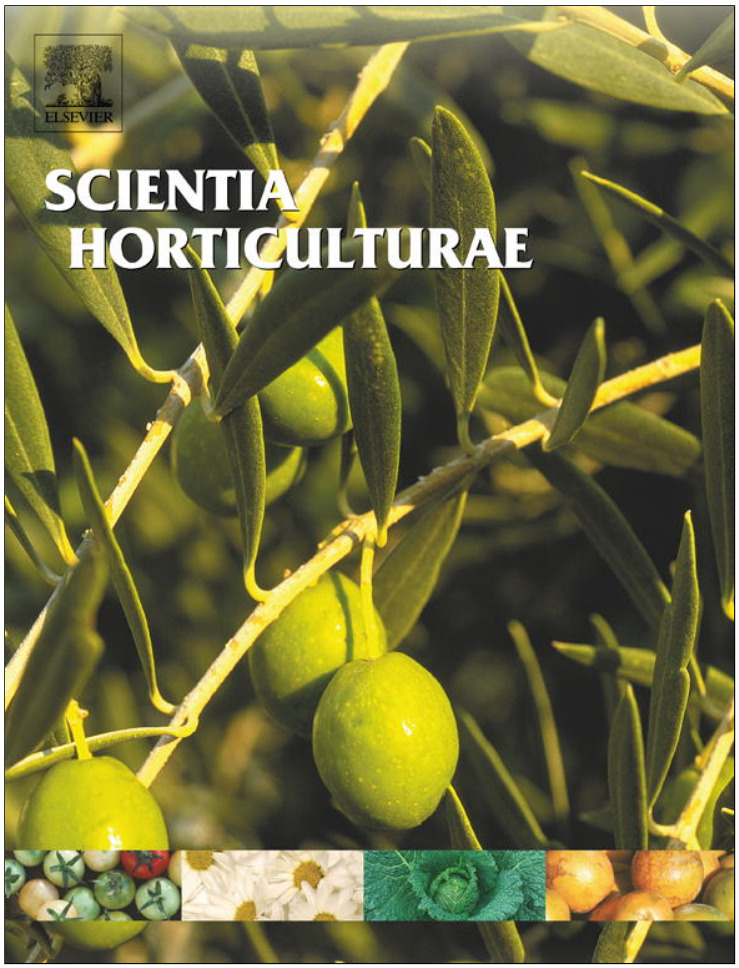

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Fruit, yield, and vegetative growth responses to photosynthetically active radiation during oil synthesis in olive trees

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ABSTRACT

Maximizing productivity in super high density and intensive olive orchards requires proper management of illumination of the canopy walls and their interior. Currently, this is difficult to achieve due to the limited knowledge about the responses to incident photosynthetically active radiation (PAR) of yield determinants and components. We determined the response functions for PAR during the oil synthesis phase of yield components (fruit dry weight and oil concentration) of fruit at a height of 2 m on the canopy periphery by applying several radiation levels (3, 20, 40, and 70% of incident PAR) to the north side (S hemisphere) of well-illuminated trees. The experiment was initiated after endocarp hardening as fruit number had already been established at that time. This avoided possible confounding effects due compensation between fruit number and size. Absence of differential fruit fall in response to treatments and of changes in (endocarp + seed) dry weight after application of treatment confirmed the achievement of this objective. Fruit dry weight, oil concentration, and, consequently, yield increased linearly with mean daily PAR receipt up to a threshold of 15 mol PAR m^{-2} d^{-1} (i.e., 40% of PAR). In treatments with irradiance levels below this threshold the fruit became the priority sinks for assimilates, although their growth rate and oil concentration were reduced. Increments in length of non-fruiting branches and of trunk cross-sectional areas were substantially reduced in response to shading. We conclude that manipulation of PAR levels during the oil synthesis phase can reduce final fruit dry weight and oil concentration, confirms the existence of upper thresholds to PAR responses for these variables, and provides evidence that fruit growth has priority in the partitioning of photosynthate over vegetative growth under low to moderate levels of PAR.

1. Introduction

The potential productivity of olive, as well as that of other fruit trees, has increased in the last twenty years largely due to increases in planting density. Densities in modern olive orchards range from 200 to 2000 plants ha^{-1} (De la Rosa et al., 2007; Tous et al., 2010). As plant density increases, the proportion of PAR intercepted by the crop is greater and consequently the biomass and yield per unit soil surface increases proportionally (Mariscal et al., 2000; Villalobos et al., 2006). However, increases in interception to values above 50% of the incident PAR do not generate much increase in yield because orchard structures that ensure high interception generate excessive shading between and within trees, a condition that it is associated with a decrease in the number of fruiting sites per unit area (Villalobos et al., 2006).

