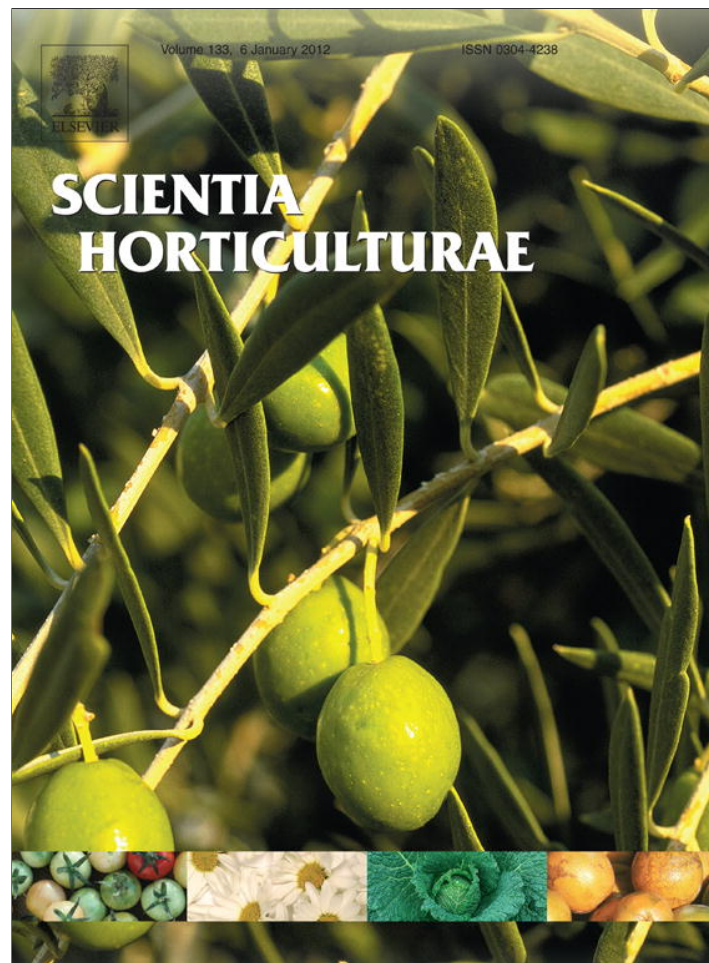


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Influence of light environment on yield determinants and components in large olive hedgerows following mechanical pruning in the subtropics of the Southern Hemisphere

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ABSTRACT

Olive cultivation has expanded considerably beyond the Mediterranean Basin to include new areas in the Southern Hemisphere. This study evaluated the response functions of yield determinants and components to photosynthetically active radiation (PAR) in a large olive hedgerow (cv. 'Arbequina') in subtropical Argentina, and assessed whether mechanical pruning altered these relationships. Mechanical pruning was applied at the end of the winter dormant period to the east side and top of hedgerows oriented North–South, while the other side was left unpruned. The PAR distribution and leaf density at different positions within the hedgerow were measured over the two subsequent growing seasons with inflorescence density, fruit set, fruit density, individual fruit dry weight, and oil content (%) being assessed the second growing season. Hedgerow size increased substantially during the first season, especially on the pruned side and top, reducing transmitted PAR in much of the canopy to less than 20% of full Sun incident PAR values above the orchard. The relationship between leaf density (and thus number of axillary buds) and PAR was bilinear for the canopy positions within the unpruned side with a threshold of about 15% of full Sun PAR, above which leaf density did not increase. No relationships between leaf density and PAR were found within the pruned side and top. In contrast, inflorescence density exhibited a threshold of 18% of PAR for canopy positions within both the pruned and unpruned sides, although no relationship was apparent for the pruned top. Neither fruit set nor yield component relationships with PAR were affected by pruning. Fruit set had a linear response to PAR for the observed range of PAR values within the hedgerow (approx. 0–50% of full Sun). Individual fruit dry weight and oil content (%) also showed linear responses to PAR. The results suggest that oil production in large olive hedgerows (height × width) is limited by low solar radiation within the canopy, and that substantial vegetative growth triggered by mechanical pruning may be an important contributor to this limitation under current management practices in subtropical climates.

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1. Introduction

Olive cultivation has expanded significantly in the last 20 years in the arid and semi-arid subtropical valleys (28–31°S) of Argentina due to tax deferral laws and the availability of deep groundwater for irrigation (MAGPyA, 2004). The climate of these production zones includes average annual air temperatures and summer

precipitation that are typically higher than in the Mediterranean Basin where olive is traditionally grown (Ayerza and Sibbett, 2001). These conditions often result in high rates of vegetative growth (Correa-Tedesco et al., 2010), which leads to the formation of large hedgerows that are maintained through mechanical pruning and harvested with over-the-row contact harvesters (Ferguson et al., 2010).

