



Fruit, mesocarp, and endocarp responses to crop load and to different estimates of source: sink ratio in olive (cv. Arauco) at final harvest



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ABSTRACT

The annual fluctuations in olive crop load due to alternate bearing and other factors often lead to large differences in fruit size and oil content between years at harvest. A better understanding of how fruit parameters respond to the different leaf: fruit (i.e., source: sink) ratios that occur with contrasting crop loads would provide important information for crop management. Thus, the primary objectives of this study conducted with the cv. Arauco in three growing seasons were to: 1) determine the weight and size responses of the fruit and its main tissues, mesocarp (pulp) and endocarp (pit), to crop load; and 2) obtain relationships between different estimates of the source: sink ratio versus various fruit and oil parameters. Fruit thinning was performed by hand on uniform trees with high initial crop loads four weeks after full bloom the first season to obtain different crop loads at harvest. The thinning percentages the first season were 24%, 48% and 87%, along with an unthinned control. The same trees were then monitored the following two seasons without any further thinning. Fruit were sampled at harvest each season to determine fruit and tissue weights and diameters, oil weight per fruit, and oil concentration (%). Fruit weight was reduced 30–40% by high crop loads in each growing season with the mesocarp being much more affected than the endocarp. Oil weight per fruit (–50%) showed a somewhat greater reduction than fruit weight to crop load due to both fruit diameters and fruit oil concentration being decreased at high crop loads. Fruit and tissue weights and oil weight per fruit all displayed bilinear functions versus source: sink ratio when the source was expressed as canopy volume (a surrogate for leaf area) and sink on both a fruit number and glucose equivalent (GE) basis. Source limited fruit growth at both medium and high crop loads due to limited photoassimilate availability based on the bilinear functions, and the slope of the endocarp response to source: sink ratio was 15 times less than that of the mesocarp when expressed on a GE basis. A quantitative comparison with previously published studies indicated that maximum fruit weight appears to be obtained in olive between 1–2 m² of leaf area per kg of GE. The bilinear relationships of source: sink ratio versus fruit weight observed in this study could contribute to crop modelling, and further research concerning how and when the mesocarp and endocarp respond to crop load is needed to aid crop management in obtaining sufficient fruit size and quality for table olive cultivars.

1. Introduction

Olive trees often exhibit alternating low and high production years that result in large differences in fruit size (Monselise and Goldschmidt, 1982; Lavee, 2007; Samach and Smith, 2013). The responses of fruit size to crop load are fundamentally related to source: sink ratio. In other words, fruit size is affected by the ratio between leaves (source)

that provide photoassimilates for growth and the number of fruit and other organs (sinks) that compete for photoassimilates (Grossman and DeJong, 1994). A recent study has shown that the sink activity of individual olive fruit (i.e., relative growth rate) is limited by high crop load during the first 30–60 days after flowering, while shoot growth is limited most of the growing season (Fernández et al., 2015). Such limitations on fruit growth due to lack of photoassimilate availability

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under sufficiently high crop loads are common in a wide range of fruit tree species such as apple (e.g., Haller and Magness, 1933; Beers et al., 1987; Palmer, 1992), cherry (Whiting and Lang, 2004; Cittadini et al., 2008) and peach (Pavel and DeJong, 1993; Grossman and DeJong, 1995).

The olive fruit is a drupe in which the major tissues are the mesocarp (pulp) and the endocarp (pit). The growth of these two tissues is closely interrelated due to their common origin in the ovary pericarp (Gucci et al., 2009), yet they also appear to compete as sinks, as long proposed in interpreting the double sigmoid growth pattern in which the slowdown of overall fruit growth has been associated with pit hardening (Hartmann, 1949; Barabé and Jean, 1995). Furthermore, endocarp growth occurs early, whereas mesocarp growth occurs throughout olive fruit development (Hammami et al., 2011; García-Inza et al., 2016), suggesting possible sink competition in early fruit growth (Fernández et al., 2015). Also, during reduced growth under early water deficits, endocarp development often extends over a longer period and successfully competes for assimilates to the detriment of the mesocarp (Rapoport et al., 2004; Gucci et al., 2009). These different tendencies during fruit development may influence the quantitative source: sink response to crop load at the tissue level at final harvest.

The existing literature related to source: sink relationships in olive provides mostly general conclusions of the response of fruit size and its tissues to crop load based on whether statistically significant differences were found between crop load treatments at final harvest. That is, significant differences between treatments have been used to establish that high crop loads often lead to smaller fruit, decreased mesocarp: endocarp tissue ratios, and less oil per fruit (Barone et al., 1994; Gucci et al., 2007; Dag et al., 2009; Lodolini et al., 2011). While it is well understood that fruit and oil yield per tree do largely increase with crop load, reductions in fruit size under high crop loads can be detrimental to the successful commercialization of table olives. Less consistent responses to crop load have been found for oil concentration (%) than for fruit size. Mesocarp oil concentration may either decrease at high crop load (Gucci et al., 2007; Beyá-Marshall and Fichet, 2017), or be unaffected (Lavee and Wodner, 2004; Trentacoste et al., 2010). Although most oil accumulates in the mesocarp rather than the endocarp tissue, little emphasis has been placed on the potential role of the endocarp in determining whole fruit oil concentration (%), which is a relevant parameter for the olive oil industry.

A greater emphasis on studies assessing fruit size and other variables as a function of source: sink ratios would lead to detailed quantitative information that may be more universally applicable for modelling olive production and predicting the consequences of different management strategies (Morales et al., 2016). Proietti et al. (2006) reported that five leaves per fruit ($26 \text{ cm}^2 \text{ fruit}^{-1}$) were needed to maximize fruit weight as well as mesocarp and endocarp tissue weights in fruit growing on girdled branches of the Italian oil cv. Frantoio. Girdling was used as an experimental technique in that study to block the translocation of leaf photoassimilates, which permitted a fairly controlled evaluation of fruit weight responses to leaf: fruit ratio. Under more natural conditions in whole trees of the Spanish oil cv. Arbequina, both fruit weight and oil weight per fruit were source-limited in medium and high crop load trees with weights increasing linearly up to a source: sink ratio of approximately 2 m^3 of tree canopy volume per one thousand fruit (Trentacoste et al., 2010).

Sink activity involves the use of substrate for growth, differentiation, and storage (Loomis and Connor, 1992), and can be energetically quantified by using glucose equivalents (GE). Glucose equivalents represent the production costs for individual plant organs such as fruit based on the amount of glucose a plant requires to construct one gram of biomass of that organ (Penning de Vries et al., 1974). In annual crop species, GE have been used successfully to compare species with very different biochemical compositions (Andrade, 1995; Munier-Jolain and Salon, 2005). For example, while corn yield was more than twice that of sunflower on a dry weight basis, the yield difference on a GE basis was

much less because corn kernels have a high percentage of low cost carbohydrates and sunflower achenes (seed + pericarp) are costly to produce due to high seed oil content (Andrade, 1995). In olive trees, GE have been used to incorporate the role of production costs of different plant organs in modelling plant growth and yield in the cv. Arbequina (Villalobos et al., 2006; Morales et al., 2016). At a finer scale, a GE approach would allow the biochemical composition of mesocarp and endocarp tissues to be considered when evaluating their role as sinks. Mesocarp cells contain large amounts of oil with a single large oil droplet per cell resulting from the fusion of several smaller oil bodies in the cytoplasm during fruit development (Rangel et al., 1997; Bodoira et al., 2015). In contrast, the endocarp is fully sclerified with very high fractions of lignin, cellulose, and hemicellulose (Rodríguez et al., 2008). The expression of source: sink relationships on a GE basis may also be an advantage relative to a fruit number basis when comparing different studies and olive cultivars because fruit size can differ greatly between olive cultivars.