Modeling crop structures that combine appropriately high PAR interception with high fruiting requires information about critical thresholds for vegetative growth, flower density, fruit set, and fruit dry weight as a function of PAR (Connor, 2006). For apple and peach, the most widely studied fruit trees, several studies have analyzed the response function to PAR of yield determinant and components. In apple, fruit bud number increased with PAR up to a threshold of 37% of full sunlight the season after shade treatments were applied (Jackson, 1980). On the other hand, a 23% threshold was determined for fruit density in peach (Marini and Corelli-Grappadelli, 2006; Mirás-Avalos et al., 2011). In olive, pioneering studies showed that trees shaded (15% transmittance PAR) for 10 months prior to flowering had eight times less inflorescences per node and three times less fruits per inflorescence compared to unshaded plants (Tombesi and Cartechini, 1986; Tombesi and Standardi, 1977). When olive

Abbreviations: DAF, days after flowering; °Cd, degree–day; PAR, photosynthetically active radiation.

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Table 1
Average dry weights of fruit pit (endocarp + seed) and pulp (mesocarp + exocarp) from trees receiving 70% of incident PAR (control treatment). Endocarp hardening occurred 60 days after full flowering ($n = 4$).

Fruit part	Dry weight (g fruit^{-1})					
	30 DAF	90 DAF (start of experiment)	120 DAF	150 DAF	180 DAF	210 DAF (end of experiment)
Endocarp + seed	0.12 ± 0.02	0.30 ± 0.02	0.30 ± 0.01	0.31 ± 0.03	0.32 ± 0.03	0.32 ± 0.01
Mesocarp + exocarp	0.06 ± 0.02	0.19 ± 0.02	0.29 ± 0.01	0.44 ± 0.03	0.52 ± 0.03	0.56 ± 0.01

trees were shaded (10% transmittance PAR) during the phase of active oil synthesis (i.e., mesocarp growth phase), fruit dry weight decreased by 55%, while oil content decreased 70% compared with the unshaded trees (Proietti et al., 1994). Since only one level of shading was used in these studies with olive, it was not possible to establish the response functions of these variables to PAR.

Recently, Connor et al. (2009, 2012) analyzed the relationships between yield components (fruit density per unit hedgerow surface, fruit size and fruit oil content) and PAR across layers of narrow olive hedgerows using intercepted PAR values for October (or March, S Hemisphere) as a proxy for seasonal (i.e., bloom to harvest) intercepted PAR. Cherbiy-Hoffmann et al. (2012), using a similar layered hedgerow approach, extended these results by examining the relationships between yield components and determinants (including inflorescence density and fruit set) and intercepted PAR on pruned and unpruned sides and tops of the hedgerow. In this experiment, response variables were related to intercepted PAR values for the monthly periods judged to be most appropriate to each response variable as a function of tree phenology. Analyses of the kind referenced above provide valuable insights into the possible relationships between yield determinants and components and PAR (associated, in the cited cases, with position on the hedgerow), but outcomes are subject to some extent to decisions as to which calendar period is used to compute intercepted PAR. Clearer relationships can be expected to emerge in experiments in which incident PAR is manipulated in such a way as to target a specific phenophase and a single position on the hedgerow.

As in most fruit trees, source–sink relationships are likely to be important in olive (Rallo and Suarez, 1989; Rallo and Cuevas, 2008), particularly because vegetative and reproductive growth occurs simultaneously. This often leads to competition between branch and fruit growth, as in peach where the proportion of assimilates allocated to a given sink type during the growth season depends on its demand and the competitive ability of other sink types (Grossman and DeJong, 1995a; DeJong and Grossman, 1995; review by Marcelis et al., 1998). Such inter-sink adjustments in olive have been little studied.

The objectives of this study were: (i) to determine, for fruit growing at a single position on the hedgerow, the response functions of fruit dry weight and oil concentration to PAR during the oil synthesis phase (i.e., after final fruit set has occurred), and (ii) to contrast the effects of PAR on vegetative (branch and trunk growth) and reproductive (fruit) growth rates. The general hypothesis tested was that fruit growth during the oil synthesis phase is the priority sink for the assimilates under limiting PAR. In consequence, it was predicted that with a decrease in PAR the fruit growth would be affected to a lesser extent than the growth of branches.

2. Materials and methods

2.1. Experimental site and shading treatment

The study was conducted from January 23 to May 22, 2008 in a commercial orchard of 8-year-old trees (*Olea europaea* L. var. "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 is 100 mm, mean annual temperature 20 °C and the potential reference evapotranspiration 1600 mm y^{-1} (Searles et al., 2011). Tree spacing was 4 m × 6 m 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.

Measurements of fruit growth and oil concentration ran from flowering to harvest, and all responses to shading were followed during 16 consecutive weeks from 90 to 210 days after flowering (DAF). This latter period coincided with the rapid expansion of the mesocarp (which had reached only 11% of its final weight at the start of treatments), active oil synthesis, and little endocarp + seed growth (Conde et al., 2008; Hammami et al., 2011), conditions we confirmed by periodical harvests of fruit (Table 1). Final fruit number is normally defined in olive by the time of pit hardening (Gómez-del-Campo and Rapoport, 2008), so we started the shading treatments after that event to avoid possible compensations between fruit number and fruit size.

