetative shoots were without fruit, while reproductive shoots had crop loads similar to that of the whole tree. The tree crop loads 1061, 818, 539, and 132 in 2007–08 represent the unthinned control and the 24%, 48%, and 87% thinned treatments, respectively. The same symbol is used for the crop load of the same group of trees in 2007–08 and 2008–09. The dates of fruit thinning (Th), pit hardening (PH), and harvest of green table olives (H) are indicated with arrows. Thermal time was approximately 3800 and 4300 degree days in 2007–08 and 2008–09, respectively, for the periods in which elongation was measured. Each point represents the mean of $n=6 \pm$ standard error.

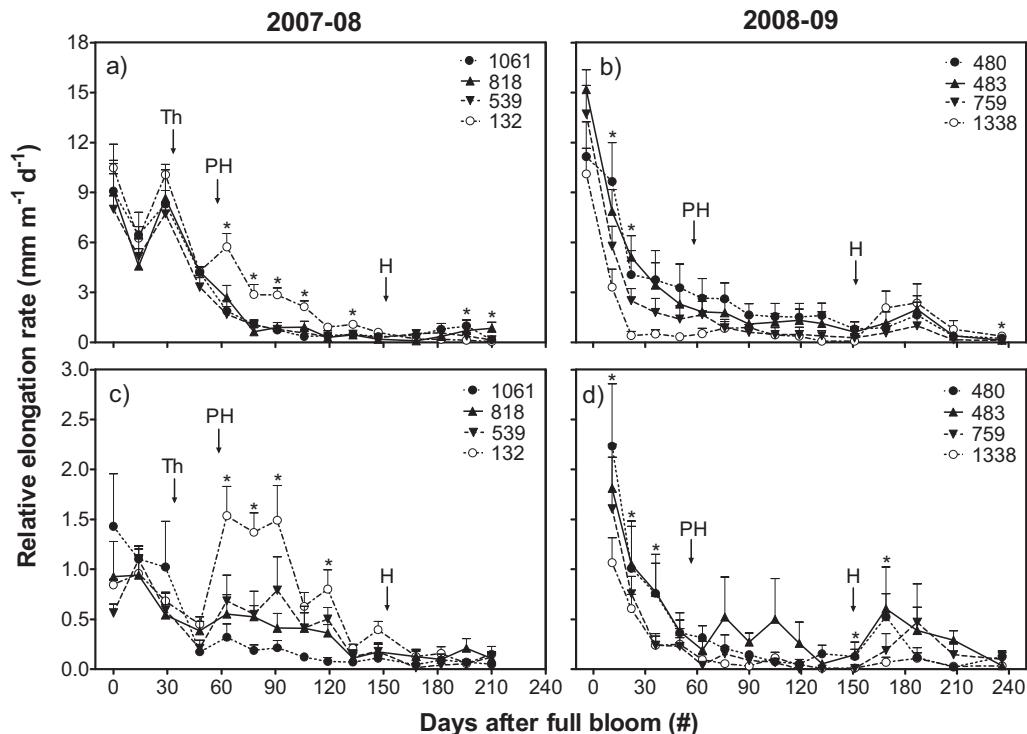


Fig. 3. Relative elongation rate of apical growth on vegetative (a, b) and reproductive (c, d) shoots under different tree crop loads ($\# \text{ m}^{-3}$) in the same season as fruit thinning (2007–08) and in the subsequent season (2008–09). All vegetative shoots were without fruit, while reproductive shoots had crop loads similar to that of the whole tree. The tree crop loads 1061, 818, 539, and 132 in 2007–08 represent the unthinned control and the 24%, 48%, and 87% thinned treatments, respectively. The same symbol is used for the crop load of the same group of trees in 2007–08 and 2008–09. The dates of fruit thinning (Th), pit hardening (PH), and harvest of green table olives (H) are indicated with arrows. Thermal time was approximately 3800 and 4300 degree days in 2007–08 and 2008–09, respectively, for the periods in which elongation was measured. Each point represents the mean of $n=6 \pm$ standard error. Asterisks indicate significant differences between crop loads for a given date ($P < 0.05$).

Table 2

Apical, lateral, and total shoot elongation of non-bearing vegetative shoots and fruit-bearing reproductive shoots under different crop loads. Fruit thinning was applied in 2007–08 and the indirect effects of thinning were observed in 2008–09.