The primary objectives of this study conducted with the olive cv. Arauco over three growing seasons in Northwest Argentina were to: 1) determine the weight and size responses of both the fruit and its main tissues (i.e., mesocarp and endocarp) to a wide range of crop loads; and 2) obtain relationships between different estimates of the source: sink ratio versus various fruit and oil parameters. Secondly, we quantitatively compared the source: sink relationships from our study with those from other published studies.

2. Materials and methods

2.1. Experimental orchard and experimental design

The study was conducted in a commercial olive orchard (*Olea europaea* cv. Arauco) located near Bañado de Los Pantanos in the Province of La Rioja, Argentina (28.4°S , 66.8°W ; 805 m above sea level) over three growing seasons. The cv. Arauco has large fruit that are used for either table olive or olive oil production and is grown widely in Argentina where it originated (International Olive Oil Council, 2000). The trees were 9 years-old at the start of the experiment with a spacing of 6 m within rows \times 8 m between rows ($208 \text{ trees ha}^{-1}$), east-west row orientation, and an initial canopy volume of $13 \pm 3 \text{ m}^3$. The orchard was well-irrigated using a drip irrigation system with a crop coefficient (Kc) of 0.7 employed most of the year based on results from a near-by orchard (Correa-Tedesco et al., 2010). Fertilization (N, P, K, Mg) was provided by the grower via the drip irrigation. If periodic foliar nutrient analyses conducted at a commercial laboratory (La Buena Tierra, Catamarca ARG) detected any deficiencies, supplemental fertilizer was added manually to the soil under the drip emitters of the experimental trees. The maximum daily temperatures were often above 35°C during the summer and freezing temperatures ($< 0^\circ\text{C}$) occurred on an average of about 35 days during the winter. Yearly crop reference evapotranspiration in this arid region is approximately 1600 mm with a rainfall of about 100 mm (Searles et al., 2011). Further orchard management and climate details can be found in Fernández et al. (2015), and some preliminary results from one growing season were presented in Fernández et al. (2014).

Fruit thinning was performed the first growing season on uniform trees with a high initial crop load four weeks after full bloom on November 13–14, 2007 to obtain a broad range of crop loads. Different target percentages (approx. 33, 66, or 95%) of fruit were removed by hand from the entire tree canopy for six trees per treatment level by removing from each branch one of every three fruit (33%), two of every three fruit (66%), or 19 of every 20 fruit (95%). Six remaining trees were used as controls and were not thinned. After the final harvest, the actual percentage of thinned fruits was determined to be 24%, 48%, and 87% based on the number of fruit thinned in November and the number of fruit harvested at the end of the season. The same trees were used during the second and third growing seasons, but no thinning was

Table 1

Crop load for the trees (cv. Arauco) in three growing seasons. Fruit thinning was performed the first season to obtain a wide initial range of crop loads. The same trees were monitored during the second and third seasons, but no thinning was performed. $n = 6 \pm$ standard error.

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

performed. These trees maintained a wide range of crop loads due to the alternate bearing behavior generated by the initial thinning event. The crop loads for each season are shown in Table 1. The experimental design was a randomized complete block design with one tree from each of the four experimental groups assigned to a given block and there were 6 blocks (i.e., 4 trees per block × 6 blocks = 24 trees).

2.2. Fruit harvest and measurements

At harvest each season (mid- to late-March), a sample of 20 fruit from each tree was collected randomly from the periphery of the tree canopy at a height of approximately 1.6 m. The fruit longitudinal and transverse diameters were measured using a digital caliper (Mahr GmbH, model MarCal 16 EWR, Germany) and fresh weight was determined using a precision balance (Denver Instrument Company, model XP 3000, USA). The fruit were then dried in an oven at 75 °C until reaching a constant dry weight and re-weighed. A second sample of 50 fruit per tree was frozen at harvest to later determine the mesocarp: endocarp ratio on a dry weight basis. Freezing and thawing the fruit facilitated the separation of the two tissues.

2.3. Fruit oil concentration, oil content, and maturity index

Approximately 2 kg of fruit per tree were collected at harvest the first and second seasons to determine fruit oil concentration (%), oil content per fruit (g oil fruit⁻¹), and fruit maturity index (0–7). For fruit oil concentration, a subsample of 100 whole fruit were dried to a constant weight, 10 g of the dried material was then finely ground, and the oil was extracted using ethyl ether for 6 h in a Soxhlet apparatus (Frías et al., 1991). The oil concentration was expressed as a percentage (%) of fruit dry weight. Oil weight per fruit was quantified as the fraction of oil in the fruit multiplied by the dry weight per fruit. The maturity index was determined by classifying 100 fruit per tree according to skin and mesocarp color using a scale of 0–7 (García and Yousefi, 2005; Uceda et al., 2010).

2.4. Source: sink calculations

Relationships were obtained for our experimental data by graphing individual fruit and tissue weights, or their glucose equivalents, versus source: sink ratio. Similar to Trentacoste et al. (2010), the source was estimated for most calculations as the tree canopy volume (V ; m³), which was defined as the average of the canopy volumes for each tree determined at the beginning and the end of each growing season. A spherical cap formula ($V = \pi d^2 h / 6$) was used, where d is the average of canopy diameter in the east-west and north-south directions and h is canopy height (i.e., tree height minus the distance between the soil surface and the tree skirt). The sink was expressed either as 1000 fruit or as fruit GE. Thus, the source: sink ratio was shown as m³ of tree canopy volume per 1000 fruit or m³ per kg of fruit GE.

The amount of glucose necessary to construct oil, proteins, carbohydrates, lignin, and minerals was estimated for the mesocarp and

endocarp using fractional values of biochemical composition obtained from the existing literature (Heredia-Moreno et al., 1987; Conde et al., 2008; Rapoport, 2008; Ghanbari et al., 2012) and our measured fruit oil concentrations (%). For the last growing season (2009–10), fruit oil concentration was not measured, but it could be estimated from the crop loads of the previous two growing seasons ($r^2 = 0.94$).

The biochemical composition values were multiplied by the standard coefficients from Penning de Vries et al. (1974) for each of the main categories: oil (3.11), proteins (1.70), carbohydrates (1.24), lignin (2.17), and minerals (0.05). This calculation provided the production cost (i.e., g of glucose required per unit of dry matter produced) of the mesocarp and endocarp for the fruit of each tree with its given crop load. The whole fruit production cost was then determined as a weighted average of the two tissues. Lastly, the mesocarp and endocarp dry weights were multiplied by their respective production costs to obtain the number of GE for each tissue, which were summed to obtain GE per fruit.

In order to quantitatively compare our results with those of previously published studies with different olive cultivars, the source: sink values above which maximum fruit weight was obtained were calculated for each study. Source was expressed using leaf area (m²), and the source: sink ratio was calculated as leaf area per 1000 fruit, fresh weight, dry weight, or GE. While leaf area density (LAD; m² m⁻³ of tree canopy volume) was not measured in our study, we estimated LAD as 2.5 m² m⁻³ based on prior published values from the same orchard (Searles et al., 2009) in order to convert canopy volume to leaf area. A single study with apple fruit (Palmer, 1992) and another with sunflower achenes (Ruiz and Maddonni, 2006) were also included to provide some initial comparison between source: sink ratios of olive with disparate species.