A randomized complete block design with four levels of artificial shading (3, 20, 40, and 70% of incident PAR measured on a horizontal plane) and 4 replicate trees per treatment was employed. At the beginning of the experiment, the tree height was 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).

The selected trees had a high fruit load (approximately 1500 fruit m^{-3}) as defined by Trentacoste et al. (2010) for cv. 'Arbequina'. The different shading levels were achieved using plastic netting of different transmittances stretched over metal frames 4 m high and 3.5 m wide. Shades were placed on the N side (which receives higher levels of irradiance in the Southern Hemisphere) of the trees and the S side remained unshaded (Fig. 1). This allowed free movement of air within the structure and minimized changes in microclimatic conditions often associated with the artificial shading treatments. Previous studies have indicated that the carbon balance of a main branch of a mature tree is relatively autonomous (Proietti and Tombesi, 1996). Although transmittance of the shade

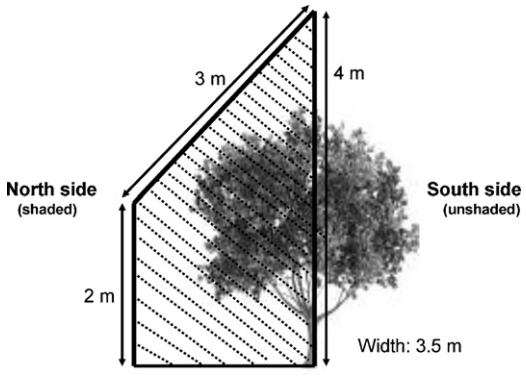

Fig. 1. Diagrammatic side view of the shading structure.

cloth was 90% in the control under full sun conditions, partial shading produced by the neighboring tree within the row reduced this value to 70%. Moderate pruning of the neighboring tree was performed during the experimental period to avoid any further reduction in the PAR received by the control. A similar pruning of neighboring trees was done for the other treatments.

The irradiance transmitted by the shade clothes (I) was measured in situ once a month during the experiment using a 1 m × 0.01 m integrating light bar (Cavadevices, Buenos Aires, Argentina), placed horizontally at a height of 2 m and at 0.25 m from the outer edge of canopy and perpendicular to the row (i.e., in an east–west direction). Incident radiation (Io) was measured in the center of the row, far from the trees. All PAR measurements were made at solar noon because in a preliminary study the fraction of intercepted PAR measured under the shade clothes at noon was within 6% of the value calculated by integrating values from five different solar times (8, 10, 12, 14, 16 h). Mean daily incident PAR for the entire period, estimated from short-wave radiation data obtained from a weather station (Davis Instrument, CA, USA) located 8 km away, was 42.9 mol m^{-2} d^{-1}. Values of PAR incident on the shaded sides of each individual tree were obtained by multiplying daily PAR incident on a horizontal plane by shade-specific transmittances values, and they varied from 1 to 36 mol m^{-2} d^{-1}. Air temperature and relative humidity under the shades were measured once a month using a digital thermohygrometer (Hygropalm 2, Rotronic Ag, NY, USA) and compared with paired measurements made at the center of the interrow far from the influence of the shading structures.

2.2. Dynamics of fruit growth, oil concentration and vegetative growth

Fruit dry weight and oil concentration were determined once a month from flowering until ripening, with the fourth harvest coinciding with the imposition of treatments. At each harvest, 100 g of fresh fruit was collected from the external part of the canopy (i.e., within 0.25 m from the outer surface) at a height of 1.75–2.25 m on the shaded (N) side of each tree. Individual harvest canopy volumes were separated from neighboring harvest volumes by at least 0.20 m to minimize changes in source–sink relationships which might affect the subsequent growth of non-harvested fruit. Fruit and pulp (exocarp + mesocarp) fresh and dry weights were determined on subsamples of 10 fruit before and after the fruit being oven-dried at 70 °C to constant weight. To determine oil concentration, the remaining fruit of each sample were ground in a hammer mill and the oil was extracted with hexane from the oven-dried paste using a Soxhlet extractor for 6 h. Average dry weight and average oil concentration per fruit, fruit number, and yield for each side were determined separately.

The vegetative growth of the trees was estimated by measuring the length of branches without fruit (non-bearing branches) and the cross-sectional area of the trunk. Branch length was measured once a month during the shading period on ten marked branches (initial lengths between 5 and 7 cm) located at the periphery of the shaded side of the trees and 2 m height. Trunk cross-sectional area (TCSA) was estimated from trunk circumference measured at 0.30 m from the ground with a flexible tape at the beginning and at the end of the shading period.

On May 22, 2008 the N (shaded) and S sides of the trees were harvested separately and then weighed for yield determination. For a given side, yield density was calculated as fruit weight (kg) per canopy volume (m^3). Fruit number was estimated for each side by dividing yield by average individual fruit fresh weight. Oil yield density and fruit density were calculated by dividing oil yield or fruit number by the volume corresponding to each tree side. Before harvesting, fruit fall was evaluated visually by comparing fruits on the ground under the different shading treatments and constructing a visual scale.