Season	Crop load (#m ⁻³)	Vegetative shoot			Reproductive shoot		
		Apical(mm)	Lateral(mm)	Total(mm)	Apical(mm)	Lateral(mm)	Total(mm)
2007–08	1061	81 ± 16a	10 ± 9a	91 ± 23a	33 ± 7a	6 ± 6a	39 ± 10a
	818	77 ± 15a	5 ± 2a	82 ± 16a	42 ± 6a	16 ± 7a	58 ± 10a
	539	91 ± 28a	20 ± 12a	111 ± 39a	39 ± 10a	7 ± 2a	46 ± 10a
	132	139 ± 14b	11 ± 9a	150 ± 19a	71 ± 7b	89 ± 29b	160 ± 33b
2008–09	1338	22 ± 5a	3 ± 1a	25 ± 2a	10 ± 2a	35 ± 13a	45 ± 15a
	759	45 ± 22ab	2 ± 1a	47 ± 23a	8 ± 2a	28 ± 10a	36 ± 8a
	483	78 ± 25ab	53 ± 50a	131 ± 72a	20 ± 12a	27 ± 11a	47 ± 22a
	480	115 ± 45b	38 ± 24a	153 ± 66a	14 ± 5a	35 ± 11a	49 ± 11a

Unthinned control = 1061 fruit m⁻³ in 2007–08; 24%, 48%, and 87% thinning treatments were 818, 539, and 132 fruit m⁻³, respectively. Values with different letters indicate significant differences between crop loads in the same season using the Fisher LSD post-test ($P < 0.05$). $n = 6 \pm$ standard error

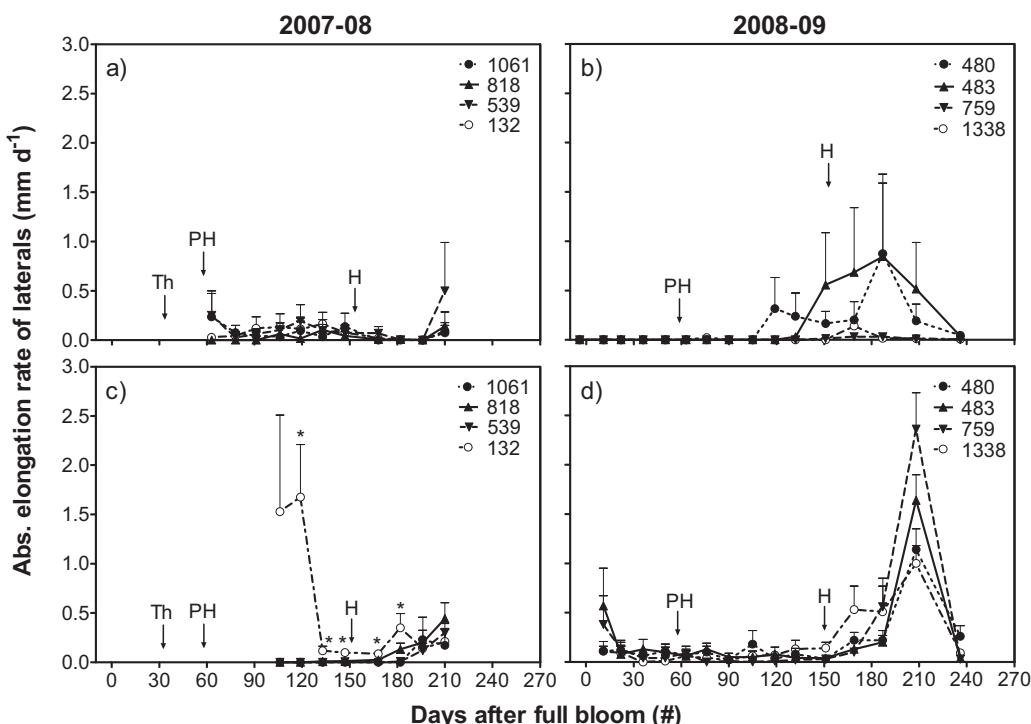


Fig. 4. Absolute elongation rate of laterals on vegetative (a, b) and reproductive (c, d) shoots under different tree crop loads (# m⁻³) in the same season as fruit thinning (2007–08) and in the subsequent season (2008–09). All vegetative shoots were without fruit, while reproductive shoots had crop loads similar to that of the whole tree. The tree crop loads 1061, 818, 539, and 132 in 2007–08 represent the unthinned control and the 24%, 48%, and 87% thinned treatments, respectively. The same symbol is used for the crop load of the same group of trees in 2007–08 and 2008–09. The dates of fruit thinning (Th), pit hardening (PH), and harvest of green table olives (H) are indicated with arrows. Each point represents the mean of $n = 6 \pm$ standard error. Asterisks indicate significant differences between crop loads for a given date ($P < 0.05$).