In fruit trees, it is desirable to maximize the interception of solar radiation in conjunction with an appropriate distribution of radiation within the tree canopies (Jackson, 1980; Rom, 1991; Lauri et al., 2009). This allows for maximum efficiency of radiation use for photosynthesis, flower bud formation, growth, and fruit quality. In such a context, yield and product quality depend on the light environment in which the fruits develop. For example; by using shade cloths of known transmittances, it was found that flower density (# per unit canopy volume) increased linearly with increasing

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solar radiation, up to a threshold of 40% of full solar radiation for apple (Jackson and Palmer, 1977a) and 23% for peach (reviewed by Marini and Corelli-Grappadelli, 2006). Similarly, fruit weight in apple increased up to a threshold of 40%. Variables of fruit quality, such as color development, exhibited higher thresholds in both apple (60%) and peach (30%) (Jackson and Palmer, 1977b; Marini and Corelli-Grappadelli, 2006). Results of several studies in these species demonstrated that light environment close to the potential sites of fructification is the variable most strongly linked to spatial within-canopy variations in yield and fruit quality (e.g., Corelli-Grappadelli et al., 1994; Wünsche et al., 1996; Wünsche and Lakso, 2000; Willaume et al., 2004).

Yield of olive trees, similar to other fruit crops, is related to the amount of photosynthetically active radiation (PAR) intercepted by the orchard (Villalobos et al., 2006). In experiments that compared shaded trees (<15% of incident PAR) versus unshaded trees, number of inflorescences, fruit set, fruit size, and fruit oil content (%) all decreased drastically with artificial shading (e.g., Tombesi and Standardi, 1977; Tombesi and Cartechini, 1986; Proietti et al., 1994; Tombesi et al., 1999). These results suggest that yield will be reduced if tree canopies or hedgerow volume become too large due to self-shading within the hedgerow and accompanying low PAR values.

To model optimal canopy design in olive (cv. 'Arbequina'), Connor et al. (2009) analyzed the relationships between yield components and PAR for narrow, high porosity hedgerows using the averages of all fruit in vertical canopy intervals and a single value of PAR intercepted daily by each interval. They found a linear relationship between fruit density ($\# \text{ m}^{-2}$) and intercepted PAR up to a threshold of 37% of horizontally incident PAR above the orchard. Fruit dry weight and oil content also exhibited threshold responses, but the threshold was much larger (60% of incident PAR).

Considering that the yield of olive orchards is often best explained by fruit number rather than fruit size or oil content (%) (Gómez-del-Campo et al., 2009; Trentacoste et al., 2010), there is surprisingly little or no information available concerning the relationships between the number of axillary buds, inflorescence density, and fruit set with PAR. Additionally, although pruning practices influence the amount of PAR inside the canopy, it is not known whether the responses of yield determinants and components to PAR are altered by pruning. The objectives of this study, conducted on trees forming part of large olive hedgerows typical of Northwest Argentina, were to: (i) characterize the PAR distribution within the hedgerow during two growing seasons; (ii) determine the PAR response functions of both yield determinants and yield components (fruit weight and oil content); and (iii) determine if pruning alters these PAR response functions.

2. Materials and methods

2.1. Experimental site and hedgerow architecture

The study was conducted over two growing seasons from September 1, 2005 to April 15, 2007 in a commercial orchard with 8-year-old olive trees (*Olea europaea* L. cv. 'Arbequina'). The orchard was located in the Central Valley of the Province of Catamarca near the town of Miraflores, Argentina (28°37'S, 65°54'W; 550 m above sea level). This area is part of the Arid Chaco phytogeographic region with historic average annual rainfall values of 423 mm, an average annual temperature of 20.6 °C, and an annual reference evapotranspiration of 1700 mm (<http://www.smn.gov.ar>). Tree spacing was 5 m × 7 m with a north–south (15% deviation to the east) row orientation and irrigation was provided by eight 4 L h⁻¹ drip emitters per tree. The orchard received approximately 950 mm of irrigation per year in addition to the lower than average rainfall using a crop

coefficient (K_c) of 0.7. A reduction coefficient (K_r) of 0.9 was also applied to correct for crop cover according to Fereres and Castel (1981).

Following the management practices of the region where one side of the hedgerow and its top are pruned every one or two years, the east-facing side and the top of the hedgerow were pruned mechanically at the end of the winter rest period (August 2005) using a large, tractor mounted rotary-saw pruner with four cutting heads. The east-facing side was pruned at an angle of 10° from vertical (i.e., hedging) and the top of the hedgerow was pruned horizontally (i.e., topping), while the west-facing side was left untouched. Given the N–S orientation, we assumed that the major effects of pruning would be similar whether either the east or the west facing-side of the hedgerow was pruned. No further pruning was conducted during the study period.

Three individual trees were selected for detailed tree size, PAR distribution, and yield measurements based on tree height (3.5 m), trunk diameter, and row porosity. Each tree was located near the center of a 100-m long row with at least one row separating it from the next tree. Measurements of tree size were conducted four times during each growing season (September, December, February and April) to coincide respectively with the phenological stages of flowering, flower induction, fruit growth, and harvest. Tree height was determined using a graduated pole centered on the trunk of each tree. Canopy width perpendicular to the row was measured at 0.5-m intervals up to a height of 5 m using a grid system to assess growth of both the pruned and unpruned sides of the hedgerow.