2.3. Meteorological data and growth rate

Air temperature and solar radiation were recorded every 15 min by an automatic weather station (Davis Instruments, Hayward, CA, USA) located 8 km from the study site. Thermal time was calculated (in °C d^{-1} units) using the single sine, horizontal cut-off method (http://www.ipm.ucdavis.edu/WEATHER/ddretrieve.html), with critical temperatures of 7 °C (lower limit estimated for peach fruit growth by DeJong and Goudriaan, 1989) and 40 °C (upper limit suggested for olive fruit growth by Pérez-López et al., 2008). The relative growth rate (RGR) of the fruit during the filling phase was estimated as the rate of increase in weight per unit dry weight per degree–day (Hunt, 1982). RGR was calculated as $[\ln(w_2) - \ln(w_1)]/(t_2 - t_1)$ where w_2 and w_1 are the mean individual fruit dry weights at harvest dates t_2 and t_1 in units of thermal time. The RGR of non-bearing branches and the trunk during fruit filling were calculated similarly by substituting branch length or TCSA for weight (Solari et al., 2006). To evaluate the competitive ability of the reproductive and vegetative sinks during the filling phase, RGR of both sinks were expressed as percentage of the 70% of PAR treatment, considered as a control.

2.4. Statistical analyses

Linear or bilinear functions were fitted to the relationships between yield and yield components (fruit number, fruit dry weight, and oil concentration) and average daily PAR (mol m^{-2} d^{-1}) or thermal time (°Cd, T_{base}7 °C) using the nonlinear routine of TBLCURVE software (TBLCURVE 2D, 1994). The fitting of bi-linear functions with an unknown break-point followed the conditional model $y = a + bx$ for $x \leq c$; $y = a + bc$ for $x > c$, where y were the variables mentioned above (i.e. the dry weight, the oil concentration, etc.), x was time in degree days or PAR, a was the intercept y, b was the slope of the linear function, and c was an unknown breakpoint (the x value which maximizes the variable response).

The dynamics of fruit dry weight and oil concentration and the elongation of vegetative branches were analyzed using the PROC MIXED procedure of SAS (SAS Institute, Cary, NC, USA) for repeated measurements ANOVA following recommendations of Littell et al. (1998). Treatment means were contrasted using the ESTIMATE function of PROC MIXED. Relative growth rates for vegetative and reproductive structures were analyzed by ANOVA from PROC GLM procedure of SAS. Duncan's Multiple Range Test was used to compare treatment means.

3. Results

Daily PAR and maximum and minimum temperatures decreased progressively throughout the fruit filling phase (Fig. 2). Air temperature and relative humidity under the shade structures was, on average, 0.4 °C and 0.8% lower, respectively, than the values recorded outside the structures, with no differences between treatments ($P > 0.05$) for either variable.

3.1. Seasonal and treatment period responses to PAR

Fruit fall was minimal during the oil synthesis phase, and thus fruit density (# m^{-3}) was similar across shade treatments (Fig. 3a) This allowed for changes in fruit weight and oil concentration in response to the treatments to be evaluated as a function of PAR during the oil synthesis phase, without confounding effects arising from possible compensations between fruit number and size.

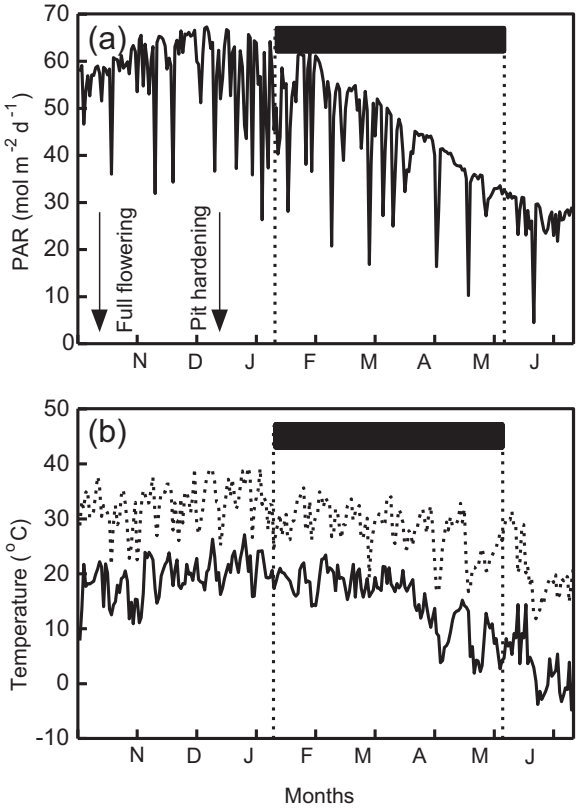

Fig. 2. (a) Daily incident photosynthetically active radiation (PAR), and (b) maximum and minimum daily temperatures recorded during the 2007/2008 growing season. Dotted vertical lines and black rectangles indicate the shading period.

