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Responses of olive tree yield determinants and components to shading during potentially critical phenological phases

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ABSTRACT

Shading for short periods during potentially critical phenological phases can improve our understanding of the processes underlying the reductions in crop performance when solar radiation is limiting in high density orchards. Our objective was to evaluate the effects of three separate 30 day-long shade periods imposed during fruit set (FS), endocarp sclerification (ES), and early oil accumulation (OA) on some oil yield determinants and components in olive. Four shading levels (3, 20, 40, and 70% of incident photosynthetically active radiation; PAR) were applied in each period using shade cloths that surrounded one-half of large individual trees. Individual fruit dry weight, oil concentration (%) on a dry weight basis, and non-fruiting branch growth were determined at the end of each shading period, 45 days after their completion, and at the end of the season. The previously shaded- and the unshaded-halves of each tree were also harvested at the end of the season to obtain fruit number and oil yield for each half-tree. Individual fruit dry weight and oil concentration at the end of all three shading periods were decreased by shading due to reduced absolute rates of fruit growth and oil accumulation, respectively. However, at final harvest, there were no statistically significant treatment differences in individual fruit weight. By contrast, a small reduction in oil concentration persisted in the fruit from trees subjected to heavy shading during the OA period. Oil yield per half-tree at end of the season was decreased by shading applied during FS and OA periods, principally due to decreases in fruit number and oil concentration, respectively. Final oil yield was not affected by shading during the ES period. Elongation of non-fruiting branches was only decreased by shading during the early spring FS period, when vegetative growth was somewhat more sensitive to shading than fruit growth. Lastly, no consistent response of return bloom to the shading periods was detected the following spring. Our results suggest that the FS period when fruit number is defined and the OA period are more critical for determining final oil yield than the ES period. This information could provide guidance for the design of more effective management strategies in high density orchards where shading can play a key role.

1. Introduction

Fruit tree yield potential per hectare increases with planting density in the low to intermediate range due to the greater interception of solar radiation by the orchard (e.g., Wünsche and Lakso, 2000; Villalobos et al., 2006). However, yield becomes limited when PAR interception exceeds around 50% at greater planting densities because shading of flowering and fruit positions by neighboring trees can result in lower fruit number, smaller fruits, and poorer fruit quality (e.g., Jackson and Palmer, 1977; Ferree et al., 2001; Marini and Corelli-Grappadelli, 2006).

Abbreviations: AGR, absolute growth rate; DAFB, days after full bloom; °Cd, degree-day; PAR, photosynthetically active radiation.

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In olive, correlations between seasonal PAR receipt and yield components in transects across the vertical surfaces of hedgerows or across positions within the hedgerow volume have recently been reported (Connor et al., 2009, 2012; Cherbiy-Hoffmann et al., 2012). The effects of shading during four months of the main oil synthesis phase on fruit growth and final fruit oil concentration have also been examined (Cherbiy-Hoffmann et al., 2013). In that study, at least 15 mol m^{-2} d^{-1} (i.e., ≥40% of incident PAR) were needed to maximize individual fruit dry weight and oil concentration (%). Notwithstanding these advances, a number of important gaps in the understanding of how yield determinants and components respond to the timing and intensity of shading still remain.

Olive trees have a biennial cycle in which buds are formed during the first season on new vegetative growth, and flowering, fruit set, fruit growth and oil accumulation take place in the second season in organs derived from the reproductive buds formed in the first season (Rallo and Cuevas, 2008). Fruit number definition and vegetative growth of branches occur predominantly during the 40 days after full bloom (DAFB) (Rallo and Suarez, 1989). Fruit growth usually lasts six months and three phases can be distinguished: Phase I which overlaps with the greatest rates of vegetative growth and in which 70% of total fruit cell number is formed, Phase II when massive endocarp sclerification occurs and oil synthesis is initiated, and Phase III during which most mesocarp cell expansion and linear oil accumulation take place (Sánchez, 1994; Hammami et al., 2011).

In many fruit tree and vine species, shading during fruit set can reduce photosynthate availability and thus fruit growth rate, triggering the abscission of those fruits growing at lower rates (Byers et al., 1991; Ferree et al., 2001; Iglesias et al., 2003; Lakso, 2011). The percentage of fruit set in olive has been shown to be decreased by a number of factors including high flowering density (Lavee et al., 1996, 1999), water stress (Rapoport et al., 2012), and high temperature (Vuletin Selak et al., 2014). As is the case for other fruit trees, the little information available for olive suggests that shading during the fruit set period may be critical. An early study found a dramatic increase in fruit abscission during the fruit set period when severe long-term shading treatments (<15% PAR transmittance) were initiated shortly after flowering (Tombesi and Standardi, 1977). More recently, Cherbiy-Hoffmann et al. (2012) determined that fruit density at harvest across a range of positions within the canopy in an olive hedgerow was more strongly associated with PAR receipt around the fruit set period than with irradiance received during other phenological periods. Fruit abscission in that study was also found to increase sharply when incident PAR dropped below 20%. The use of different percentage shading treatments for fairly short periods should allow for a better determination of when fruit abscission is most sensitive to low PAR receipt.