2.2. Distribution of photosynthetically active radiation in the hedgerow

Light environment within the hedgerows was characterized four times per season at approximately the same phenological stages used for the tree-size measurements, and was based on the determination of PAR at 60 positions per tree (30 per side). These 30 positions per side were located at 5 distances from the trunk (0.75–1.75 m) in the direction of the interrow with a spacing of 0.25 m and at 6 heights (1.0–3.5 m) separated by 0.5 m. In the 2006–2007 growing season, some additional points were added to the east and west sides to accommodate the tree growth that occurred during the previous season. Unfortunately, it was not possible to increase the PAR measurement area above 3.5 m in height due to logistical difficulties. All measurements were made using a 1.0 m × 0.01 m integrating light bar (Cavadevices, Buenos Aires, Argentina), placed horizontally and parallel to the tree row (north–south direction) in all 60 positions. Readings were taken five times a day at 8, 10, 12, 14, and 16 solar hours under clear sky conditions. Additionally, incident PAR was measured every 5 min above the orchard at a height of 6 m using an individual PAR sensor and recorded with a datalogger (Cavadevices, Buenos Aires, Argentina). The integrating light bar and individual PAR sensor were cross-calibrated and had equivalent cosine responses. To estimate the daily radiation received at each position, trapezoidal integration of the five PAR values at each canopy position and the incident values above the orchard was performed. Daily radiation at each position was expressed as mol PAR m⁻² d⁻¹ and as the percentage of incident radiation above the orchard.

2.3. Determinants and components of yield

At the end of each growing season, non-destructive leaf counts were carried out at each of the 60 positions within the hedgerow as an approximation of new branch growth for the same positions and as a proxy for the number of potentially reproductive axillary buds for the following season. The counts were performed within a metal-framed, box-like structure of known dimensions and

volume (1 m long \times 0.1 m wide \times 0.1 m high; 0.01 m³) that was placed in the same positions as the integrating light bar used in the PAR measurements. A leaf was counted when greater than one-half of its surface area was within the sampling volume. As with the PAR measurements, detailed leaf count measurements were not obtained above 3.5 m, although an approximation was obtained by harvesting branches from neighboring trees.

Inflorescence number at each position was determined at flowering in September 2006 (second season) within the same sampling volume, and the number of fruit was similarly counted at harvest on March 9, 2007. The harvest was carried out at a fruit maturity index of 3.5, approximately two weeks before the estimated date of maximum oil accumulation. Fruit fresh and dry weights for each of the 60 positions were determined in the laboratory with the fruit being oven-dried at 70 °C until a constant weight was obtained. Each dry fruit sample was crushed, ground in a porcelain mortar, and the oil was extracted with hexane for 6 h using a Soxhlet apparatus. Reproductive variables were not assessed during the first growing season because of a severe, late-winter frost (−7 °C) that damaged most of the inflorescences shortly before flowering.

2.4. Data analysis

Linear or bilinear regression functions were fitted to measured yield determinant or component values versus daily PAR using TBLCURVE software (TBLCURVE 2D, 1994). Data for the pruned and unpruned sides including data from both the external canopy face and its interior were evaluated separately unless pooling proved appropriate. Results for the top of the canopy corresponded to the 10 observations distributed across the 3.5 m-high measurement plane, and were also evaluated separately as a first approximation. To obtain the best relationship, the measured PAR values from each of the four measurement dates from the previous season or from the current season were considered taking into account measurement dates that could potentially be the most influential over a given study variable. For example, to evaluate fruit set, its relationships with PAR values measured in late-September during flowering and those measured in December posterior to fruit set were tested, and the best fit selected.

3. Results

During the two growing seasons (2005–2006, 2006–2007), the mean monthly values of daily PAR averaged about 20 mol m^{−2} d^{−1} in the winter and 40 mol m^{−2} d^{−1} in the summer with only minor deviations from historical values (Fig. 1a). Temperature values were also similar to previously recorded values (Fig. 1b). By contrast, total monthly rainfall in both seasons was low (Fig. 1c), which resulted in lower annual totals (2005–2006: 245 mm; 2006–2007: 267 mm) than the historical average (423 mm).

Hedgerow dimensions increased substantially during the two growing seasons, particularly on the pruned top and side compared to the unpruned side (Fig. 2). During the first growing season, new branch growth was more than 1.0 m on the pruned top (i.e., vertical watersprouts) and pruned side, while growth was about 0.3 m on the unpruned side (Fig. 2b). Because of the high growth rates, the hedgerow reverted to an approximately spherical shape by the end of the first season. Although the frost just prior to flowering markedly reduced fruit load and thus likely increased photoassimilate availability for branch growth, no substantial damage to vegetative apices or leaf drop were observed. Hedgerow growth was lower during the second growing season with width increasing only 0.3 m on the pruned side and less than 0.1 m on the unpruned side (Fig. 2c). The final hedgerow dimensions measured in April 2007 were 4.6 m (width) and 5.5 m (height) in contrast to 3 m