The responses of final fruit dry weight, oil concentration, and yield to PAR incident on the external portion of the N face of the canopy were best fitted by bilinear functions (Fig. 3b–d). Final fruit dry weight increased linearly with irradiance up to a maximum weight of 0.9 g fruit^{-1} at 17 mol m^{-2} d^{-1} (equivalent to 40% of PAR incident on a horizontal plane) (Fig. 3b); and oil concentration reached its plateau at 15 mol m^{-2} d^{-1} (34% PAR) (Fig. 3c). This combination resulted in a final maximum oil yield of 0.59 kg m^{-3} at 14 mol m^{-2} d^{-1} (33% PAR). Fruit maturity index (MI) at harvest was delayed by shading with MI being 1.61 under 3% PAR and 2.66 under 70% of PAR (data not shown).

During the experiment, vegetative growth was low because the seasonal growth peak occurred before the application of the treatments. The treatment-period increment in non-fruiting branch length increased linearly from 0.2 to 2.3 cm branch^{-1} over the entire range of incident PAR values (1–35 mol m^{-2} d^{-1} PAR); with no apparent threshold (Fig. 4a). Similarly, treatment-period increment in TCSA increased linearly from 2.3 cm^2 up to 7.1 cm^2 over the same PAR range (Fig. 4b).

3.2. Treatment-period relative growth rate responses to PAR

Responses of treatment-period RGR to PAR, normalized with respect to control values, differed between the fruit and vegetative organs (Fig. 5). The fruit growth response saturated at 40% of incident PAR, while the responses of non-bearing branches and that of TCSA tended to increase over the whole range of incident PAR, although there was some indication that the TCSA increment changed little at the three lowest levels of PAR (Fig. 5b; Table 2). Under very limiting PAR levels (3%, 20%), normalized RGR values for elongation of non-bearing branches and TCSA were lower than the equivalent metrics for fruit.

3.3. Dynamics of fruit dry weight, oil concentration, and branch elongation

Fruit dry weight increased in one or two linear phases throughout the fruit filling phase in all treatments, but rates of increase and number of phases were strongly dependent on PAR level (Fig. 6a). After imposition of treatments and for PAR levels ≥40%, an increase of 0.40 g fruit^{-1} took place at a rate of 0.22 mg °Cd (Fig. 6a; Table 3), a

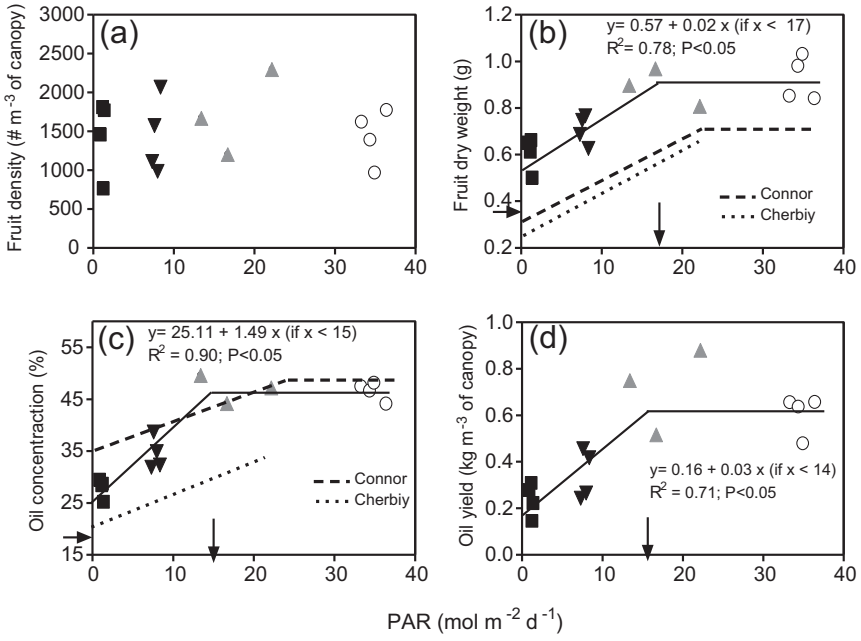

Fig. 3. Relationships between (a) fruit number, (b) fruit dry weight, (c) fruit oil concentration, and (d) final oil yield and average daily PAR for the external 0.25 m of shaded trees. Artificial shading treatments are indicated in the figures as the average proportion of PAR received by the trees during the study (■: 3%, ▼ 20%, ▲: 40%, ○: 70%). In parts b–d, the arrow placed on the *x*-axis indicates threshold value of PAR. Average daily incident PAR (Io) during the experiment was 42.9 mol m^{-2} d^{-1}. In parts b and c results obtained by Connor et al. (2009) (- - -) and Cherbiy-Hoffmann et al. (2012) (· · ·) are also shown.

Table 2
Treatment effects on the average relative growth rates of the fruit, of non-bearing branches and of the trunk cross-sectional area over the whole of the oil synthesis phase ($n = 4$). Different letters indicate significant differences between treatments ($P < 0.05$) and letters in italic indicate marginally significant differences between treatments ($P = 0.08$).