2.5. Statistical analysis

The different fruit weight and diameter variables as well as the oil-related variables were analyzed for each growing season following a general linear mixed model procedure for a randomized block design (InfoStat Version 2011, Universidad Nacional de Córdoba, Argentina). A Fisher LSD post-test was used to compare crop loads when a significant difference was detected ($P < .05$). Relationships between weight, GE, or oil variables with source: sink ratio were fitted with bilinear functions when weight or another variable reached a plateau versus source: sink ratio and the model was determined to be statistically significant ($P < .05$). The conditional model fitted was $y = a + bx$ if $x \leq c$ and $y = z$ if $x \geq c$; where y was the fruit weight, GE or oil response variable, x was the source: sink estimation, a was the y-intercept, b was the slope, and c was the unknown breakpoint that represents the source: sink ratio where a shift from source limitation to sink limitation occurred, and z was the maximum value of the response variable (i.e., the plateau).

3. Results

3.1. Fruit weight, diameter, and oil parameters

Fruit fresh and dry weight on trees with the highest crop load each growing season was 30–40% less than that of trees with the lowest crop load each season (Table 2; $P < .05$). The mesocarp showed similar large reductions in dry weight, while the endocarp dry weight was significantly reduced by only 13–19% in the first and third seasons ($P < .05$). As a consequence of the mesocarp responding more to crop load than the endocarp, the mesocarp: endocarp ratio was reduced 30–40% in trees with high fruit load.

The fruit longitudinal and transverse diameters were both decreased 10–20% by crop load during the three growing seasons (Table 3; $P < .05$). The endocarp diameters were less affected, with percentage differences of only 5–10% between high and low crop loads, although

Table 2
Fruit and tissue weights for trees (cv. Arauco) with different crop loads in three growing seasons.

Season	Crop load (# m ⁻³)	Fruit fresh weight (g)	Fruit dry weight (g)	Mesocarp dry weight (g)	Endocarp dry weight (g)	Mesocarp: endocarp dry weight ratio
2007–08	132	7.73 ± 0.15a	2.85 ± 0.06a	1.97 ± 0.03a	0.69 ± 0.02a	2.86 ± 0.09a
	539	5.93 ± 0.25b	2.32 ± 0.09b	1.65 ± 0.05b	0.66 ± 0.01a	2.49 ± 0.03b
	818	5.14 ± 0.35c	1.96 ± 0.15c	1.34 ± 0.10c	0.60 ± 0.02b	2.22 ± 0.09c
	1061	4.68 ± 0.17c	1.72 ± 0.07c	1.16 ± 0.05c	0.56 ± 0.01b	2.07 ± 0.07c
2008–09	480	6.74 ± 0.34a	2.83 ± 0.17a	1.97 ± 0.16a	0.69 ± 0.02a	2.86 ± 0.21a
	483	6.04 ± 0.28a	2.58 ± 0.14a	1.91 ± 0.08a	0.65 ± 0.01a	2.96 ± 0.19a
	759	5.72 ± 0.25b	2.30 ± 0.07b	1.55 ± 0.07b	0.64 ± 0.02a	2.41 ± 0.07b
	1338	4.36 ± 0.09c	1.66 ± 0.05c	0.98 ± 0.04c	0.58 ± 0.03a	1.72 ± 0.09c
2009–10	114	7.90 ± 0.10a	2.98 ± 0.04a	2.05 ± 0.02a	0.76 ± 0.02a	2.69 ± 0.05a
	571	6.25 ± 0.26b	2.34 ± 0.12b	1.60 ± 0.08b	0.68 ± 0.02b	2.34 ± 0.10b
	803	5.49 ± 0.16c	2.09 ± 0.08c	1.37 ± 0.08c	0.65 ± 0.02b	2.12 ± 0.07c
	825	5.66 ± 0.11c	2.06 ± 0.06c	1.27 ± 0.08c	0.66 ± 0.02b	1.93 ± 0.11c

Values with different letters indicate significant differences between crop loads in the same season using the Fisher LSD post-test ($P < .05$). $n = 6 \pm$ standard error.

Table 3
Fruit and endocarp diameters for trees (cv. Arauco) with different crop loads in three growing seasons.

Season	Crop load (# m ⁻³)	Fruit		Endocarp	
		Longitudinal diameter (mm)	Transverse diameter (mm)	Longitudinal diameter (mm)	Transverse diameter (mm)
2007–08	132	30.3 ± 0.1a	21.0 ± 0.2a	19.5 ± 0.3a	8.69 ± 0.08a
	539	28.1 ± 0.5b	19.0 ± 0.3b	19.5 ± 0.4a	8.65 ± 0.06a
	818	26.3 ± 0.7c	18.0 ± 0.5c	18.7 ± 0.4a	8.53 ± 0.09a
	1061	25.4 ± 0.4d	17.1 ± 0.2c	17.6 ± 0.3b	8.25 ± 0.08b
2008–09	480	28.4 ± 0.5a	20.0 ± 0.4a	19.6 ± 0.2a	8.86 ± 0.07a
	483	27.3 ± 0.4a	19.0 ± 0.3b	19.1 ± 0.2a	8.70 ± 0.11a
	759	27.3 ± 0.5a	19.0 ± 0.3b	19.0 ± 0.4a	8.60 ± 0.10a
	1338	25.2 ± 0.2b	17.0 ± 0.1c	18.0 ± 0.3b	8.18 ± 0.15b
2009–10	114	29.3 ± 0.2a	20.5 ± 0.2a	20.3 ± 0.1a	9.50 ± 0.06a
	571	27.8 ± 0.3b	19.2 ± 0.3b	19.2 ± 0.5b	8.99 ± 0.13b
	803	26.4 ± 0.2c	18.3 ± 0.3c	19.1 ± 0.3b	8.89 ± 0.10b
	825	26.9 ± 0.2c	18.4 ± 0.2c	19.1 ± 0.2b	8.82 ± 0.08b

Values with different letters indicate significant differences between crop loads in the same season using the Fisher LSD post-test ($P < .05$). $n = 6 \pm$ standard error.

these differences were still statistically significant. In contrast, neither the fruit nor the endocarp longitudinal: transverse diameter ratios (i.e., form) responded to crop load (data not shown).

The fruit oil concentration on a dry weight basis (%) was 5.3 points lower the first growing season (36.9% vs. 42.2%) and 6.1 points lower the second season (34.4% vs. 40.5%) due to high crop load (Table 4; $P < .05$). Oil concentration was not determined the third season. The

Table 4
Fruit oil concentration, oil weight per fruit, and maturity index (MI) for trees (cv. Arauco) with different crop loads in two growing seasons.

Season	Crop load (# m ⁻³)	Oil conc. (%)	Oil weight (g fruit ⁻¹)	MI (0–7)
2007–08	132	42.2 ± 1.5a	1.20 ± 0.04a	2.12 ± 0.06a
	539	40.5 ± 1.1b	0.94 ± 0.05a	1.33 ± 0.16b
	818	37.7 ± 0.9b	0.74 ± 0.07b	1.13 ± 0.05b
	1061	36.9 ± 1.7b	0.64 ± 0.05c	1.12 ± 0.06b
2008–09	480	40.5 ± 2.8a	1.15 ± 0.10a	1.41 ± 0.07a
	483	41.9 ± 1.5a	1.08 ± 0.20a	1.43 ± 0.02a
	759	39.3 ± 1.2a	0.91 ± 0.05a	1.27 ± 0.09a
	1338	34.4 ± 1.3b	0.57 ± 0.02b	1.09 ± 0.03b

Values with different letters indicate significant differences between crop loads in the same season using the Fisher LSD post-test ($P < .05$). $n = 6 \pm$ standard error.

amount of oil per fruit was about 50% lower under high crop load because of both the decrease in oil concentration and in fruit diameters. Fruit maturity was also lower to some degree under high fruit load (Table 4).