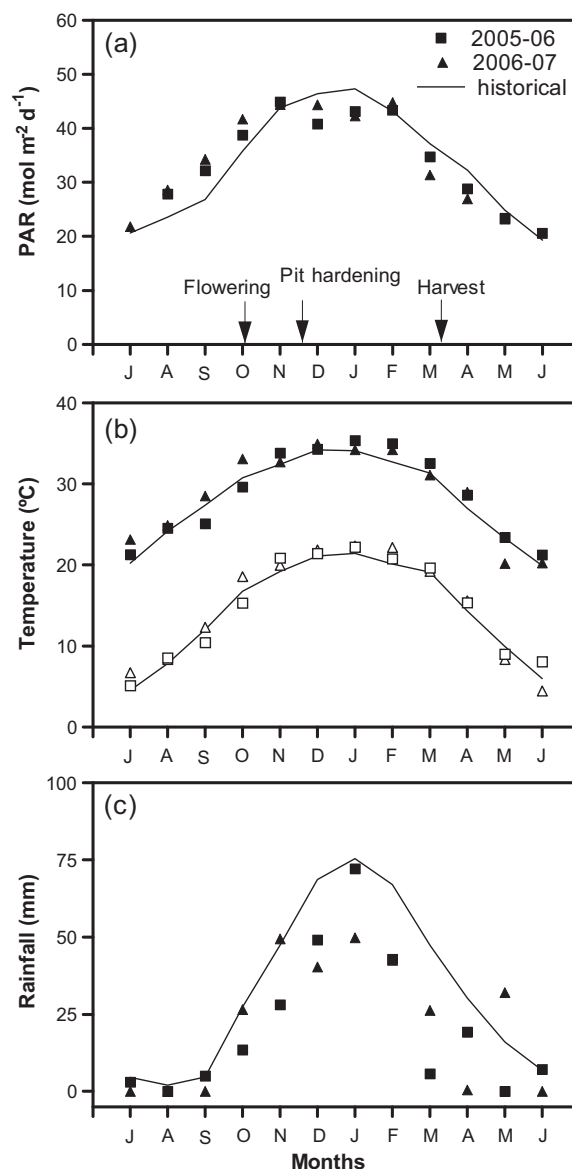


Fig. 1. Mean monthly values of (a) daily photosynthetically active radiation (PAR), (b) daily maximum and minimum temperatures, and (c) total monthly rainfall for 2005–2006 and 2006–2007. Continuous lines show historical values (1991–2007) from the National Meteorological Service weather station at the Catamarca airport (14 km from the experimental site).

(width) and 3.5 m (height) immediately after pruning (September 2005).

PAR received within the hedgerow (as % of incident above the orchard) was high (>60%) or intermediate (20–60%) in a little over half of the measurement positions just after pruning (Fig. 2a). By the end of the first season, most of the positions within the original canopy volume received 20% or less of incident PAR although more external portions of the canopy on the pruned and unpruned sides had intermediate receipts (Fig. 2b). At the end of the second season, the only portions of the hedgerow below 3.5 m with PAR values in the intermediate category were a narrow strip on the unpruned side and a single position on the pruned side (Fig. 2c).

Leaf density (# L^{−1}) measured the first season in autumn of 2006 (April); an estimator of new branch growth during the first season and potentially reproductive axillary buds for the second season, showed a significant bilinear relationship with midsummer PAR (February) for the canopy positions within the unpruned

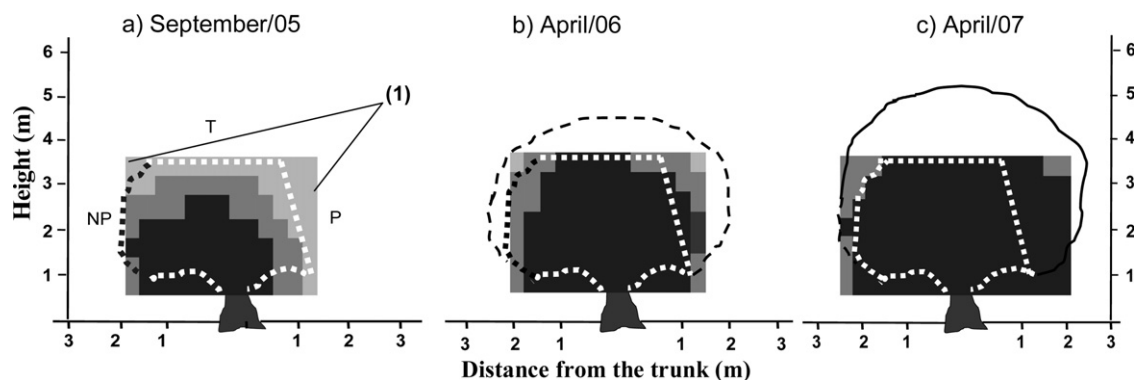


Fig. 2. Hedgerow dimensions and light environment at (a) the beginning of the 2005–2006 season (dotted line), (b) the end of the 2005–2006 season (dashed line) and (c) the end of 2006–2007 season (continuous line). P is the pruned side, NP is the unpruned side, and T is the top. Categories of PAR received within the hedgerow (as % of daily incident radiation above the orchard) are shown by shading: PAR > 60% (light gray), between 20% and 60% (dark gray), and $\leq 20\%$ (black). The number (1) indicates the limits of the measured PAR area. Values are means of 3 trees.