Treatments	Relative growth rate (RGR)		
	Fruits (mg g^{-1} °Cd^{-1})	Branches (mm cm^{-1} °Cd^{-1})	Trunk cross-section (mm^{-2} cm^{-2} °Cd^{-1})
3% PAR	0.169 ± 0.021 a	0.00016 ± 0.0000 *a*	0.130 ± 0.084 a
20% PAR	0.283 ± 0.018 b	0.00063 ± 0.0003 *ab*	0.208 ± 0.101 a
40% PAR	0.373 ± 0.043 c	0.00083 ± 0.0001 *ab*	0.114 ± 0.045 a
70% PAR (control)	0.375 ± 0.023 c	0.00158 ± 0.0007 *b*	0.408 ± 0.076 b

Table 3
Treatment effects on rates of fruit dry matter and fruit oil concentration increase during the treatment period. Values are slopes of the linear functions fitted to the data ($n = 4$). Different letters within a column indicate significant differences ($P < 0.05$). These slopes correspond to post-imposition of treatment lines shown in Fig. 6.

Treatments	Fruit dry matter increase rate (mg °Cd^{-1})	Oil concentration increase rate (% °Cd^{-1})
3% PAR	0.074 ± 0.001 a	0.007 ± 0.001 a
20% PAR	0.144 ± 0.010 b	0.011 ± 0.001 b
40% PAR	0.225 ± 0.021 c	0.017 ± 0.001 c
70% PAR (control)	0.224 ± 0.005 c	0.018 ± 0.001 c

rate indistinguishable from that of the pre-treatment period. Below 40% PAR fruit growth rates decreased in relation to those obtaining before imposition of shades, but even under severe shading (3% incident PAR) fruit growth rates were slightly positive right up to final harvest.

Oil concentration in the control treatment increased slowly during the first 60 DAF (or 1200 °Cd) and then linearly until the final harvest (Fig. 6b, Table 3). At PAR levels ≥40%, oil concentration increased an average of 30 percentage points during the oil synthesis phase at a rate of 0.018% °Cd (Fig. 6b, Table 3). After imposition of treatments and for PAR levels lower than 40%, oil accumulation rates and final oil concentrations were reduced (Fig. 6b and Table 3). Under severe shading (3% of PAR), oil accumulation continued to occur (albeit at a rate 2.5 times smaller than in fruits that received ≥40% of PAR; Table 3).

By contrast with the sustained linear growth rates of fruit dry weight and oil concentration, and the lack of differences between control and 40% PAR treatments for these variables, non-fruiting branch elongation rates exhibited a curvilinear response over thermal time and the rate under 40% PAR was consistently different from that of the control. Notably and at least for the measurements

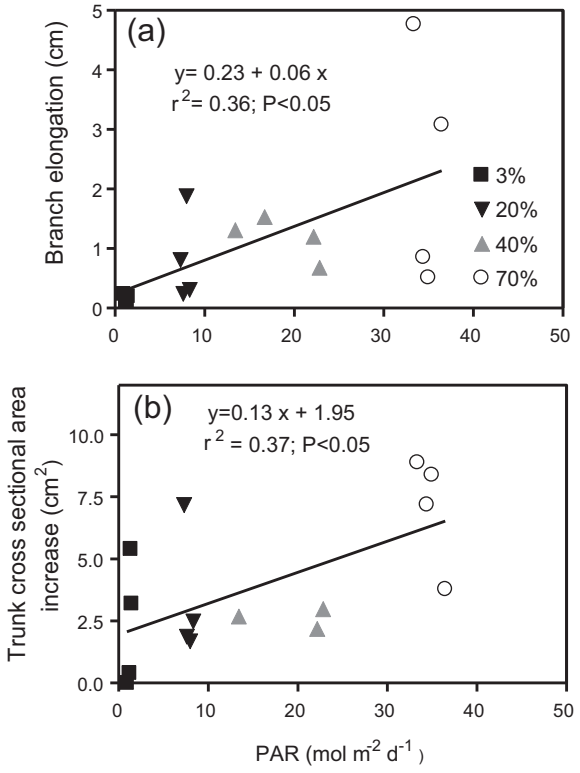

Fig. 4. Relationships between increases during the treatment period in (a) length of non-bearing branches and (b) in TCSA and average daily PAR. Artificial shading treatments are indicated in the figures as the average proportion of PAR received by the trees during the study (■: 3%, ▼ 20%, ▲ :40%, ○: 70%). Average incident daily PAR (Io) during the experiment was 42.9 mol m^{-2} d^{-1}.