3.2. Fruit source: sink relationships

Both total fruit and mesocarp dry weight increased linearly with increasing source: sink ratio (m³ per 1000 fruit) until reaching a plateau for the data pooled from all three growing seasons (Fig. 1a and b). The slope of the mesocarp relationship represents an increase of 0.61g of mesocarp dry weight per unit of source: sink ratio. In contrast, the slope of the endocarp response (0.08 g per unit of source: sink) was 7.6 times lower than that of the mesocarp (Fig. 1c). Nevertheless, a similar breakpoint of about 2.5 m³ of canopy volume per 1000 fruit occurred for the whole fruit and both tissues above which any increase in source: sink ratio did not increase dry weight. The mesocarp: endocarp dry weight ratio reached a maximum value of 2.84 at a slightly lower source: sink ratio of 2.16 m³ per 1000 fruit (Fig. 1d).

The estimated production costs (g glucose g dry matter⁻¹) were greater in the mesocarp than the endocarp (Table 5). Consequently, the whole fruit had slightly lower values than the oil-rich mesocarp due to the presence of cheaper lignin and hemicellulose in the endocarp. Estimated production costs did not differ between the different crop loads for the mesocarp tissue. Statistically significant lower costs were only determined for whole individual fruit under high crop load conditions due to the lower mesocarp: endocarp ratio in fruit from high crop load trees. A singular value of 1.60 g glucose g dry matter⁻¹ is presented for the endocarp because a constant biochemical composition was assumed, although it is recognized that minor changes due to crop load could have occurred.

By combining production costs with dry weight values, bilinear relationships were obtained between GE (e.g., g glucose per fruit or per mesocarp) and the source: sink ratio, also expressed using glucose values (m³ of canopy per kg of fruit glucose) (Fig. 2). The overall shape of the relationships was similar when source: sink was expressed on a glucose basis or as fruit number (Fig. 1), although substantial differences in the relative values of the slope were apparent for the mesocarp and endocarp tissues. The slope of the mesocarp GE response to source: sink was 9.32 (Fig. 2b), while that of the endocarp was only 0.63 (Fig. 2c). This means that the endocarp response to source: sink was 14.8 times lower than that of the mesocarp response on a glucose equivalent basis in comparison to 7.6 times lower when expressed as dry weight versus fruit number. Additionally, the maximum value of the mesocarp: endocarp ratio was 3.94 on a glucose equivalent basis (Fig. 2d) and only 2.84 on a dry weight basis (Fig. 1d).

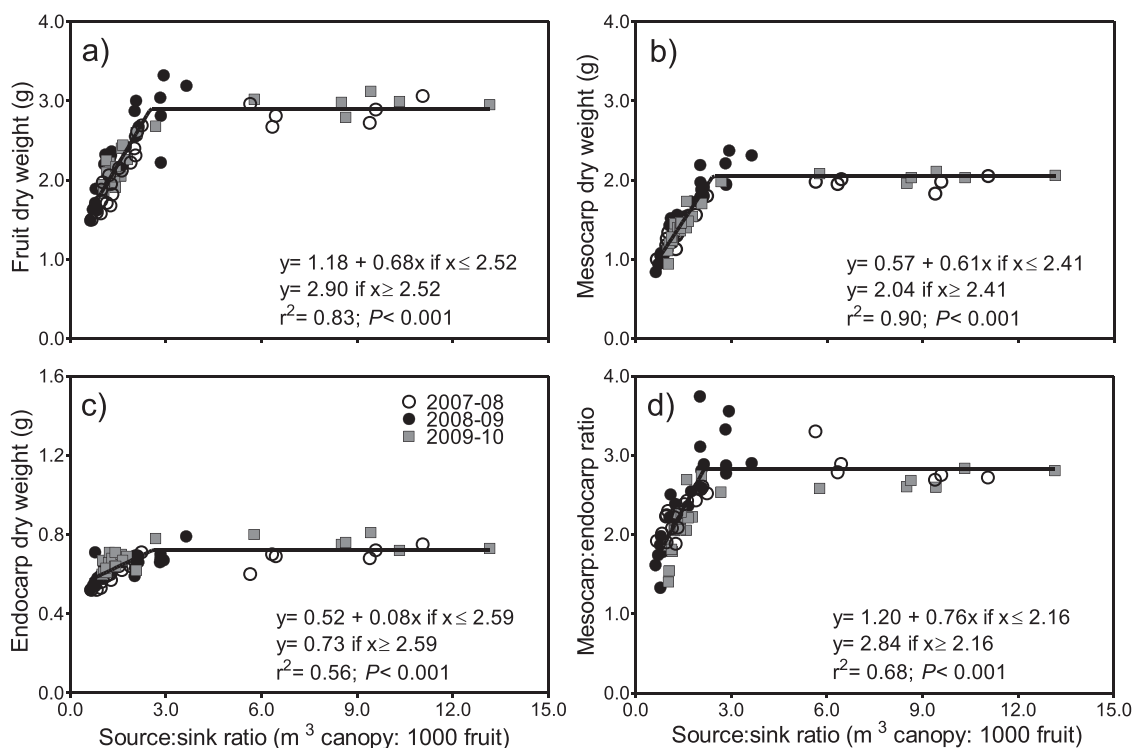


Fig. 1. The dry weight of individual fruit (a), the mesocarp (b) and endocarp (c) tissues, and the mesocarp: endocarp dry weight ratio (d) versus the source: sink ratio expressed as m³ of canopy volume per 1000 fruit. A bilinear function was determined for each dry weight variable using the pooled data from the three growing seasons. The equation for each line segment as well as r² and P values are shown. n = 24 trees per growing season.

Table 5

Estimated production costs (g glucose g dry matter⁻¹) of individual fruit, mesocarp, and endocarp tissues for trees (cv. Arauco) with different crop loads in three growing seasons.

Season	Crop load (# m ⁻³)	Fruit (g gluc g dm ⁻¹)	Mesocarp (g gluc g dm ⁻¹)	Endocarp (g gluc g dm ⁻¹)
2007–08	132	2.07 ± 0.03a	2.23 ± 0.03a	1.60
	539	2.04 ± 0.02ab	2.22 ± 0.03a	1.60
	818	2.00 ± 0.01bc	2.18 ± 0.01a	1.60
	1061	1.99 ± 0.03bc	2.18 ± 0.04a	1.60
2008–09	480	2.04 ± 0.05a	2.19 ± 0.07a	1.60
	483	2.06 ± 0.03a	2.22 ± 0.04a	1.60
	759	2.02 ± 0.02ab	2.20 ± 0.03a	1.60
	1338	1.96 ± 0.03b	2.17 ± 0.06a	1.60
2009–10	114	2.09 ± 0.001a	2.27 ± 0.003a	1.60
	571	2.04 ± 0.005ab	2.23 ± 0.01a	1.60
	803	2.02 ± 0.002ab	2.23 ± 0.02a	1.60
	825	2.02 ± 0.01bc	2.24 ± 0.02a	1.60

Fruit and mesocarp values with different letters indicate significant differences between crop loads in the same season using the Fisher LSD post-test ($P < .05$). n = 6 ± standard error. A single value was assumed for the endocarp.

3.3. Oil relationships

Oil weight per fruit showed a strong linear relationship with fruit dry weight in the two seasons for which data was available (Fig. 3a). In contrast, fruit oil concentration (%) appeared to increase only up to a plateau of 41.7% at a breakpoint of about 2.5 g of fruit dry weight (Fig. 3b). The initial increase in fruit oil concentration with fruit weight was likely related to an increasing contribution of the mesocarp relative to the endocarp in determining whole fruit oil concentration as fruit weight increased. In this regard, fruit oil concentration (%) increased with mesocarp: endocarp dry weight ratio until the ratio reached a plateau of about 2.7 in 2007–08 (Fig. 4a), and a similar tendency was

apparent in 2008–09 (Fig. 4b).