side of the hedgerow (Fig. 3a; $R^2 = 0.59$). When leaf density was regressed against autumn PAR (April), a similar significant relationship was obtained, although the coefficient of determination was lower ($R^2 = 0.45$). The threshold PAR value above which leaf density did not increase was $5 \text{ mol m}^{-2} \text{ d}^{-1}$, or equivalent to about 15% of the incident PAR above the orchard. No relationship between leaf density and PAR was apparent for canopy positions within the pruned side and top (Fig. 3b and c). Leaf density was much greater on the pruned side and top of the hedgerow with an average of $12.5 \text{ leaves L}^{-1}$ in comparison to a maximum of 6.9 L^{-1} on the unpruned side. This difference in leaf density is most likely due to the high number of new branches that resulted from the mechanical pruning. During the spring (September 2006) of the second growing season, inflorescence density ($\# \text{ L}^{-1}$) increased up to a PAR value of $7 \text{ mol m}^{-2} \text{ d}^{-1}$ (equivalent to 18% of incident PAR) for the canopy positions within the unpruned side of the hedgerow (Fig. 4a). The bilinear relationship was obtained using midsummer PAR values (February 2006) that coincided with the floral induction phase of the previous growing season. Inflorescence density showed poorer relationships with PAR received at other phenological stages (data not shown). The PAR threshold for canopy positions within the pruned side (Fig. 4b) was similar to that of the unpruned side, although the plateau of the fitted function was somewhat lower. This likely occurred because the percentage of axillary buds that differentiated inflorescences (i.e., # inflorescences/# axillary buds) was smaller on the pruned side (40%) than on the unpruned side (70%). No clear relationship between inflorescence density and PAR was found for the pruned top of the hedgerow (Fig. 4c), and the percentage of axillary buds that differentiated inflorescences was only 20%.

The fruit set and yield component (fruit density, dry weight, and oil content) relationships with PAR were not affected by pruning during the second season, and a single response function per variable was fitted to the data from all three sections of the hedgerow (Figs. 5 and 6). Fruit set ($\# \text{ inflorescence}^{-1}$) showed a significant linear relationship with springtime (late September 2006) canopy PAR values over the range of observed PAR values ($0\text{--}22 \text{ mol m}^{-2} \text{ d}^{-1}$) (Fig. 5a). Fruit density ($\# \text{ L}^{-1}$) showed a bilinear relationship with PAR including a PAR threshold of $8 \text{ mol m}^{-2} \text{ d}^{-1}$ (20% of incident PAR above the orchard) (Fig. 5b). Both individual fruit dry weight and oil content (%) on a dry weight basis had significant linear relationships at harvest with canopy PAR values over the range of observed PAR values (Fig. 6). In all cases, the best fit for the yield component relationships with PAR was obtained when using PAR values from the spring (late September 2006), rather than summer or autumn values (data not shown). It is likely that potential fruit size based on cell number is defined during

this time period, although the response of oil content (%) is less clear.

4. Discussion

Large hedgerows are common in olive orchards in the subtropical latitudes of Northwest Argentina due to a combination of climate and management practices (Gómez-del-Campo et al., 2010), and provided an opportunity to measure yield determinants and components within the hedgerow interior over a wide range of PAR levels and pruning conditions. After dormant season pruning of one hedgerow side and the top, overall hedgerow dimensions increased from $3 \text{ m} \times 3.5 \text{ m}$ (width \times height) to $4.6 \text{ m} \times 5.5 \text{ m}$ over two growing seasons with concomitant decreases in PAR in the canopy interior. Most of the increase in hedgerow size occurred in the first season on the pruned side and top when fruit load was low due to the pruning itself as well as a hard frost. Although mechanical pruning of fruit trees often leads to a short-term increase in PAR penetration into the canopy, the indiscriminate head cutting (i.e., shortening) of young branches can greatly stimulate the formation and growth of new branches, which may decrease PAR levels in the canopy over the longer-term (Forshey and Elfving, 1989; Gucci and Cantini, 2000; Lombardini, 2006).

Leaf density within a canopy is the result of the appearance of new leaves and the senescence of old leaves. The values of the more external canopy positions measured on the pruned side and top in our study were double those of the unpruned side by the end of the first season due to the high number of new branches formed at the heading cuts. Similarly, Gucci and Cantini (2000) have stated that a mat of shoots forms on the outer edge of olive hedges after mechanical pruning that prevents light penetration to the inner part of the canopy. Thus, mechanical pruning in olive may lead to a less desirable tree architecture compared to hand pruning as suggested for pistachio by Spann et al. (2008). For all canopy positions (i.e., external and internal), the pruned side and top did not show clear relationships between leaf density and the amount of PAR received, likely because new leaf appearance was driven more by the loss of apical dominance (and new branching) due to pruning than by PAR. In contrast, leaf density for the unpruned side showed a linear increase up to a PAR threshold value of $5 \text{ mol m}^{-2} \text{ d}^{-1}$, or slightly less than 15% of the incident PAR above the orchard. In this case, the balance between new leaf appearance associated with the more external canopy positions and leaf loss in the canopy interior resulted in PAR playing a major role in determining leaf density. Drastic reductions of PAR (<10%) in the summer using shade cloth have previously been shown to increase leaf senescence in olive (Proietti et al., 1994).