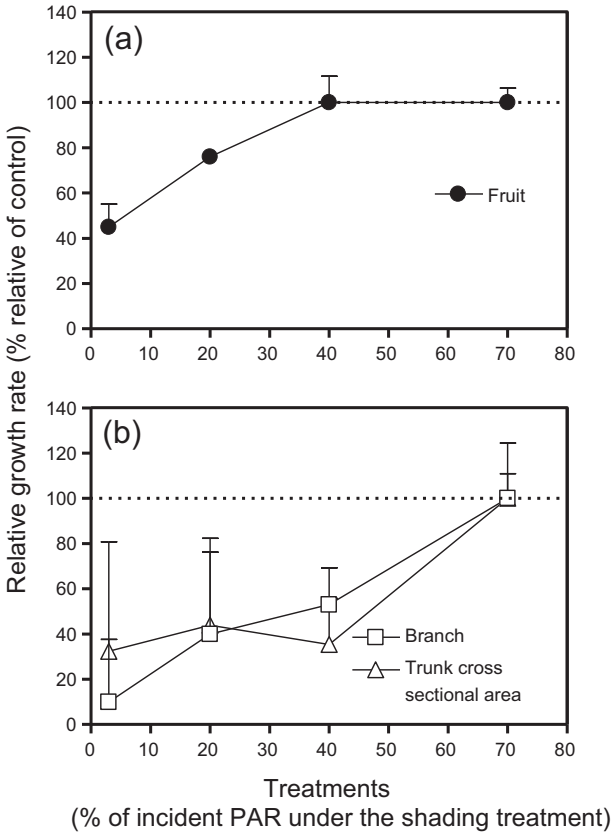

Fig. 5. Relationship between normalized (with respect to control [70% PAR] values) relative growth rates over the treatment interval and relative (to incident) PAR for (a) fruit dry weight and (b) non-bearing branch elongation and trunk surface area. Capped vertical lines represent one standard error ($n = 4$).

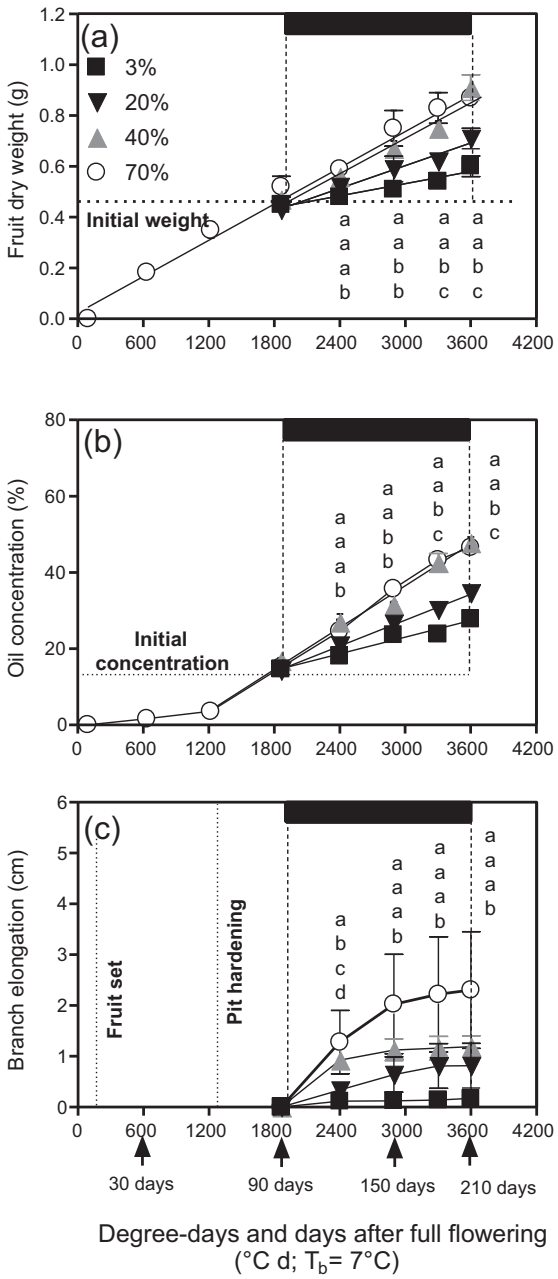

Fig. 6. Dynamics of (a) dry weight per fruit, (b) oil concentration and (c) increase in the length of non-bearing branches. The shaded rectangle identifies the period over which treatments were applied (January–May 2008) and the dotted horizontal line indicates the weight and oil concentration of the fruit at the beginning of the study. Artificial shading treatments were expressed as percentage of incident PAR. Each data point is the average of 4 trees per treatment and vertical lines ± one standard error (not shown when smaller than symbol). Time in days after full flowering (DAF) is indicated below the *x*-axis. Different letters in the vertical sets above or below the data points for each measurement data indicate significant difference between treatments ($P < 0.05$).

made at 2400 °Cd, the incremental elongation of these branches was statistically different between all four levels of PAR (Fig. 6c). Branch elongation rates under 3% PAR fell almost to zero.