fairly constant until harvest with a slight increase the month following harvest in some treatments (Fig. 3b and d). Unlike the first season when all trees had similar crop loads until thinning was applied 35 DAFB, the different crop loads from the start of the second season resulted in differences in apical RER between treatments very early in the season, but not later. The apical RER for trees with fairly low crop load (480, 483 fruit m⁻³) was greater than trees with moderate to high crop loads (759, 1338 fruit m⁻³) during the first 30–40 DAFB in both shoot types (Fig. 3b and d). Although there were some minor differences in apical RER between crop loads after harvest, the results are not consistent with high crop loads having greater RER after harvest as occurred the first season.

3.4. Lateral and total shoot growth

At the end of both growing seasons, the contribution of elongation by newly-formed lateral shoots to total shoot elongation

was much lower than that of apical elongation for the non-bearing, vegetative shoots (Table 2). This occurred because very few laterals formed on the vegetative shoots. In contrast, the thinning event in the first season significantly stimulated the formation of laterals and their elongation on reproductive shoots in trees with low fruit load (132 fruit m⁻³), but not in trees with moderate or high crop loads. This led to lateral elongation being more than 50% of total elongation at the end of the first season for these low crop load, reproductive shoots. Although lateral elongation was greater than apical elongation for all reproductive shoots the second season, there was no significant effect of crop load, likely because the lowest crop load (480 fruit m⁻³) was much greater than that of the first season.

To assess the dynamics of lateral shoot growth, the absolute elongation rates (AER) were calculated. Although measurements were not initiated until 90 DAFB the first season on the reproductive shoots, there appears to have been a peak around this time in

the AER of lateral shoots on reproductive branches in trees with low crop load (132 fruit m^{-3}) (Fig. 4c). Indeed, the AER was significantly greater in the low crop load trees than in the other trees from 120 DAFB until after harvest (180 DAFB). This agrees with the large difference in the elongation of lateral shoots in the low crop load treatment in comparison to that of the other treatments at the end of the first season (Table 2). No differences in absolute elongation rate were detected in vegetative branches the first season (Fig. 4a). When measurements were conducted over the full growing season (0–240 DAFB) in 2008–09, the number of laterals on both vegetative and reproductive shoots was very low for the first 100 DAFB. The AER reached maximum values after harvest very late in the season for laterals of both vegetative and reproductive shoot types including a pronounced peak for the laterals of reproductive shoots at 210 DAFB (Fig. 4b and d). However, no statistically significant differences were apparent between crop loads for either shoot type.

Lastly, it should be mentioned that the dynamics of total shoot elongation (apical + laterals) for non-bearing, vegetative shoots were similar to those of apical elongation in Fig. 3a, b for both seasons because few laterals were formed (Table 2). In contrast, the considerable elongation of laterals on reproductive shoots with low crop loads in 2007–08 led to significant differences in total shoot RER between crop loads up to 180 DAFB (Fig. 5), rather than 120 DAFB when only apical elongation was evaluated (Fig. 3b). The laterals on the reproductive shoots did not affect the response of total shoot RER to crop load during the second season (data not shown).

3.5. Fruit growth

Individual fruit dry weight increased linearly the first season for each crop load ($r^2 \geq 0.98$ in all four cases; $P < 0.001$) from fruit thinning to green table olive harvest (35–152 DAFB; Fig. 6a). Fruit

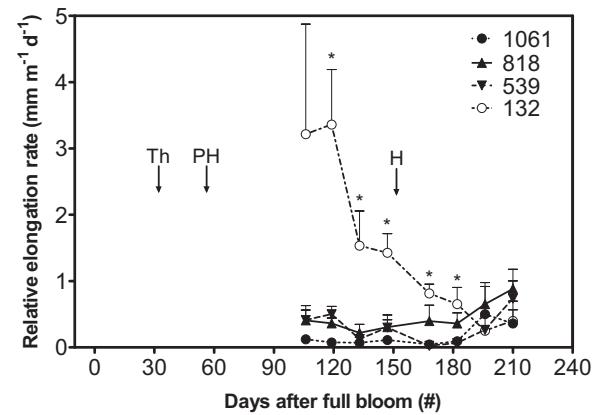


Fig. 5. Relative elongation rate of the total shoot including apical plus lateral elongation for reproductive shoots under different tree crop loads ($\# \text{ m}^{-3}$) in the same season as fruit thinning (2007–08). Reproductive shoots had crop loads similar to that of the whole tree. The tree crop loads 1061, 818, 539, and 132 represent the unthinned control and the 24%, 48%, and 87% thinned treatments, respectively. The dates of fruit thinning (Th), pit hardening (PH), and harvest of green table olives (H) are indicated with arrows. Each point represents the mean of $n=6 \pm$ standard error. Asterisks indicate significant differences between crop loads for a given date ($P < 0.05$).