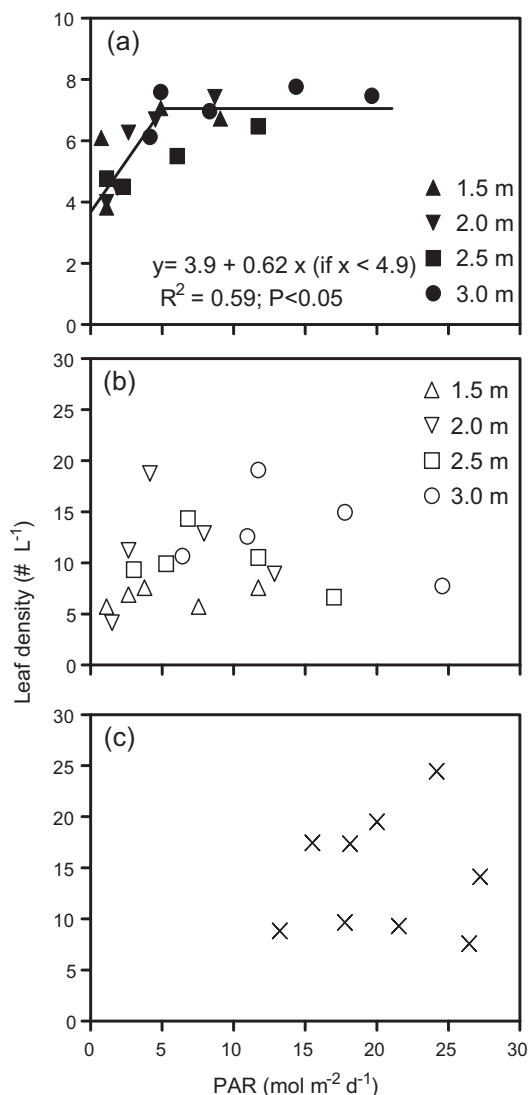


Fig. 3. Relationships between leaf density (number of leaves per liter) near the end of the first growing season (April 2006) and mid-summer photosynthetically active radiation (February 2006; PAR) received at different canopy positions within the hedgerow for the (a) unpruned side, (b) pruned side, and (c) the pruned top. Daily incident PAR above the orchard on the day of measurement was 37.8 mol PAR m⁻² d⁻¹. Several data points are plotted for each height within the canopy, which correspond to different distances from the center of the canopy. Each data point is the average of 3 trees. Note the difference in the scale of the y-axis between panel (a) and panels (b) and (c).

To the best of our knowledge, little information exists in olive concerning the responses of yield determinants (i.e., number of axillary buds, inflorescence density, fruit set) to PAR received within the hedgerow. Leaf density, in addition to partially reflecting vegetative growth, provides an estimate of potentially reproductive axillary buds. Although the number of axillary buds at the end of the first growing season (2005–2006) was larger within the pruned side and the top as seen in the greater leaf density than in the unpruned side, the inflorescence density the following spring was smaller. In other words, the exuberant growth associated with pruning promoted the induction of vegetative buds at the expense of reproductive buds, as reviewed for fruit trees by Mika (1986), Genard et al. (2008) and Bangerth (2009). As discussed in the previous paragraph, only the leaf density (and thus the number of axillary buds) on the unpruned side showed a relationship with PAR. In contrast, the canopy positions for both the pruned and unpruned sides showed bilinear relationships between

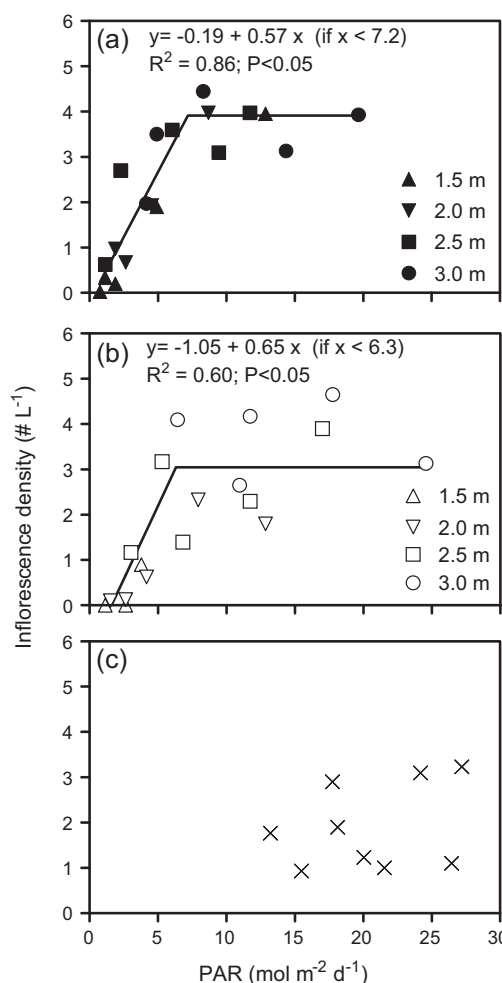


Fig. 4. Relationships between inflorescence density (number of inflorescences per liter) in spring 2006 (late September) and mid-summer photosynthetically active radiation (February 2006; PAR) received at different canopy positions within the hedgerow for the (a) the unpruned side, (b) pruned side, and (c) pruned top. Daily incident PAR above the orchard on the day of measurement was 37.8 mol PAR m⁻² d⁻¹. Several data points are plotted for each height within the canopy, which correspond to different distances from the center of the canopy. Each data point is the average of 3 trees.

inflorescence density and PAR with a PAR threshold of about 7 mol m⁻² d⁻¹ (equivalent to 18% of incident PAR) in both cases. An early, pioneering study in olive found that inflorescence density was markedly reduced under a PAR transmittance of less than 10% when shading whole trees (Tombesi and Cartechini, 1986).