Similar to fruit dry weight (Fig. 1a), oil weight per fruit increased linearly with increasing source:sink ratio (m³ per 1000 fruit) until reaching a plateau (Fig. 5a). Fruit oil concentration had a somewhat weaker relationship with source: sink ratio due to variability in the second season data (Fig. 5b).

3.4. Comparison between studies

The source: sink ratio at which maximum fruit weight was obtained was quantitatively compared between our study and those of two previous publications (Proietti et al., 2006; Trentacoste et al., 2010) with other olive cultivars (Table 6). As would be expected, the leaf area needed to maximize fruit weight was much greater in the large-fruited cv. Arauco than in the two smaller cultivars. More direct comparisons on a weight or GE basis showed that the source: sink ratios obtained for the cv. Arauco were similar to those of cv. Frantoio (Proietti et al., 2006), but lower than those of cv. Arbequina (Trentacoste et al., 2010).

When comparing the source: sink values of olive with those of apple and sunflower, it can be seen that up to 200 m² per 1000 fruit were needed to maximize the fruit weight of a large apple cultivar (Palmer, 1992), while only about 0.45 m² were needed for sunflower achenes (Ruiz and Maddonni, 2006). In contrast, the values for olive cultivars were intermediate (2.6–4.9). On a GE basis, the leaf area per kg of glucose was somewhat less in olive (1.1–1.9) than in apple (2.9) and sunflower (3.3).

4. Discussion

The cv. Arauco is a traditional, large-fruited cultivar in Argentina of significant economic and cultural importance (Searles et al., 2012). A recent study of the seasonal dynamics of fruit and shoot growth and alternating production behavior in this cultivar indicated that fruit growth was source-limited by crop load in the first 60 days after full bloom and that fruit thinning by about 50% of initial crop load the first

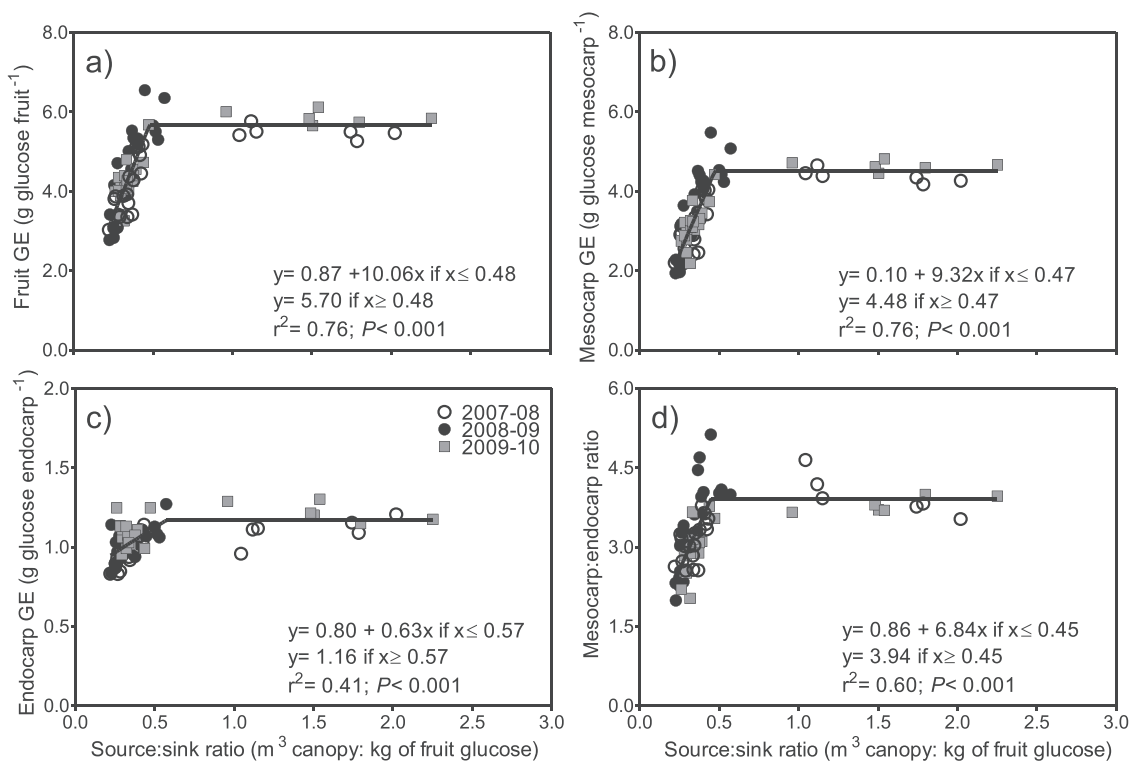


Fig. 2. Glucose equivalents (GE) of individual fruit (a), the mesocarp (b) and endocarp (c) tissues, and the mesocarp: endocarp GE ratio (d) versus the source: sink ratio expressed as m³ of canopy volume per kg of fruit glucose. A bilinear function was determined for each variable using the pooled data from the three growing seasons. The equation for each line segment as well as r² and P values are shown. n = 24 trees per growing season.

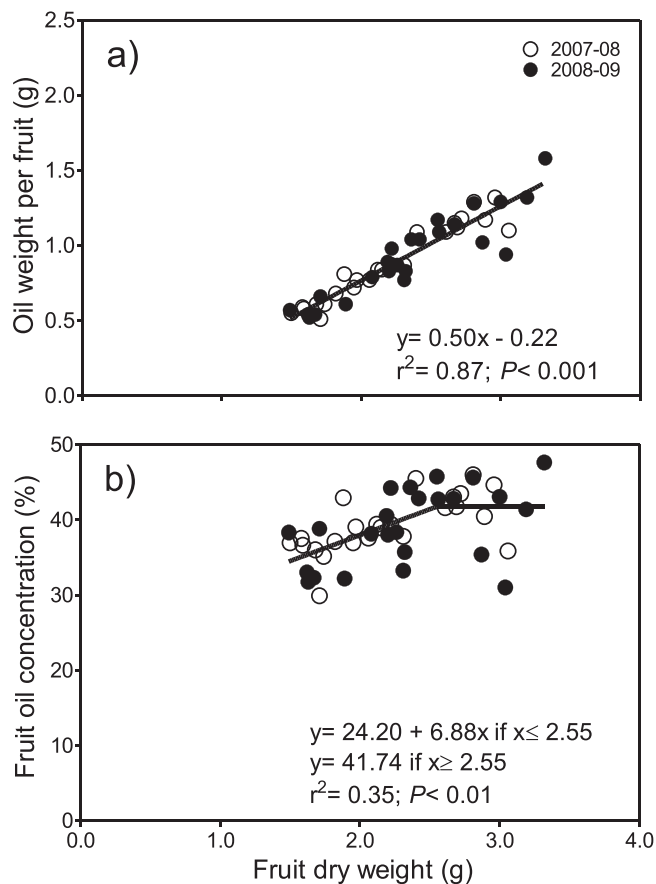


Fig. 3. Oil weight per fruit (a) and fruit oil concentration (b) versus fruit dry weight for two growing seasons. The equations for each line as well as r² and P values are shown. n = 24 trees per growing season.