After shading early in the season, final fruit size at harvest could be affected by several factors. It might be expected that shading during fruit set and early fruit growth could lead to potential fruit size not being reached at harvest given that most cell division occurs early in olive fruit growth (Hammami et al., 2011). On the other hand, greater fruit abscission associated with shading could allow for greater carbon allocation per fruit to the remaining fruit, leading to partial recovery in fruit size between the end of shading and harvest. Final fruit size at harvest might also be affected by changes in the allocation of carbon between fruit and branch due to shading in this phase, as seen for other fruit species such as apple (Bepete and Lakso, 1998).

The distinguishing characteristic of Phase II fruit growth in olive is endocarp sclerification, although in this phase oil biosynthesis also starts and the rates of mesocarp cell division and branch elongation decrease (Sánchez, 1994; Rallo and Cuevas, 2008). In high density orchards, irrigation is often reduced during Phase II because fruit growth is considered to be relatively insensitive to water stress during this period compared to Phases I and III (Fereres and Soriano, 2007; Gómez-del-Campo, 2013). It therefore might be expected that shading during endocarp sclerification may have little consequence for final fruit size and oil yield, but this has not been tested.

As mentioned earlier, radiation receipt below 40% of incident PAR during the main oil synthesis period (Phase III; 120 d of shading) in olive was associated with marked reductions in fruit dry weight and oil concentration, and therefore in oil yield (Cherbiy-Hoffmann et al., 2013). Proietti et al. (1994) determined that when olive leaves and fruits were heavily shaded (12% of incident PAR) during all of Phase III, fruit dry weight and oil concentration decreased dramatically. However, there is no information about responses to resource restriction at the start of Phase III in olive, although it could be expected that shading at this time might result in lower fruit dry weight and oil concentration at harvest if the duration of the post-shading period is not sufficiently long to allow for fruit recovery. In peach, the reduction in fruit weight due to resource limitation early in the season could not be fully recovered after fruit thinning at 5, 10 and 15 weeks after flowering (Grossman and DeJong, 1995).

Along with fruit load, the radiation environment in fruit tree orchards during a given season often affects the intensity of return bloom the following season (e.g., Jackson and Palmer, 1977; Marini and Corelli-Grappadelli, 2006). A pioneering study in olive found that 10 months of severe shading before flowering reduced the return bloom considerably (Tombesi and Standardi, 1977). Other factors such as early fruit removal can also affect bloom the following season (Dag et al., 2010), but the importance of short shading periods on return bloom in olive is not known. On the basis of observed responses to long shading periods and alterations in fruit load, it might be expected that radiation environment early in the season is likely to be fairly critical for return bloom.

The present study imposed a 30-day long shading period during each of three different phenological phases (fruit set, endocarp sclerification, and early oil accumulation) in order to determine the effects of shading on some oil yield determinants and components. Such information should help to better define the critical periods for oil yield in olive. Four shading levels were used to evaluate the shading responses of the measured variables.

2. Materials and methods

2.1. Experimental site and shading treatments

The study was conducted in a commercial orchard of 8-year-old olive trees (*Olea europaea* L. cv. 'Arbequina') located 15 km northeast of Aimogasta, province of La Rioja, Argentina (28°55′ S, 66°51′ W; 800 m above sea level) within the Arid Chaco phytogeographic region (Ayerza and Sibbett, 2001). Mean annual rainfall and temperature are 100 mm and 20 °C; respectively, and potential reference evapotranspiration is about 1600 mm y^{-1} (Searles et al., 2011). Tree spacing was 4 m within the row × 6 m between rows with a north-south row orientation. Supplementary irrigation was 650 mm y^{-1} (crop coefficient = 0.7; reduction coefficient = 0.6) and was provided by four 4 L h^{-1} drip emitters per tree.

During the 2007–2008 growing season, three separate 30-day long shading periods were applied after full bloom (October 18, 2007) corresponding to the periods of fruit set (FS; October 22–November 21), endocarp sclerification (ES; November 21–December 22), and early Phase III oil accumulation (OA; December 22–January 23, 2008). Massive endocarp sclerification was estimated to be December 10, 2007 (54 days after full bloom; DAFB). Four levels of artificial shading (3, 20, 40, and 70% of daily incident PAR measured on a horizontal plane) were employed

during each period, and there were 4 replicate shaded trees per treatment arranged in a randomized complete block design. More replicate trees were not practical because of the need to install very large metal frames over the trees in order to implement the shading levels (see details in next paragraph). All of the trees used during the shading periods were selected at the beginning of the season based primarily on uniformity in canopy volume and flowering intensity. Different, pre-selected trees were used for each shading period (total number of trees used = 48). Tree height averaged 3.1 m with an average canopy volume of 15 m^3. Canopy volume ($V = 4/3\pi r^2 h$) was calculated as a spheroid, where r was the radius and h was the canopy depth (i.e., tree height minus the distance between soil surface and the tree skirt). Final harvest of all trees took place on April 3, 2008.