For fruit set, a single linear relationship with PAR received by the canopy positions within the hedgerow for the entire range of observed PAR values (i.e., 0–22 mol m⁻² d⁻¹, equivalent to 0–50% of incident PAR above the orchard) was obtained during the second growing season when combining the data from the pruned and unpruned sections of the hedgerow. This indicates that the relationship between fruit set and PAR was not affected by pruning the previous year. Tombesi and Standardi (1977) also found that fruit set was limited by solar radiation at low light levels using an unshaded control and two shading treatments (i.e., 3 and 16% light transmittance). Our results suggest that fruit set is less sensitive to PAR than inflorescence density under low PAR conditions due to the low slope of the fruit set vs. PAR relationship, and indicate that a high PAR value (>50%) is needed to maximize fruit set. Such a PAR value is slightly greater than the 40% threshold observed in apple trees (Jackson and Palmer, 1977a), and is much greater than that found in hazelnut (25%; Hampson et al., 1996). Further analysis

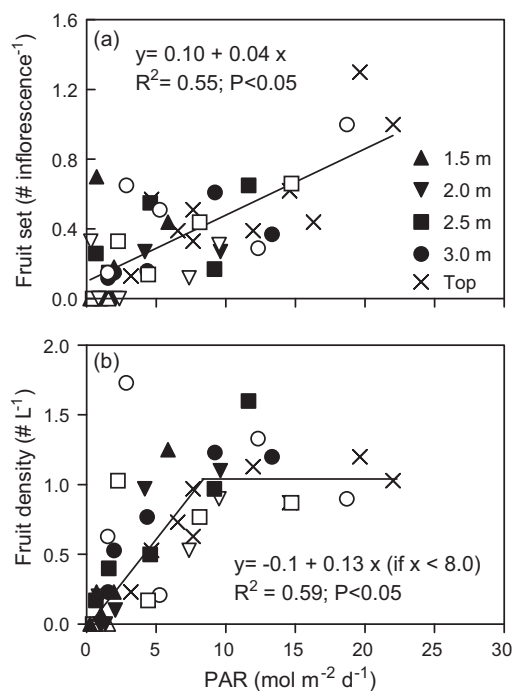


Fig. 5. Relationships between (a) fruit set (number of fruit per inflorescence) and (b) fruit density (number of fruit per liter) with photosynthetically active radiation (PAR) received at different canopy positions within the hedgerow during the spring (late September 2006) of the second growing season. Daily incident PAR above the orchard on the day of measurement was $45.7 \text{ mol PAR m}^{-2} \text{ d}^{-1}$. Several data points are plotted for each height within the canopy, which correspond to different distances from the center of the canopy. Each data point is the average of 3 trees. Unpruned side (closed symbols); pruned side (open symbols); pruned top (X).

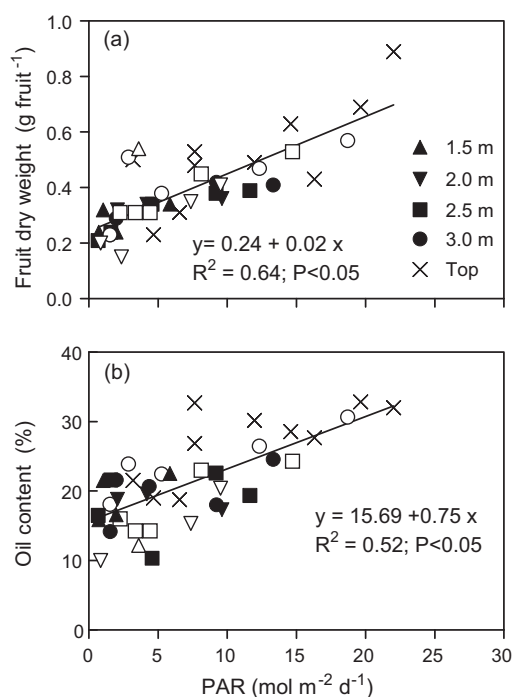


Fig. 6. Relationships between (a) individual fruit dry weight and (b) oil content (%) on a dry weight basis with photosynthetically active radiation (PAR) received at different canopy positions within the hedgerow during the spring (late September 2006) of the second growing season. Daily incident PAR above the orchard on the day of measurement was $45.7 \text{ mol PAR m}^{-2} \text{ d}^{-1}$. Several data points are plotted for each height within the canopy, which correspond to different distances from the center of the canopy. Each data point is the average of 3 trees. Unpruned side (closed symbols); pruned side (open symbols); pruned top (X).

suggests in part that fruit set showed a linear rather than a bilinear relationship with PAR because although inflorescence density was low within the upper portion of the pruned and topped sections of the hedgerow, fruit set (# fruit per inflorescence) was greatest in these positions. In other words, fewer inflorescences resulted in a greater fraction of the inflorescences producing harvestable fruits, likely due to little carbohydrate competition between fruits. Rosati et al. (2010) for olive and Iglesias et al. (2003) for citrus have previously suggested that early carbohydrate competition between growing fruits often leads to fruit drop.