weight over the course of the season in trees with a low crop load (132 fruit m^{-3}) was significantly greater than in trees with a moderate crop load (539 fruit m^{-3}) using repeated measures analysis, while fruit weight in trees with higher crop loads (818, 1061 fruit m^{-3}) was much lower than that of the moderate crop load trees. When an early measurement (15 DAFB) of fruit weight was added the second season, fruit growth of trees with low and moderate crop loads initially appeared to increase slowly (15–30 DAFB) and then to increase more linearly until harvest. Individual

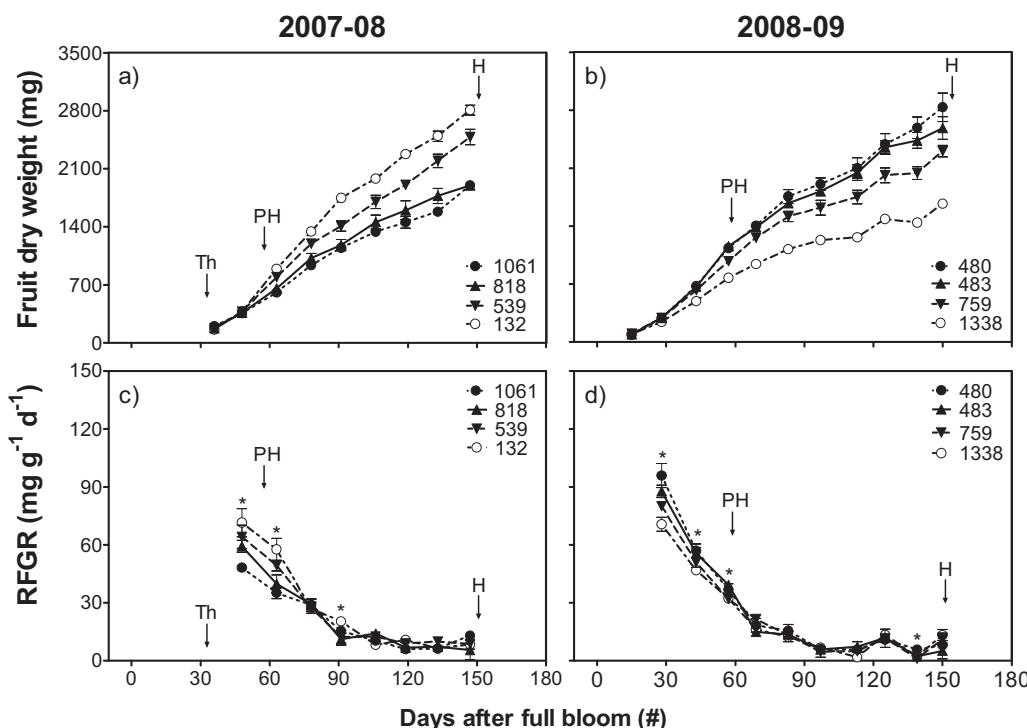


Fig. 6. Individual fruit dry weight (a, b) and relative fruit growth rate (RFGR) (c, d) under different tree crop loads ($\# \text{ m}^{-3}$) in the same season as fruit thinning (2007–08) and in the subsequent season (2008–09). The tree crop loads 1061, 818, 539, and 132 in 2007–08 represent the unthinned control and the 24%, 48%, and 87% thinned treatments, respectively. The same symbol is used for the crop load of the same group of trees in 2007–08 and 2008–09. The dates of fruit thinning (Th), pit hardening (PH), and harvest of green table olives (H) are indicated with arrows. Thermal time was approximately 2830 and 2760 degree days in 2007–08 and 2008–09, respectively, from full bloom to harvest. Each point represents the mean of $n=6 \pm$ standard error. Asterisks indicate significant differences between crop loads for a given date ($P < 0.05$).

Table 3

Inflorescence number per shoot, inflorescence density, and fruit set for the two subsequent seasons following the fruit thinning in the Spring of 2007. Crop load is given for the previous season.