The different levels of artificial shading were generated using neutral density, polyethylene plastic mesh shade cloths of different PAR (%) transmittances (Agroredes S.R.L., Buenos Aires, Argentina) stretched over metal frames 4 m high and 3.5 m wide. The frames and accompanying shade cloths were placed on the north side of the trees, which receives the greatest irradiance in the Southern Hemisphere. Frame extensions were added to the east and west sides of the trees such that the entire northern half of the trees were shaded, while the southern half remained unshaded (Cherbiy-Hoffmann et al., 2013). This design allowed for significant air movement within the structure given that the predominant winds were from the southeast and minimized changes in microclimatic conditions often associated with artificial shading treatments. As to the potential influence on the results of not shading the south side, a previous study in olive has indicated that the carbon balance of a main branch of a mature tree is relatively autonomous (Proietti and Tombesi, 1996), although some carbon translocation from the unshaded to the shaded sides cannot be discounted (Cherbiy-Hoffmann et al., 2013).

The PAR transmitted by the shade cloths (I) was measured once in situ for each shading period at solar noon using a 1 m × 0.01 m integrating bar (Cavadevices, Buenos Aires, Argentina), placed horizontally at a height of 2 m and at a distance of 0.25 m outside the canopy and perpendicular to the row (i.e., in an east-west direction). At the same time, full incident PAR (Io) was measured in the center of the interrow where tree row effects on shading were minimal. A preliminary study showed that the fraction of PAR transmitted by the shade cloths at noon was within 6% of the estimated value obtained by integrating values taken at five different solar times (8, 10, 12, 14, and 16 h). The measured transmittance of the control shade cloth was 90% under full sun conditions, but the partial shading produced by neighboring trees within the row reduced this value to 70%. Moderate pruning of the neighboring trees was performed during the experimental period to avoid any further reduction in the PAR received by the experimental trees.

To obtain average incident PAR values for each treatment during the entirety of each shading period, daily incident PAR (mol m^{-2} d^{-1}) was estimated from shortwave radiation data recorded every 15 min at an automatic weather station fitted with a pyranometer (Davis Instruments, Hayward, CA, USA) located in an open area 8 km from the study site. These daily integrals were then multiplied by the shade-specific transmittances. Air temperature and relative humidity under the shade cloths were also measured once for each shading period using a digital thermohygrometer (Hygropalm 2, Rotronic Ag, NY, USA), and compared with paired measurements made at the center of the interrow.

2.2. Vegetative growth and return bloom

Ten non-fruiting branches located at a height of 2 m and within 0.25 m of the outer canopy surface were marked just before each shading period on the northern, shaded half of each tree. The initial lengths of these branches were 5–7 cm and were subsequently re-measured at the end of each shading period and at final harvest. Return bloom was assessed in the spring of the following season (2008–2009) by counting inflorescences and leaf axillary buds on the previously tagged, non-fruiting branches from the previous season.

2.3. Fruit growth and oil concentration

Individual fruit dry weight and oil concentration (% on a dry weight basis) were determined at the beginning and at the end of each shading period, 45 days after the end of the shading treatment, and at final harvest. The only exception to this protocol was that initial fruit samples at the beginning of the FS period (i.e., 4 DAFB) were not feasible. For the samples of each shading period and 45 days after shading, fresh fruit (50 g) were collected from the outer part of the canopy at a height of 1.75–2.25 m on the shaded side of each tree. Fruit dry weight was determined on subsamples of 10 fruits which were oven-dried at 70 °C to constant weight. To determine oil concentration, the remaining fruit from each sample were ground in a hammer mill to obtain a homogenized paste, the paste was then oven-dried at 70 °C, and the oil was extracted with hexane for 6 h using Soxhlet apparatus. At final harvest, the samples were taken from fruit harvested from the entire volume of the shaded side of each tree.

2.4. Yield and fruit number at harvest

On April 3, 2008 the shaded and unshaded sides of the trees were harvested separately and then weighed for yield determination. For a given side, samples of 500 g were taken to determine average fruit fresh and dry weights and fruit oil concentration. Fruit and oil yield density were calculated as fruit or oil weight (kg) per unit canopy volume (m^3). Fruit number was estimated for each side by dividing yield by average individual fruit fresh weight, and fruit density was calculated by dividing fruit number by the corresponding canopy volume.

2.5. Absolute growth rates

The absolute growth rates (AGR) of fruit were determined for each shading level and phenological phase over three separate intervals: (1) the 30-day shading period, (2) the 45 days after the end of each shading period, and (3) the interval from 45 days after the end of each shading period to final harvest; using the equation:

$$\mathrm{AGR} = (w_2 - w_1)/(t_2 - t_1)$$

where w_2 and w_1 are the mean individual fruit dry weight at harvest dates t_2 and t_1 in units of thermal time, which was calculated as degree days (in °Cd^{-1} units) using the single sine, horizontal cutoff method (http://www.ipm.ucdavis.edu). Although little direct experimental evidence exists concerning olive fruit, oil, and branch growth responses to temperature (García-Inza et al., 2014), the lower and upper limit temperatures were set to 7 °C and 40 °C based on some previous studies (DeJong and Goudriaan, 1989; Pérez-López et al., 2008). Air temperature data were registered every 15 min by the same automatic weather station used to measure solar radiation. Absolute oil accumulation rates for the three intervals were calculated using mg of oil per fruit as the weight values at each harvest date. Branch AGR calculations substituted branch length for weight (Solari et al., 2006) to obtain AGR estimates for two periods, the 30-day shading period and from the end of shading to final harvest.