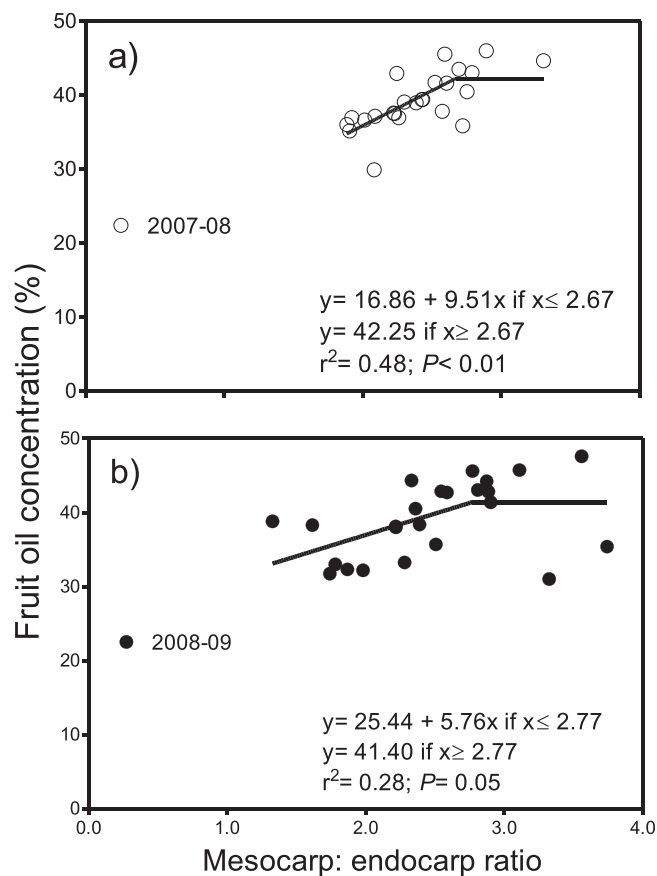


Fig. 4. Fruit oil concentration versus the mesocarp: endocarp dry weight ratio in the first (a) and second (b) growing seasons. The equation for each line segment as well as r² and P values are shown. n = 24 trees per growing season.

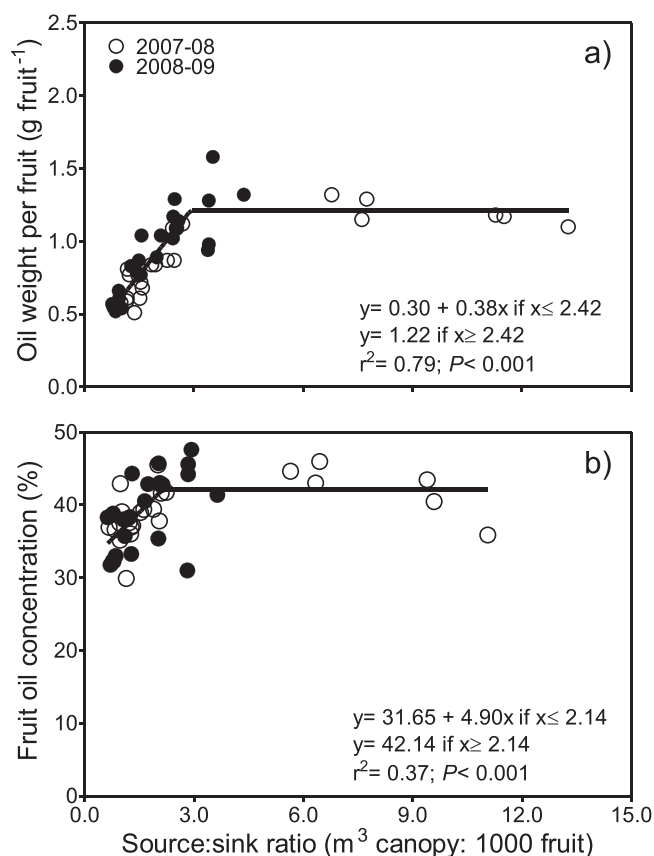


Fig. 5. Oil weight per fruit (a) and fruit oil concentration (b) versus source: sink ratio expressed as m³ of canopy volume per 1000 fruit for two growing seasons. The equation for each line segment as well as r² and P values are shown. n = 24 trees per growing season.

season reduced alternate bearing over subsequent seasons (Fernández et al., 2015). In the present study, we examined how crop load affected fruit and tissue weight at harvest and obtained bi-linear relationships of source: sink ratio versus various fruit and oil parameters. Secondly, we quantitatively compared these source: sink relationships from our study with those from other published studies.

4.1. Fruit weight, oil concentration, and tissue responses to crop load

Fruit fresh and dry weight were significantly decreased at harvest by crop load in each of the three growing seasons with the mesocarp weight (–30 to –40%) being much more affected than the endocarp weight (–13 to –19%) (Table 2). The endocarp has previously been shown to decrease slightly due to crop load under well-watered conditions in the cv. Leccino in Italy, but not under moderate deficit irrigation (Lodolini et al., 2011). For the cv. Barnea in Israel, the endocarp

weight remained fairly constant over a range of almost no fruit per tree up to 50,000 fruit per tree (Dag et al., 2009). It may be that the endocarp size of large-fruited cultivars like ‘Arauco’ has a potentially more plastic response to crop load than smaller cultivars. Nevertheless, fruit weight decreased with increasing crop load in all of these cases because of substantially reduced mesocarp growth. The lesser sensitivity of the endocarp than the mesocarp to crop load could be related to its greater sink activity, which may arise from evolutionary pressures associated with its role in seed protection and dispersal (Alcántara and Rey, 2003).

In addition to fruit weight, crop load also affected the oil weight per fruit (Table 4). The decrease in oil weight per fruit (–50%) was even greater than the reduction in fruit weight (–35 to –40%) over the range of crop loads examined in the first two growing seasons. This occurred because although fruit weight and oil weight per fruit had a strong linear relationship (Fig. 3a), fruit oil concentration (%) on a dry weight basis was also reduced by intermediate to high crop loads (Fig. 3b). Although oil concentration in the mesocarp may not be affected by crop load in some olive cultivars and locations (Lavee and Wodner, 2004; Proietti et al., 2006; Trentacoste et al., 2010), oil concentration of the whole fruit may still show a response to crop load. This may be related to delayed or reduced oil accumulation due to sink competition from the endocarp and/or a “dilution effect” from the low oil concentration in the endocarp. In our study, fruit with a low mesocarp: endocarp ratio, such as occurs with high crop load, had a lower fruit oil concentration than fruit with high mesocarp: endocarp ratios (Fig. 4). Barone et al. (1994) and Proietti et al. (2006) also found that whole fruit oil concentration was reduced by the response of the mesocarp: endocarp ratio to crop load. More recently, Rosati et al. (2015) reported there was no change in mesocarp oil concentration under nitrogen and potassium fertilization, but whole fruit oil concentration increased as a consequence of the increase in the mesocarp: endocarp ratio with fertilization.

The maximum fruit oil concentration (42%; Fig. 5b) in our study was slightly lower than the maximum concentrations (46–48%) reported previously for cv. Arauco in our immediate growing region (Rondanini et al., 2014). This occurred because the trees in the orchard were harvested principally for preparing commercial green table olives. Thus, the fruit had a fairly low maturity index (MI) that varied from 1.09 and 2.12, depending on the crop load and growing season (Table 4). Nevertheless, it is quite unlikely that the lower fruit oil concentration in the high crop load trees would have reached values similar to low crop load trees if harvested later because the concentration differences appeared to be largely related to the mesocarp: endocarp ratio and not to differences in oil synthesis in the mesocarp *per se*. Additionally, fruit mature very slowly under high crop loads, and harvesting trees with higher crop loads at a later date to obtain the same maturity index as low crop load trees may not have been feasible before considerable risk of frost.

Table 6
A comparison of source: sink ratios at maximum fruit weight in some olive cultivars, apple, and sunflower.