Spring	Previous crop load (#m ⁻³ canopy)	Inflorescences (# shoot ⁻¹)	Inflorescence density (# cm ⁻¹)	Fruit set (fruit/infl. x 100%)
2008	1061	6.3 ± 0.8a	0.50 ± 0.03a	25.3 ± 9.4a
	818	8.5 ± 2.2a	0.51 ± 0.17a	25.7 ± 8.3a
	539	13.6 ± 2.8b	0.76 ± 0.07b	25.3 ± 3.7a
	132	22.2 ± 1.0c	0.92 ± 0.04b	17.4 ± 2.6a
2009	1338	0	0	0
	759	3.0 ± 0.6a	0.41 ± 0.10a	46.5 ± 9.5a
	483	5.6 ± 1.1b	0.62 ± 0.11a	19.7 ± 4.6b
	480	5.1 ± 0.6b	0.54 ± 0.10a	21.6 ± 8.4b

Unthinned control = 1061 fruit m⁻³ in 2007–08; 24%, 48%, and 87% thinning treatments were 818, 539, and 132 fruit m⁻³, respectively. Values with different letters indicate significant differences between crop loads in the same season using the Fisher LSD post-test ($P < 0.05$). $n = 6 \pm$ standard error

Table 4

Tree canopy volume parameters and trunk cross-sectional area (TCSA) growth at the end of each growing season under different crop loads. Fruit thinning was applied in 2007–08 and the indirect effects of thinning were observed in two subsequent seasons (2008–09, 2009–10).

Season	Crop load (# m ⁻³)	Canopy Vol. increase (m ³)	Canopy Volume (m ³)	TCSA increase (cm ²)
2007–08	1061	1.3 ± 0.2b	15.5 ± 0.8c	24.8 ± 3.0b
	818	1.3 ± 0.2b	15.3 ± 0.9c	19.7 ± 1.9b
	539	1.8 ± 0.2a	16.4 ± 0.9b	25.5 ± 3.1b
	132	2.2 ± 0.2a	18.0 ± 0.9a	46.5 ± 2.0a
2008–09	1338	0.9 ± 0.2b	19.8 ± 0.9a	13.6 ± 1.3c
	759	1.1 ± 0.9b	18.5 ± 0.9a	25.8 ± 1.9b
	483	2.0 ± 0.3a	19.3 ± 1.3a	35.8 ± 3.4a
	480	2.2 ± 0.2a	19.7 ± 0.9a	44.4 ± 5.3a
2009–10	825	1.3 ± 0.3b	22.3 ± 0.9a	NA
	803	1.1 ± 0.2b	21.6 ± 1.4a	NA
	571	2.1 ± 0.5a	22.6 ± 1.5a	NA
	114	2.6 ± 0.5a	25.1 ± 1.8a	NA

Unthinned control = 1061 fruit m⁻³ in 2007–08; 24%, 48%, and 87% thinning treatments were 818, 539, and 132 fruit m⁻³, respectively. Values with different letters indicate significant differences between crop loads in the same season using the Fisher LSD post-test ($P < 0.05$). $n = 6 \pm$ standard error. NA = data not available.

fruit dry weight the second season was greater in trees with low crop loads (480, 483 fruit m⁻³) than trees with moderate or high crop load (Fig. 6b). The maximum reduction in fruit dry weight within the range of crop loads examined was approximately 40% in both seasons.

The relative fruit growth rate (RFGR) of all crop loads decreased from early in the season until 90 DAFB in 2007–08 and 2008–09, and then remained low until harvest (Fig. 6c and d). Greater RFGR values were observed in trees with low and moderate crop loads the first season than in high crop load trees shortly after fruit thinning until 90 DAFB ($P < 0.05$; Fig. 6c). Statistically significant differences in RFGR were also apparent between crop loads fairly early in the second season (Fig. 6d).

3.6. Return bloom and fruit set

The number of inflorescences per shoot was significantly greater in the spring of 2008 on shoots with low and medium crop loads the previous season due to fruit thinning than on shoots that were not thinned (1061 fruit m⁻³; Table 3). Similar results were observed in the spring of 2009 including no inflorescences on the observed shoots of trees with the previous season's highest crop load (1338 fruit m⁻³). Inflorescence density (inflorescences per cm of shoot) was also greater in the spring of 2008 on shoots with low and moderate crop loads the previous season than on shoots with high crop loads the previous season. In contrast, no significant effect of previous crop load on inflorescence density was detected for the spring of 2009. Fruit set (%) was not affected in the spring of 2008 by fruit thinning the previous season, but differences in fruit set were apparent in the spring of 2009. The results for the flower-

ing parameters were similar when expressed on either a per cm of shoot or per node basis (data not shown).