In order to compare the competitive ability of the reproductive and vegetative sinks, the AGR of both fruit dry weight and branch length in the PAR reduction treatments (3, 20, 40%) were normalized as percentages of the AGR values to the highest PAR level (70%). The reproductive sink was calculated by multiplying the mean dry weight of individual fruit by the number of fruit per cm of branch length on external, fruit-bearing branches. Due to the minimal branch growth after the FS period, this analysis was performed for the FS period only.

2.6. Statistical analysis

Most data were analyzed by one-way ANOVA using the PROC GLM procedure of SAS (SAS Institute, Cary, NC, USA). Duncan's multiple range test was employed to separate differences between treatments means at $P < 0.05$ for each shading period.

3. Results

Average daily incident PAR values were similar for the three shading periods and averaged 58 mol PAR m^{-2} d^{-1} (Fig. 1). Daily PAR values for the different shading levels (3, 20, 40, and 70% PAR) were approximately 2, 12, 23, and 41 mol PAR m^{-2} d^{-1}; respectively. Average maximum (32.5 °C) and minimum (19.5 °C) daily temperatures did not differ significantly between shading periods (Fig. 1). Air temperature and relative humidity were 0.4 °C and 0.8% lower under the shading structures than the values registered outside the structures, and no differences ($P > 0.05$) were found among shading treatments (data not shown) for these variables.

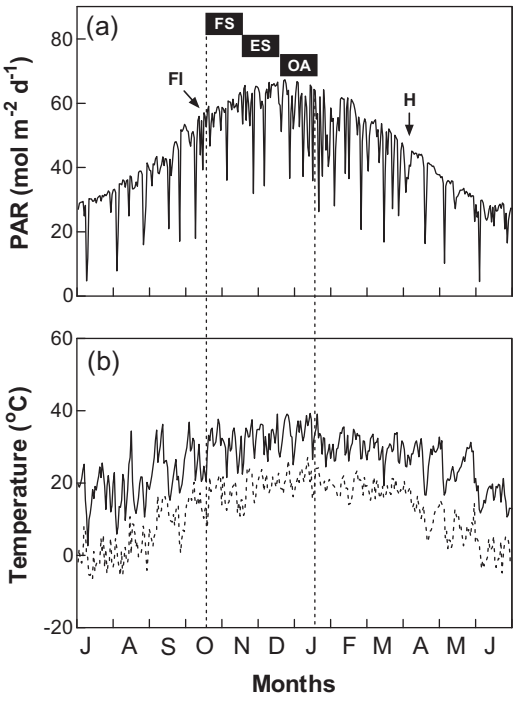

Fig. 1. (a) Daily incident photosynthetically active radiation (PAR) and (b) maximum (continuous line) and minimum (dotted line) daily temperatures during July 2007–June 2008. Black rectangles indicate the timing of the three separate 30-day shading periods that were applied during fruit set (FS), endocarp sclerification (ES), and early Phase III oil accumulation (OA). Dates of full flowering (FI) and final harvest (H) are indicated with arrows.

3.1. Fruit and oil responses at the end of shading and 45 days later

At the end of each of the three shading periods, individual fruit dry weight on external branches decreased as shading became more severe (Fig. 2a). Fruit oil concentration was also reduced by shading in all three periods even though the concentrations at the end of the FS and ES shading periods were very low (Fig. 2c). Forty-five days after the end of shading, no significant effects on individual fruit dry weight were evident (Fig. 2b). A significant decrease in fruit oil concentration was still present 45 days after the end of shading for the trees shaded in the OA period, but trees