Species and cultivar	Study	Max. fresh weight (g)	Max. dry weight (g)	LA (m ²): 1000 fruit	LA (m ²): FW (kg)	LA (m ²): DW (kg)	LA (m ²): GE (kg)
Olive cv. Frantoio	Proietti et al. (2006)	2.6	1.1	2.6	1.0	2.3	1.1
Olive cv. Arbequina	Trentacoste et al. (2010)	2.5	1.1	4.6	1.8	4.1	1.9
Olive cv. Arauco	This study	7.7	2.9	6.9	0.9	2.4	1.3
Apple cv. Crispin	Palmer (1992)	390	59	200	0.5	3.4	2.9
Sunflower hybrids (DK 3900, DK4030, Paraiso 20, Paraiso 30)	Ruiz & Maddonni (2006)	NA	0.06	0.45	NA	7.5	3.3

LA = leaf area; FW = fresh weight; DW = dry weight; GE = glucose equivalents; NA = not available.

4.2. Source: sink relationships for fruit and oil parameters

Fruit and tissue weights as well as oil weight per fruit were fitted to bilinear relationships versus source: sink ratios with source: sink expressed as m^3 of canopy volume per 1000 fruit (Figs. 1; 5a). In all cases, weight increased linearly until reaching a source: sink ratio of about 2.5 m^3 per 1000 fruit. This indicates that individual fruit growth and oil accumulation were limited by photoassimilate availability when crop load was medium to high (i.e., $> 400 \text{ fruit m}^{-3}$). Crop loads of $500\text{--}700 \text{ fruit m}^{-3}$ have been considered to provide both good-sized fruit and high annual yields for table olive production in the cv. Arauco (Fernández et al., 2015). Similar to our results, Trentacoste et al. (2010) also found medium to high crop loads to limit fruit growth and oil accumulation in cv. Arbequina on a per fruit basis. Given the frequency of alternate bearing in olive, such results provide needed information for crop managers interested in fruit thinning using chemical agents to obtain commercially viable fruit size for table olives.

Expressing source: sink relationships using GE provided additional insights into the responses of the mesocarp and the endocarp to source: sink (Fig. 2). While the slope of the source-limited line segment was 7.6 times lower in the endocarp than the mesocarp on a per fruit basis, it was 14.8 times lower when a GE basis was used. This further accentuates the lower sensitivity of the endocarp than the mesocarp to source: sink ratio, and suggests that in addition to the role of relative sink activity early in fruit growth, the high production cost of oil synthesis in the mesocarp may contribute to the difference in sensitivity of the two tissues to source: sink ratio. In a similar manner, Villalobos et al. (2006) reported that radiation use efficiency of above-ground biomass production was much lower in trees with fruit than in juvenile trees with no fruit, and that much of this difference was related to the greater production costs of fruit due to their high oil concentration compared to the lower costs of leaves or wood. We are not aware of other studies that have used a GE approach at the tissue level in olive fruit.

4.3. Comparison between studies

When assessing the various means of expressing of source: sink ratio, direct comparisons between olive cultivars were difficult on a leaf area per 1000 fruit basis because of the large differences in fruit weight between cultivars (Table 6). The cv. Arauco had a maximum fruit weight that was three times greater than that of cvs. Frantoio or Arbequina, and leaf area per 1000 fruit was also two to three times greater in cv. Arauco. A more direct comparison between cultivars could be obtained when sink was expressed on a weight or GE basis, and there was no apparent relationship between source: sink ratios on a per fruit basis and the other measures of sink. Differences between the three olive cultivars tended to decrease from a fresh weight (FW) to a dry weight (DW) basis and finally to a GE basis. For example, the relative difference (%) in source: sink ratio at maximum fruit weight between cv. Arbequina and cv. Arauco decreased from 100% to 71%, and then to 46%, on a FW, DW, and GE basis; respectively. This suggests that expressing source: sink on a GE basis in olive studies may be recommended because differences in fruit oil and water concentrations (%) are accounted for.

The comparison between studies of the source: sink values at maximum fruit weight also provides some potential insight. In the fairly small-fruited cultivars, the cv. Frantoio (Proietti et al., 2006) reached maximum fruit weight at a much lower source: sink ratio on a weight or GE basis than that observed in cv. Arbequina (Trentacoste et al., 2010). The lower source: sink ratio may have occurred in cv. Frantoio because fruit weight at different leaf: fruit ratios was primarily assessed on girdled branches rather than at the whole tree level, which meant that photoassimilate availability was high due to lack of export from the branch (Proietti et al., 2006). Similar to Trentacoste et al. (2010), our study with cv. 'Arauco' assessed source: sink relationships at the whole tree level. Interestingly, the source: sink value at maximum fruit weight

in cv. Arauco, a large-fruited cultivar, was much less than that of cv. Arbequina trees on a weight or GE basis and similar to that of girdled cv. Frantoio branches. It has previously been suggested that large-fruited cultivars have a greater potential to respond to differences in source: sink ratio due to their larger ovaries being stronger sinks (Rosati et al., 2010).

Lastly, an initial comparison between olive and other crop species was undertaken. The comparison of different crops or organs that accumulate different cost compounds (e.g., potato starch versus peanut oil) is clearly not direct unless production costs are considered (Lakso and Denning, 1996). Olive fruit have high fractions of expensive lipids in the mesocarp and fairly expensive lignin in the endocarp with an approximate production cost of $2.0\text{--}2.1 \text{ g glucose g dry matter}^{-1}$ (Table 5). Sunflower achenes also have high production costs (2.22) due to the high lipid content (Andrade, 1995), while apples have very low production costs (1.16) associated with their high water and sugar contents (Walton et al., 1999). On a GE basis, our calculations indicated that the source: sink ratio at maximum fruit weight tended to be lower in olive cultivars than in apple or sunflower (Table 6). When comparing evergreen trees (olive) with deciduous ones (apple), it has long been suggested that leaf life span may improve carbon balance in evergreen species (Chabot and Hicks, 1982). In other words, although instantaneous rates of leaf or canopy conductance and CO_2 assimilation are often greater in broadleaved deciduous species such as apple or peach than in sclerophyllous-leaved olive (Larsen et al., 1989; Marchi et al., 2007; Villalobos et al., 2013), olive trees have a fairly constant leaf area density providing photoassimilates daily throughout the year without the need to construct a considerable number of new leaves each spring. A similar phenomenon may occur in sunflower due to its annual life form and seasonal leaf area development. For this reason, the duration of leaf area index is likely to be a better measure of source in sunflower than merely using leaf area at a particular phenological stage (Ruiz and Maddonni, 2006).

5. Conclusion

Our results demonstrate that the response of fruit weight to crop load, and thus to source: sink ratio, depends to a large degree on the differential response of the fleshy mesocarp and the stony endocarp tissues. Although a great deal of progress has been made in the last decade, further research concerning how and when the mesocarp and endocarp respond to crop load is needed to aid crop management in obtaining sufficient fruit size and quality for table olive cultivars. Lastly, the bilinear relationships of source: sink ratio versus fruit weight obtained in this study and the analysis of tissue level energy costs as glucose equivalents could contribute to crop modelling efforts. The use of glucose equivalents may also serve to better assess differences between species.

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References

- Alcántara, J., Rey, P., 2003. Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*. *J. Evol. Biol.* 16, 1168–1176.