3.7. Tree canopy and trunk growth

The increase in tree canopy volume from the beginning to the end of the season (i.e., growth) was consistently reduced by crop load each of the three seasons examined ($P < 0.05$, Table 4). This led to the canopy volume being 18% lower in trees with high crop load than those with low crop load at the end of the first season. The alternation of high and low crop loads between seasons in the same trees resulted in similar canopy volumes at the end of the second season. In the third season, some indication of a difference (12%) in canopy volume was again apparent, but it was not statistically significant. Crop load also affected trunk cross-sectional area growth during the two seasons that were measured.

3.8. Fruit number, tree yield and alternate bearing index

As expected, fruit number per tree at harvest showed a wide range between crop loads in the first season when fruit thinning was applied and in the subsequent two seasons ($P < 0.05$, Fig. 7a). Similar to fruit number, fresh fruit yield per tree was also significantly greater under high crop loads in each season (Fig. 7b). Nevertheless, biennial yields were little affected (Table 5). The biennial yield of the heavily thinned trees (87%) was only decreased during the second biennial period compared to the other trees ($P < 0.05$; Table 5). The fluctuations in yield between seasons were greatest in the trees that originally received the 87% thinning, whereas the trees that received 48% thinning showed a relatively constant yield over the three seasons (Fig. 7b). This is indicated

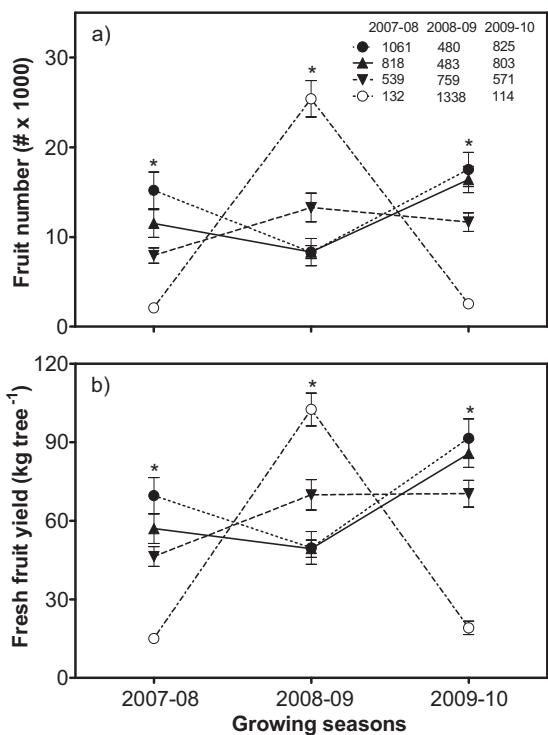


Fig. 7. Fruit number (a) and fresh fruit yield (b) per tree under different crop load levels over three growing seasons (2007–08, 2008–09, 2009–10). Fruit thinning was applied in 2007–08 and the indirect effects of thinning were observed in two subsequent seasons. In 2007–08, there were 1061 fruit m⁻³ of tree canopy in the control trees and 818, 539, and 132 fruit m⁻³ in the 24, 48, and 87% thinning treatments, respectively. Each point represents the mean of $n=6 \pm$ standard error. Asterisks indicate significant differences between crop loads for a given season ($P < 0.05$).

Table 5

The alternate bearing index (ABI) and the total fresh fruit yield per tree of each fruit thinning treatment or the control for two biennial periods. Fruit thinning was applied only in the 2007–08 season.

Biennium	Fruit thinning (%)	ABI (0–1)	Yield (kg tree ⁻¹)
2007–08 + 2008–09	Control	$0.22 \pm 0.05a$	$119 \pm 8a$
	24%	$0.13 \pm 0.04a$	$106 \pm 7a$
	48%	$0.20 \pm 0.03a$	$116 \pm 9a$
	87%	$0.75 \pm 0.03b$	$118 \pm 7a$
2008–09 + 2009–10	Control	$0.30 \pm 0.07a$	$141 \pm 9a$
	24%	$0.27 \pm 0.03a$	$135 \pm 7a$
	48%	$0.10 \pm 0.03b$	$140 \pm 8a$
	87%	$0.69 \pm 0.03c$	$122 \pm 7b$

Values with different letters indicate significant differences between thinning treatments in the same biennial period using the Fisher LSD post-test ($P < 0.05$). $n = 6 \pm$ standard error. 0 = no alternate bearing; 1 = complete alternate bearing.

by the greater alternate bearing index (ABI) in the heavily thinned trees (87%) than in the other thinned trees and control for the two biennial periods assessed (Table 5). In contrast, the moderately thinned trees (48%) had a statistically significant lower ABI than the lightly thinned (24%) and the control trees during the second biennial period.