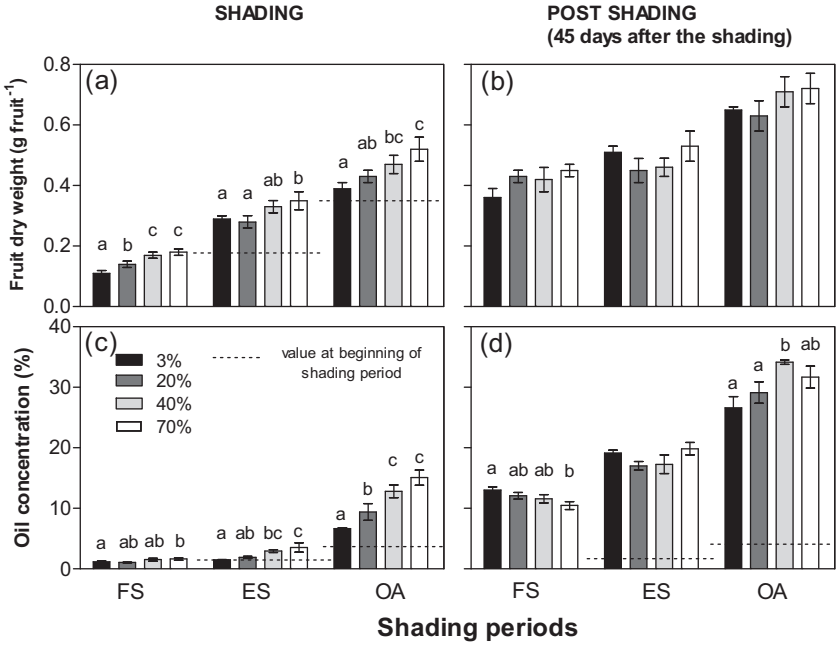

Fig. 2. Individual fruit dry weight (g $fruit^{-1}$) and oil concentration (% on a dry weight basis) at the end of each shading period (a, c) and 45 days later (b, d). The 30-day shading periods were applied during fruit set (FS), endocarp sclerification (ES), and early Phase III oil accumulation (OA). Bars represent means and capped vertical lines are SEs ($n = 4$). Codes for levels of shading (as % of incident PAR) are shown in (c). Different letters above bars indicate statistically significant ($P < 0.05$) differences between treatments within each shading period.

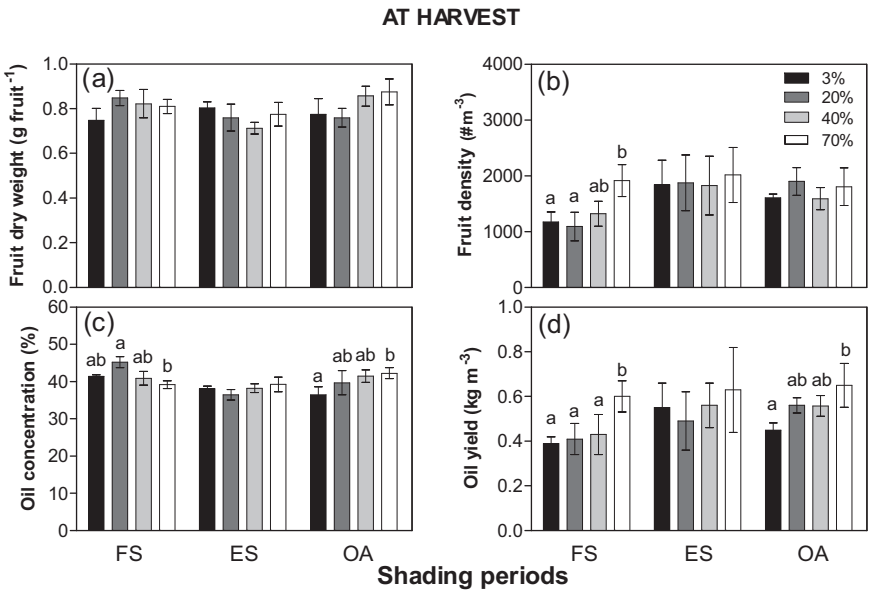

Fig. 3. (a) Individual fruit dry weight (g fruit^{-1}), (b) fruit density (# m^{-3} tree canopy), (c) oil concentration (% on a dry weight basis), and (d) oil yield (kg m^{-3} tree canopy) at final harvest for all three shading periods. The 30-day shading periods were applied during fruit set (FS), endocarp sclerification (ES), and early Phase III oil accumulation (OA). Bars represent means and capped vertical lines are SEs ($n = 4$). Codes for levels of shading (as % of incident PAR) are shown in Fig. 3b. Different letters above bars indicate statistically significant ($P < 0.05$) differences between treatments within each shading period. In all cases, the values correspond to fruit from the entire shaded half of the trees.

shaded during the ES period did not show any difference between shading levels 45 days later (Fig. 2d). Although the trees shaded during the FS period had shown a decrease in oil concentration at the end of the shading period (Fig. 2c), an increase in the most heavily shaded treatment (3% PAR) was detected 45 days after the end of the shading period (Fig. 2d).

3.2. Yield and fruit number responses at final harvest

In agreement with the responses found 45 days after the end of shading in fruit from external branches, no significant effects of shading on individual fruit dry weight of fruit from the entire shaded half of the tree at final harvest were observed for any of the three periods (Fig. 3a). Visual observation at harvest suggested that most fruit were on external branches as is common in modern orchards with high leaf density (Connor et al., 2014). In contrast to individual fruit weight, a small but significant decrease in fruit oil concentration with shading was still apparent in trees shaded in the OA period, and the modest increase in oil concentration for more heavily shaded, FS trees detected 45 days after the end of shading continued through to final harvest (Fig. 3c). This increase was presumably an indirect response related to the much lower fruit density values determined at final harvest for the trees that received low PAR levels during the FS period (Fig. 3b). In other words, low fruit density likely led to a greater oil concentration in individual fruit.

Oil yield for the shaded half of the trees at final harvest decreased with shading in the FS period due to the lower fruit density and in the OA period due to the lower oil concentration of individual fruit, but showed no response to shading in the ES period (Fig. 3d). Oil yield for the unshaded-half of the trees was not affected by the shading levels applied to the other half of the tree for any of the three periods examined (data not shown).