As in other crops, fruit number is the component that best explains yield in olive trees (Gómez-del-Campo et al., 2009; Trentacoste et al., 2010). Fruit density in our study for the entire hedgerow including both pruned and unpruned sections increased with PAR up to a PAR threshold of $8 \text{ mol m}^{-2} \text{ d}^{-1}$ (20% of incident PAR). Comparing fruit density with single values of radiation intercepted by vertical intervals (0.5 m in height and depth) of narrow, high porosity hedgerows, Connor et al. (2009) obtained a somewhat greater PAR threshold of $15 \text{ mol m}^{-2} \text{ d}^{-1}$ (37% of incident PAR) for the same cultivar ('Arbequina') in Toledo, Spain. However, direct comparison between the two studies is difficult because our study considered horizontal variation in PAR within the hedgerow, while Connor et al. (2009) considered essentially vertical gradients. Given that many variables besides PAR within the hedgerow are likely to affect yield determinants and subsequent fruit density, more manipulative experiments examining either the role of individual yield determinants on fruit density (Lavee et al., 1996, 1999) or the importance of other climatological variables such as temperature could improve our understanding of the controls of fruit density.

In contrast, many of the responses of fruit dry weight and oil content (%) in Catamarca to PAR received within the hedgerow were similar to those of Connor et al. (2009) in Spain despite the differences in canopy structure and experimental methodology. Connor et al. (2009) found that both variables increased linearly with PAR up to a threshold of about $25 \text{ mol m}^{-2} \text{ d}^{-1}$ (60% of incident PAR), while in our study these two variables responded linearly to PAR up to the maximum observed value of $22 \text{ mol m}^{-2} \text{ d}^{-1}$. The slopes of the relationships were also similar in the two studies with a slope of approximately 0.02 g mol^{-1} of PAR for fruit dry weight and of about $0.75\% \text{ mol}^{-1}$ of PAR for oil content. Nevertheless, the environment did appear to affect maximum oil content. Although the slope was the same, the oil content (%) was considerably higher at Toledo than in our study for the same level of PAR. Low oil content (%) is common in Catamarca, possibly due to the depression of fatty acid synthesis under high summer temperatures (García-Inza, personal communication). In Catamarca, the highest rate of oil synthesis in 'Arbequina' occurs in mid-summer with a mean temperature of 27°C and a mean daily PAR of $43 \text{ mol m}^{-2} \text{ d}^{-1}$ (Fig. 1), while it occurs in early fall in Toledo with a mean temperature of 15°C and a fairly similar mean daily PAR (Gómez-del-Campo et al., 2009).

The role of crop load should likely be considered in assessing fruit weight and oil concentration responses to PAR. In our study, tree crop load was medium to high with maximum values of around $1000 \text{ fruit m}^{-3}$ of canopy volume in some canopy positions. At such values, Trentacoste et al. (2010) determined that source:sink ratio limits both individual fruit weight and oil weight per fruit in cv. 'Arbequina'. More directly, shading (<10% PAR) has been found to reduce fruit weight and oil concentration in heavily loaded olives trees, but not in low crop load trees (Tombesi et al., 1999). Such a source:sink perspective on PAR responses could ultimately be helpful in improving the modeling of optimum canopy structures.

In conclusion, the results of this study with a large olive hedgerow in Northwest Argentina suggest that yield determinants

such as the number of axillary buds and inflorescence density have low PAR requirements (i.e., <20% of incident radiation above the orchard), while many yield components including fruit weight and oil content need greater than 50% of full Sun PAR to obtain maximum values. Thus, large hedgerows (in height and width) with their considerable canopy interiors and corresponding low light levels appear to limit individual fruit weight and their oil content. Mechanical pruning of one side and the top of the hedgerow indirectly modified the relationship between the number of axillary buds and PAR at the end of the first growing season by generating exuberant new vegetative growth that was independent of PAR, but did not affect other yield determinants or components the following season to any great degree. While the frost at the beginning of the first growing season eliminated almost all production for that year, late-winter cold fronts of Antarctic origin are not uncommon in the region despite the subtropical latitude and often lead to alternate bearing. Limiting mechanical pruning to high crop load years when fruit growth and oil accumulation provide strong competition to vegetative growth for photoassimilates may decrease the risk of excessive growth, and would improve the distribution of light in the hedgerow. Potentially, canopy size in existing orchards of this region could be managed according to the appropriate combination of plant height and alley width as proposed by Connor (2006). Alternatively, the possibility of increasing plant density and, consequently, of reducing the size of the hedgerows could be explored.

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