4. Discussion

The need to understand how the seasonal dynamics of shoot and fruit growth are modified by different crop loads in olive trees has become more important over the last 20 years due to increasing planting densities and the greater use of irrigation (Lavee, 2007; Connor et al., 2014). Our results in a well-irrigated orchard (cv. 'Arauco') indicate that the duration of apical elongation for non-

bearing, vegetative shoots in trees with low overall tree crop load (132–480 fruit m⁻³) lasted several months (120–180 DAFB; Fig. 2a and b). Similarly, shoot elongation in "off" trees was observed to be greater than 135 DAFB in an irrigated orchard in Central Tunisia (Aiachi Mezghani et al., 2012).

When overall tree crop load was higher, apical elongation on non-bearing shoots occurred predominantly over a period as short as 50 DAFB in our experiment (Fig. 2a and b). On fruit-bearing shoots, apical elongation was always less than that of non-bearing shoots of the same tree crop load, and the duration of elongation on fruit-bearing shoots was also shorter with the exception of when crop load was very low (132 fruit m⁻³; Fig. 2c). Rallo and Suarez (1989) reported in fruit-bearing shoots of an "on" year that the duration of growth was somewhere between 60 and 100 DAFB for shoot length, number of nodes, leaf area, and leaf dry weight in an irrigated orchard (cv. 'Picual') in southern Spain. Taken together, these results suggest that most apical shoot elongation in olive trees occurs early in the season during fruit set and the initial stages of fruit growth under medium or high crop loads, but can extend throughout much of the season when crop load is low.

The contribution of lateral growth to total shoot elongation has seldom been considered in olive trees. When comparing five-year-old branches from "on" and "off" trees, Castillo-Llanque and Rapoport (2011) found that the number and length of laterals for "off" trees was 2–6 times higher than for "on" trees and that the majority (i.e., 80%) of the new shoots of "off" trees were lateral shoots. In contrast, elongation for "on" trees was mostly apical. In our study, the elongation of laterals after thinning depended on shoot type and the resulting crop load. When the trees were heavily thinned (87%) the first season, lateral elongation was greater than apical elongation on the fruit-bearing shoots with low crop load, but not on non-bearing, vegetative shoots (Table 2). In medium and high crop load trees that experienced less thinning, laterals were very uncommon for both shoot types the first season. More studies on lateral growth are needed in olive, but it appears that their formation is initiated after thinning under very low crop load conditions as has been seen in defruited peach trees (Grossman and DeJong, 1995c). When crop load is fairly high, fruit-derived auxin may alter the polar auxin transport system of the shoot to inhibit lateral growth (Smith and Samach, 2013).

Fruit growth and final weight were also reduced significantly by crop load in our study as has been seen by many authors (e.g., Barone et al., 1994; Dag et al., 2010). This was apparent at the end of the first season after the thinning event and in the subsequent second season without thinning (Fig. 6a and b). The increase in fruit dry weight through harvest for green table olives was approximately linear with the possible exception of slower growth in the first 15–30 DAFB. Such an expolinear growth pattern was first suggested for lightly-cropped fruit trees by Lakso et al. (1995). A fairly linear growth pattern for fruit weight appears to be common in high-input, olive orchards even under greater crop loads (Trentacoste et al., 2010; Martín-Vertedor et al., 2011b). In some other 'stone' fruit trees such as peach and cherry, fruit weight has the tendency to follow a double sigmoid pattern with two periods of rapid growth, one during cell division and another after pit hardening (Lakso and Goffinet, 2003). More detailed fruit growth studies during pit hardening are needed in order to better understand olive fruit growth. This could potentially be done using high-resolution, linear displacement transducers to assess fruit diameter and frequent sampling to assess fresh and dry fruit weight.