Table 1
Absolute growth rates of fruit growth and oil accumulation during each 30-day shading period, the 45-day post-shading period, and the interval between the end of the 45-day post-shading period and final harvest. The shading periods were applied during fruit set (FS), endocarp sclerification (ES), and early Phase III oil accumulation (OA). Values represent means ± SEs ($n = 4$) for the four shading levels (3, 20, 40 and 70% PAR). Different letters indicate statistically significant differences between treatments within each shading period ($P < 0.05$).

Period	PAR (%)	Fruit absolute growth rate (mg °Cd^{-1})			Oil absolute accumulation rate (mg °Cd^{-1})		
		During shading	During 45 days post-shading	45 days post-shading to final harvest	During shading	During 45 days post-shading	45 days post-shading to final harvest
FS	3	0.22 ± 0.009a	0.26 ± 0.022ab	0.26 ± 0.023	0.002 ± 0.0003a	0.046 ± 0.0053	0.18 ± 0.011
	20	0.27 ± 0.023b	0.30 ± 0.017b	0.28 ± 0.005	0.003 ± 0.0002ab	0.053 ± 0.0047	0.22 ± 0.013
	40	0.33 ± 0.009c	0.23 ± 0.025a	0.28 ± 0.017	0.005 ± 0.0008bc	0.042 ± 0.0047	0.19 ± 0.016
	70	0.35 ± 0.018c	0.28 ± 0.025ab	0.24 ± 0.006	0.006 ± 0.0007c	0.046 ± 0.0053	0.18 ± 0.008
ES	3	0.17 ± 0.014	0.25 ± 0.011	0.32 ± 0.026	0.003 ± 0.0003a	0.103 ± 0.0056	0.23 ± 0.014
	20	0.16 ± 0.030	0.18 ± 0.034	0.34 ± 0.023	0.004 ± 0.0010a	0.078 ± 0.0088	0.22 ± 0.018
	40	0.24 ± 0.022	0.15 ± 0.020	0.27 ± 0.023	0.011 ± 0.0014ab	0.078 ± 0.0105	0.21 ± 0.018
	70	0.27 ± 0.046	0.20 ± 0.025	0.27 ± 0.039	0.016 ± 0.0056b	0.103 ± 0.0116	0.22 ± 0.021
OA	3	0.08 ± 0.027a	0.42 ± 0.027	0.29 ± 0.086	0.021 ± 0.0027a	0.24 ± 0.017	0.18 ± 0.043
	20	0.12 ± 0.025ab	0.32 ± 0.041	0.23 ± 0.097	0.044 ± 0.0097ab	0.23 ± 0.021	0.21 ± 0.031
	40	0.19 ± 0.04bc	0.40 ± 0.039	0.25 ± 0.064	0.075 ± 0.0113bc	0.30 ± 0.016	0.19 ± 0.035
	70	0.26 ± 0.055c	0.33 ± 0.068	0.27 ± 0.076	0.104 ± 0.0165c	0.24 ± 0.034	0.25 ± 0.050

Table 2
Non-fruiting branch elongation and absolute growth rate during the shading periods and post-shading. The 30-day shading periods were applied during fruit set (FS), endocarp sclerification (ES), and early Phase III oil accumulation (OA). Values represent means ± SEs ($n = 4$) for the four shading levels (3, 20, 40 and 70% PAR). Different letters indicate statistically significant differences between treatments within each shading period ($P < 0.05$).

Period	PAR (%)	Branch elongation (cm)	Absolute growth rate (mm ◦Cd^{-1})	
		During shading	During shading	End of shading to final harvest
FS	3	2.65 ± 0.60a	0.051 ± 0.0116a	0.018 ± 0.0058
	20	3.51 ± 0.46a	0.068 ± 0.0089a	0.019 ± 0.0016
	40	5.57 ± 1.04b	0.107 ± 0.0201b	0.012 ± 0.0040
	70	6.67 ± 0.52b	0.129 ± 0.0101b	0.007 ± 0.0046
ES	3	0.40 ± 0.38	0.006 ± 0.0062	0.038 ± 0.0152
	20	0.26 ± 0.20	0.004 ± 0.0033	0.028 ± 0.0197
	40	0.34 ± 0.15	0.006 ± 0.0025	0.016 ± 0.0139
	70	0.50 ± 0.15	0.008 ± 0.0024	0.022 ± 0.0117
OA	3	0.20 ± 0.10	0.003 ± 0.0016	0.027 ± 0.0114
	20	0.27 ± 0.11	0.004 ± 0.0029	0.107 ± 0.0447
	40	1.02 ± 0.19	0.016 ± 0.0029	0.041 ± 0.0176
	70	1.15 ± 0.61	0.018 ± 0.0094	0.021 ± 0.0137

3.3. Absolute rates of fruit growth and oil accumulation

As expected, the absolute rates of fruit growth and oil accumulation decreased for fruit on external branches during all three shading periods (Table 1). Differences in absolute rates were not observed during the 45 days after the end of the shading treatments or during the period prior to harvest, except for fruit growth rates 45 days after the end of the FS period. Thus, although the absolute rates of fruit growth and oil accumulation were decreased by shading, the rates returned to levels that were statistically indistinguishable from those of the 70% PAR control during post-shading.