4. Discussion

Application of shades after endocarp hardening ensured that most of the subsequent responses of yield were limited to the oil synthesis phase and that endocarp and seed growth during the shading period was almost nil (Table 1), and was successful in avoiding fruit fall during this period (Fig. 3a). Thus, our results can be assessed without needing to consider the effects of possible fruit number/fruit size compensations in response to PAR levels, and can be considered as representative of what may occur in high fruit load (ca. 1500 fruit m^{-3}, Fig. 3a).

Several features of our results point to the fact that fruit were the dominant sink for assimilates during the oil synthesis phase. These indicators include:

- sustained (albeit responsive to PAR levels below but not above 40%) rates of dry weight increase and oil concentration of the fruit (Table 3 and Fig. 6a and b) in contrast to non-bearing branch elongation rates that were reduced by PAR levels of 40%, 20% and 3%, falling to close to zero at 3% (Fig. 6c, Table 2).
- normalized RGR for non-bearing branch elongation and TCSA lower than that of fruit at low levels of PAR and increasing over the range of PAR levels explored, in contrast to the saturation of fruit normalized RGR at PAR levels <40% (Fig. 5).

The continued increases of fruit dry weight and oil concentration at the 3% PAR level (Fig. 5a and b, Table 2), as well as non-zero increments in TCSA (Fig. 4b) is somewhat surprising, given that incident PAR was close to light compensation point (Bongi and Long, 1987). Under this condition of minimum carbon gain, growth might have been sustained by the translocation of carbohydrate from nearby reserves (olive, Proietti and Tombesi, 1996; peach, Marsal et al., 2003; apple, Morandi et al., 2011). But translocation from the unshaded south side of the tree could also be possible as translocation between plants (e.g., Ashmun et al., 1982) and between organisms (e.g., Finlay and Read, 1986) have been documented, particularly when a carbohydrate depletion occurred. However, carbohydrate partitioning in trees is still poorly understood (Wardlaw, 1990; Allen et al., 2005). We used changes in branch length and TCSA as proxy indicators of vegetative growth. Further work is needed to transform these dimensional changes into estimates of carbon investment, as suggested for peach by Grossman and DeJong (1995b). Our data do not allow a clear judgment as to possible hierarchies of non-bearing branches and the trunk as sinks (Fig. 5b), although the trunks of two of the four trees in the 3% PAR level continued to increase in cross-sectional area when branch length increments were almost nil (Fig. 4a, Fig. 6c, Table 2). A study of the dynamics of both branch elongation and TCSA, as we used for branches (Fig. 6c) might help clarify this issue.

Our results (Fig. 3b and c) confirm the existence of bilinear responses to PAR of fruit size and oil content found by Connor et al. (2009, 2012), resulting in a bilinear response of oil yield (Fig. 3d). This last response does not emerge clearly in Connor et al., 2012 (their Fig. 2), possibly because their results are a compilation of observations from 10 different orchards, a circumstance which would make it harder to discern response functions. Interestingly, Cherbiy-Hoffmann et al. (2012) found no indication of plateau responses to PAR in fruit dry weight and oil content, possibly because the range of PAR explored in their experiments was narrower than in the one reported here.

A comparison between the present results for fruit size and oil concentration and those of Connor et al. (2009) and Cherbiy-Hoffmann et al. (2012) (cf. dashed lines in Fig. 3b and c) show aspects of concordance and difference (i.e., presence/absence of plateaus, differences in breakpoint values, variations in slopes and intercepts, differences in range of PAR explored). Two comments are pertinent here: (a) taken together, the results favor the existence of upper limits to fruit growth capacity which becomes evident at fairly moderate levels of PAR, and (b) more work is needed to understand the origin of differences between experiments. The first issue suggests that although low levels of

PAR can produce low yields through reductions in inflorescence density and/or fruit set (Villalobos et al., 2006; Pastor et al., 2007; Cherbiy-Hoffmann et al., 2012), fruit size and oil content, and hence, yield can be affected by PAR quite late in the fruit-filling phase. This could be important in situations in which the final phases of fruit growth take place under falling levels of incoming radiation and those in which excessive vegetative growth produces shading of leaves supplying photoassimilates to fruit left deeper in the canopy. This apparently conservative fruit growth capacity may have arisen to ensure that photosynthesis of external canopy leaves contributes to the growth of fruit placed inside the tree crown and/or adequate fruit filling under falling levels of incoming radiation. There are several candidate causes for the differences in response functions between experiments shown in Fig. 3b and c. Important among these are variations among experiments in fruit load or source–sink relationships (Tombesi et al., 1999), fruit filling temperatures (García-Inza, personal communication), differences in experimental approach (i.e., layering vs. specific target within canopy, direct vs. indirect estimates of the window of time in which PAR is presumed to affect processes). A source:sink perspective on PAR responses could ultimately be helpful in improving the modeling of optimum canopy structures.

In summary, our work has shown that manipulation of PAR levels during the oil synthesis phase can reduce final fruit dry weight and oil concentration, confirmed the existence of upper thresholds to PAR responses for these variables, and provided evidence that fruit growth has priority in the partitioning of photosynthate over vegetative growth under low to moderate levels of PAR.

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