Our results show that relative growth rates of both apical shoots and fruit decreased sharply over the first 60–90 DAFB under medium and high crop loads (Figs. 3 and 6c and d). Similar overall patterns of shoot and fruit growth have been found in peach with relative growth rates decreasing to low values 70 DAFB (Grossman and DeJong, 1995a,c). Thus, sink activity appears to be very high

early in the season in both olive (an evergreen species) and peach (a deciduous species). Spring shoot growth, floral development, anthesis, fruit set, and initial fruit growth in evergreens such as citrus have been shown to demand large amounts of carbon that are provided by a combination of current photosynthesis and carbohydrate reserves (Goldschmidt, 1999). In olive, the role of reserves in the alternate bearing cycle is still unclear, but they are likely to be important early in the growing season for flowering and initial tree growth and later in the season for survival under drought or other extreme conditions (Bustan et al., 2011).

After the thinning event the first season (35 DAFB), the apical RER of vegetative, non-bearing shoots on low crop load trees decreased to a lesser degree (Fig. 3a) than on the medium and high crop load trees, while the apical RER of the reproductive shoots actually increased after thinning on low crop load trees (Fig. 3c). When statistically significant differences are found in relative growth rates between crop loads in fruit trees, this has been suggested to indicate a source (i.e., photoassimilate) limitation (Pavel and DeJong, 1993). The RER differences in apical shoot elongation of both vegetative and reproductive shoots in our study were from about 60–135 DAFB the first season when fruit thinning was applied, but differences in total elongation continued up to 180 DAFB in reproductive shoots (Fig. 5) on low crop load trees when lateral growth was included (Fig. 4c). When a range of crop load existed from the start of the second season (480–1338 fruit m⁻³), source limitation appeared to occur much earlier (15–30 DAFB) and lateral shoots did not play a critical role later in the season.

In fruit, source limitation was apparent no later than 90 DAFB in either year (Fig. 6c and d). Thus, it appears that shoot growth can be limited by photoassimilates for much of the season if crop load is high, but fruit growth is only limited during the first part of the season. This suggests that fruit are a stronger sink than shoots from the middle of the season until harvest. When manipulating source directly by severely shading olive trees (cv. 'Arbequina'), it was found that shoot growth was more strongly limited by photoassimilates than fruit growth both early in the season during fruit set (Cherbiy-Hoffmann et al., 2015) and later during oil accumulation (Cherbiy-Hoffmann et al., 2013). The response of deciduous species may be different than that of olive with vegetative shoot growth having been shown to be a priority for photoassimilates over fruit growth early in the season in apple when shading was applied (Bepete and Lakso, 1998). Such a difference in allocation priority may be related to the need for reestablishing canopy leaf area early in the spring in deciduous species. Further research should be conducted to better compare the dynamics of carbon allocation in evergreen versus deciduous fruit trees.

As would be expected, differences in canopy volume growth between crop loads in our study (Table 4) closely followed shoot elongation, and greater shoot elongation appeared to contribute to more inflorescences the following season (Table 3). Similar results have been found by completely removing fruits from olive trees at monthly intervals throughout the course of the growing season in cv. 'Coratina' in Israel (Dag et al., 2010). Although shoot growth was affected by crop load, Martín-Vertedor et al. (2011a) did not find a noticeable response in tree canopy ground cover to crop load in cv. 'Morisca' over several years, possibly due to yearly pruning. We chose not to prune during our study to more clearly observe the responses to crop load, but realize that pruning is an important management tool for regulating canopy volume and for potentially controlling alternate bearing.

Alternate bearing is a phenomenon that affects most olive growing regions to a greater or lesser degree with negative economic consequences for the olive industry (Lavee 2006; Lavee, 2006). In our study, even though individual fruit weight increases up to 40% (Fig. 6a and b) partially compensated for reductions in fruit number due to thinning (Fig. 7a), large differences in fresh fruit yield

occurred in the season that thinning was applied and in the subsequent two seasons. On the other hand, only the heavily thinned trees (87%) showed a reduction in yield for one of the two biennia evaluated. Thinning of approximately one-half of all fruits (48%) led to good fruit size for green table olives and consistent yields. In our region, it may be that chemical thinning could be applied commercially for table olives in years when flowering is unusually high. Such thinning practices are currently employed in California (USA) and Israel (Krueger et al., 2002; Birger et al., 2008).

5. Conclusions

When fruit thinning was employed to obtain a wide range of crop loads, fruit growth appeared to be limited by photoassimilate availability fairly early in the growing season, while shoot growth was most likely limited under medium and high crop loads for most of the season. The formation and elongation of laterals was of importance in trees with very low crop loads, and contributed significantly to total shoot elongation. Further studies of crop load responses are needed to better understand competition for resources between shoots and fruit with the ultimate goal of reducing alternate bearing in olive through crop management, cultivar selection, biotechnology, or other means.

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