3.4. Branch elongation responses during shading and post-shading

Elongation of non-fruiting, externally positioned branches of control (70% PAR) trees was much greater in the early spring during the FS period than during the ES or OA periods (Table 2). Shading only led to statistically significant decreases in elongation during the FS period, although some tendency toward decreased elongation with shading was also seen in the OA period. The relationship between elongation and PAR for the FS period was well described by a bilinear function ($R^2 = 0.68$, data not shown), which indicated that the elongation increased linearly with irradiance up to a threshold of 40% PAR, above which no further increase occurred. No differences among shading levels were found in the number of nodes present on non-fruiting branches ($P > 0.05$, data not shown).

In the FS period, the AGR of heavily shaded branches (3, 20% PAR) was reduced by about half when compared to branches receiving 70% PAR (Table 2), while no statistically significant differences in AGR between shading levels were observed during the post-shading period. As expected, no differences in AGR were apparent between shading levels during or after the ES and OA shading periods.

3.5. Normalized branch and fruit responses

In order to compare the differential effect of shading (i.e., source reduction) on vegetative and reproductive growth, the normalized branch and fruit growth during the FS shading period were assessed (Fig. 4). While no difference was apparent between normalized fruit and branch growth with moderate shading (40% PAR), there was a tendency for branch growth to be more affected than fruit growth at greater shading levels (3, 20%) with a statistically significant difference being detected at the greatest shading level (3% PAR). The responses of these variables to shading during the ES and OA periods were not analyzed due to the very low branch elongation (<1 cm; Table 2) observed at all shading levels.

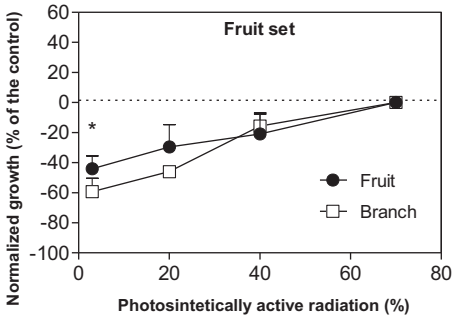

Fig. 4. Normalized growth of non-fruiting branches (empty squares) and fruit (filled circles) during the fruit set shading period for the four levels of incident photosynthetically active radiation (3–70%). The normalized values were calculated by dividing either absolute growth rate values of branch elongation or fruit dry weight per cm of branch under the different PAR reductions (3, 20, 40%) by the corresponding AGR value for the 70% PAR control. Values shown are means ± SEs ($n = 4$). The asterisk indicates a significant difference between normalized branch and fruit values.

3.6. Return bloom

Return bloom the following spring was not significantly affected by shading applied the previous season for any of the three periods (Fig. 5), and no consistent pattern between shading treatments was evident. On average, flowering intensity was low

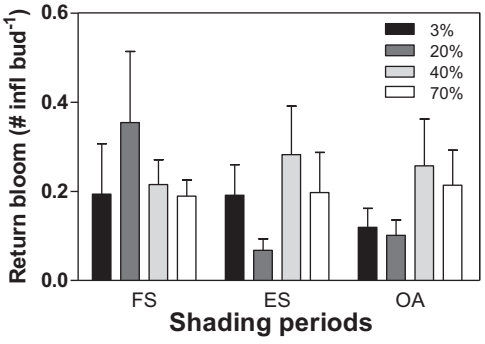

Fig. 5. Return bloom the season following the 30-day fruit set (FS), endocarp sclerification (ES) and early Phase III oil accumulation (OA) shading periods. Bars represent means and capped vertical lines are SEs ($n = 4$). Codes for levels of shading (as % of incident PAR) are also given.

(0.2 inflorescences bud^{-1}) considering that upper end values of 0.95 inflorescences bud^{-1} have been reported (Lavee et al., 1999). The low flowering intensity in our study is likely related to the high fruit load the previous season (1000–2000 fruit m^{-3} tree canopy; Fig. 3b).

4. Discussion

The results show that the responses of oil yield per half-tree at final harvest varied according to the phenological phase of the trees during which shading was applied. Final oil yield was reduced due to the 30-day FS and OA shading periods, while no response was apparent due to the ES period (Fig. 3d). The yield components responsible for these reductions also varied between periods with reductions in fruit number being important for the FS shading period initiated just after full bloom (Fig. 3b), and reductions in fruit oil concentration being the driving component for the early summer OA period (Fig. 3c). Similarly, shading around anthesis in sunflower decreased final oil yield due to a reduction in the number of grains per m^2 (Cantagallo et al., 2004), while shading during seed filling decreased oil yield due to reductions in grain oil concentration (Aguirrezábal et al., 2003).

In contrast to the different oil yield responses to shading at final harvest between the three phenological phases, individual fruit weight and oil concentration were both reduced by shading at the end of the 30-day shading periods for all three phenological phases (Fig. 2a and c). This suggests that fruit growth and oil concentration for these phenological periods from early spring to summer rely on current photosynthesis to achieve their potential and any reduction in PAR below 50–70% has negative consequences. Such limitations by current photoassimilates appeared to occur even when oil concentrations were very low during the FS and ES periods, and is consistent with results from other evergreen fruit tree species that have shown carbohydrate reserves to be rapidly depleted early in the season (Monerri et al., 2011) or under shaded conditions (Olesen et al., 2008).

Forty-five days after shading was removed, differences in the post-shading response between the FS, ES, and early Phase III OA periods were apparent. Although no differences in fruit dry weight for any shading period were observed (Fig. 2b), oil concentration was still lower in the more shaded treatments (3, 20% PAR) of the OA shading period and actually increased under heavy shading during the FS period (Fig. 2d). This greater oil concentration may be related to more photoassimilates being available per fruit due to the lower fruit density in the shaded-half of the FS trees at final harvest (Fig. 3b). Some other studies have shown that fruit oil concentration often increases in response to fruit thinning in olive (Barone et al., 1994; Gucci et al., 2007). With respect to the ES period, 45 days after shading was removed no differences in fruit weight or oil concentration were observed. This result provides additional support to the suggestion that deficit irrigation practices in olive may best be applied during this phase with little or no reduction in fruit size or oil yield (e.g. Fereres and Soriano, 2007; Gómez-del-Campo, 2013).

The lack of statistically significant differences in fruit weight 45 days after the end of shading (Fig. 2b) and at final harvest (Fig. 3a) can be assessed in terms of weight gain per fruit. If the difference in fruit weight between the most severe shading treatment (3% PAR) and the control (70% PAR) is examined for the FS period at the end of the shading (0.07 g fruit^{-1}), after 45 days (0.09 g fruit^{-1}), and at final harvest (0.06 g fruit^{-1}), it can be seen that the difference in weight per individual fruit does not change after shading. This suggests that recovery of fruit weight did not occur in the strictest sense after the FS shading period if recovery is defined as a reduction in weight difference between two treatments after source limitation is removed. Similar calculations can be applied for the OA period. In peach, Grossman and DeJong (1995) also concluded that the weight of fruit on later thinned trees could not 'catch up' with the weight of fruit on earlier thinned trees. Thus, the lack of a statistically significant difference between shading treatments during post-shading in our study may be considered to be a 'dilution effect' in that as the fruit grow, the small difference (i.e., 0.06–0.09 g fruit^{-1}) between treatments becomes relatively inconsequential. The observation that absolute rates of fruit growth and oil accumulation decreased during shading, but were not consistently greater than the AGR of the 70% PAR control after shading (Table 1) also suggests that full recovery did not occur. Similarly, the increases in transverse area of previously water-stressed olive fruits were not significantly greater than those of a well-watered control after the completion of 30-day deficit irrigation treatments (Gómez-del-Campo et al., 2014).

Responses of branch elongation in non-fruiting branches to shading differed greatly between shading periods (Table 2). Statistically significant reductions in the elongation were only evident in the FS period when elongation rates in control (70% PAR) trees were at their highest. In contrast, very low elongation values were found for all shading treatments (3, 20, 40% PAR) and the control during the ES and OA periods, presumably due to competition exerted by active fruit growth in the high crop load trees used in this study (Rallo and Suarez, 1989; Dag et al., 2010). When branch and fruit growth of each shading treatment were normalized to the control (70% PAR) for the FS period, branch elongation and fruit growth decreased with PAR over the entire range of PAR evaluated, but the decrease in fruit growth was less pronounced than that of branch growth (Fig. 4). This suggests competition for resources between organs early in the season, and that fruit growth has a greater priority than vegetative growth under limiting PAR at that time of the season. In apple, the response appears to be different than that of olive with vegetative growth having priority for assimilates over fruit growth early in the season when shaded (Bepete and Lakso, 1998). The different response between olive and apple trees may be related to the deciduous nature of apple with canopy leaf area being reestablished in the spring during early fruit formation (Wünsche and Ferguson, 2005).

Return bloom the spring following the shading periods was low with only about 20% of the potentially reproductive buds producing inflorescences, and no statistically significant differences were apparent between the shading levels (Fig. 5). There was only some tendency for flowering intensity to be lower when PAR receipt was under 40% in the ES and OA periods. Low bloom percentages were likely due to lack of flower induction the previous season due to the high crop load. Tombesi and Standardi (1977) found that flowering was considerably reduced in olive trees that were severely shaded for 10 months before return bloom, but more definitive results are still needed for shorter shading periods.

5. Conclusions

Oil yield at harvest was shown to be sensitive to shading as a consequence of increased fruit abscission due to the fruit set shading period and decreased oil concentration when shading was applied at the beginning of Phase III oil accumulation. In contrast, the importance of unrealized fruit weight during the shading periods was largely eliminated as the fruit grew over the season. The endocarp sclerification period appeared to be fairly insensitive to shading, which is consistent with the use of deficit irrigation during this period in many fruit trees.

These results may provide some guidance for the design of more effective management strategies in high density orchards. At the practical level, shading of external inflorescences by neighboring rows can occur during fruit set if pruning is inadequate, and

excessive vegetative growth may lead to the shading of fruits later in the season during oil accumulation. Additionally, simulation models of PAR estimations for hedgerow orchard walls might be used to evaluate the importance of shading for particularly critical periods (i.e., FS and OA) for different tree row geometries (Connor and Gómez-del-Campo, 2013). The effects of shading under different fruit loads or over multiple years could also be explored.

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