- Andrade, F.H., 1995. Analysis of growth and yield of maize, sunflower and soybean grown at Balcarce, Argentina. *Field Crops Res.* 41, 1–12.
- Barabé, D., Jean, R.V., 1995. On the allometric growth of tissues in fruits. *Bull. Math. Biol.* 57, 487–498.
- Barone, E., Gullo, G., Zappia, R., Inglese, P., 1994. Effect of crop load on fruit ripening and olive oil (*Olea europaea* L.) quality. *J. Hortic. Sci.* 69, 67–74.
- Beers, E.H., Hull, L.A., Grimm, J.W., 1987. Relationships between leaf: fruit ratio and varying levels of European red mite stress on fruit size and return bloom of apple. *J. Am. Soc. Hortic. Sci.* 112, 608–612.
- Beyá-Marshall, V., Fichet, T., 2017. Crop load regulates the next season's crop potential and fruit components in Frantoio olive trees (*Olea europaea* L.). *Sci. Hortic.* 215, 149–156.
- Bodoira, R., Torres, M., Pierantozzi, P., Taticchi, A., Servili, M., Maestri, D., 2015. Oil biogenesis and antioxidant compounds from "Arauco" olive (*Olea europaea* L.) cultivar during fruit development and ripening. *Eur. J. Lipid Sci. Technol.* 117, 377–388.
- Chabot, B.F., Hicks, D.J., 1982. The ecology of leaf life spans. *Annu. Rev. Ecol. Syst.* 13, 229–259.
- Cittadini, E.D., de Ridder, N., Peri, P.L., van Keulen, H., 2008. Relationship between fruit weight and the fruit-to-leaf area ratio, at the spur and whole-tree level, for three sweet cherry varieties. *Acta Hortic.* 795, 669–672.
- Conde, C., Delrot, S., Gerós, H., 2008. Physiological, biochemical and molecular changes occurring during olive development and ripening. *J. Plant Physiol.* 165, 1545–1562.
- Correa-Tedesco, G., Rousseau, M.C., Searles, P.S., 2010. Plant growth and yield responses in olive (*Olea europaea*) to different irrigation levels in an arid region of Argentina. *Agric. Water Manage.* 97, 1829–1837.
- Dag, A., Bustan, A., Avni, A., Lavee, S., Rivov, J., 2009. Fruit thinning using NAA shows potential for reducing biennial bearing of "Barnea" and "Picual" oil olive trees. *Crop Pasture Sci.* 60, 1124–1130.
- Fernández, F.J., Ladux, J.L., Searles, P.S., 2015. Dynamics of shoot and fruit growth following fruit thinning in olive trees: same season and subsequent season responses. *Sci. Hortic.* 192, 320–330.
- Fernández, F.J., Ladux, J.L., Hammami, S.B.M., Rapoport, H.F., Searles, P.S., 2014. Fruit and tissue responses of "Arauco" olive fruits to crop load in arid Argentina. *Acta Hortic.* 1057, 89–94.
- Frías, L., García-Ortiz, A., Hermoso, M., Jiménez, A., Llaveró, M.P., Morales, J., Ruano, M.T., Uceda, M., 1991. *Analistas de Laboratorio de Almazara. Serie apuntes no 6/1991.* Consejería de Agricultura y Pesca. Junta de Andalucía, Sevilla, España.
- García, J.M., Yousfi, K., 2005. Non-destructive and objective methods for the evaluation of the maturation level of olive fruit. *Eur. Food Res. Technol.* 221, 538–541.
- García-Inza, G.P., Castro, D.N., Hall, A.J., Rousseau, M.C., 2016. Opposite oleic acid responses to temperature in oils from the seed and mesocarp of the olive fruit. *Eur. J. Agron.* 76, 138–147.
- Ghanbari, R., Anwar, F., Alkharfy, K.M., Gilani, A.-H., Saari, N., 2012. Valuable nutrients and functional bioactives in different parts of olive (*Olea europaea* L.)—a review. *Int. J. Mol. Sci.* 13, 3291–3340.
- Grossman, Y.L., DeJong, T.M., 1994. PEACH: a simulation model of reproductive and vegetative growth in peach trees. *Tree Physiol.* 14, 329–345.
- Grossman, Y.L., DeJong, T.M., 1995. Maximum fruit growth potential and patterns of resource dynamics during peach growth. *Ann. Bot.* 75, 553–560.
- Gucci, R., Lodolini, E., Rapoport, H.F., 2007. Productivity of olive trees with different water status and crop load. *J. Hortic. Sci. Biotechnol.* 82, 648–656.
- Gucci, R., Lodolini, E.M., Rapoport, H.F., 2009. Water deficit-induced changes in mesocarp cellular processes and the relationship between mesocarp and endocarp during olive fruit development. *Tree Physiol.* 29, 1575–1585.
- Haller, M.H., Magness, J.R., 1933. Relation of Leaf Area and Position to Quality of Fruit and to Bud Differentiation in Apples. United States Department of Agriculture Technical Bulletin No. 338, Washington, D.C., pp. 1–36.
- Hammami, S.B.M., Manrique, T., Rapoport, H., 2011. Cultivar-based fruit size in olive depends on different tissue and cellular processes throughout growth. *Sci. Hortic.* 130, 445–451.
- Hartmann, H.T., 1949. Growth of the olive fruit. *Proc. Am. Soc. Hortic. Sci.* 54, 86–94.
- Heredia-Moreno, A., Guillén-Bejarano, R., Fernández-Bolaños, J., Rivas-Moreno, M., 1987. Olive stones as a source of fermentable sugars. *Biomass* 14, 143–148.
- International Olive Oil Council, 2000. *World Catalogue of Olive Varieties.* Madrid, Spain. IOOC, pp. 1–360.
- Lakso, A.N., Denning, S.S., 1996. Seasonal bioenergetics construction costs of apple fruits, leaves and shoots. *Acta Hortic.* 416, 163–168.
- Larsen, F.E., Higgins, S.S., Al Wir, A., 1989. Diurnal water relations of apple, apricot, grape, olive and peach in an arid environment (Jordan). *Sci. Hortic.* 39, 211–222.
- Lavee, S., 2007. Biennial bearing in olive (*Olea europaea*). *Ann. Ser. Hist. Nat.* 17, 101–112.
- Lavee, S., Wodner, M., 2004. The effect of yield, harvest time and fruit size on the oil content in fruits of irrigated olive trees (*Olea europaea*), cvs. Barnea and Manzanillo. *Sci. Hortic.* 99, 267–277.
- Lodolini, E.M., Gucci, R., Rapoport, H.F., 2011. Interaction of crop load and water status on growth of olive fruit tissues and mesocarp cells. *Acta Hortic.* 924, 89–94.
- Loomis, R.S., Connor, D.J., 1992. *Crop Ecology: Productivity and Management in Agricultural Systems.* Cambridge University Press, New York, pp. 1–538.
- Marchi, S., Guidotti, D., Sebastiani, L., Tognetti, R., 2007. Changes in assimilation capacity during leaf development in broad-leaved *Prunus persica* and sclerophyllous *Olea europaea*. *J. Hortic. Sci. Biotechnol.* 82, 69–78.
- Monselise, S., Goldschmidt, E., 1982. Alternate bearing in fruit trees. *Hortic. Rev.* 4, 128–173.
- Morales, A., Leffelaar, P.A., Testi, L., Orgaz, F., Villalobos, F.J., 2016. A dynamic model of potential growth of olive (*Olea europaea* L.) orchards. *Eur. J. Agron.* 74, 93–102.
- Munier-Jolain, N.G., Salon, C., 2005. Are the carbon costs of seed production related to the quantitative and qualitative performance? An appraisal for legumes and other crops. *Plant Cell Environ.* 28, 1388–1395.
- Palmer, J.W., 1992. Effects of varying crop load on photosynthesis, dry matter production and partitioning of crispin/M.27 apple trees. *Tree Physiol.* 11, 19–33.
- Pavel, E.W., Dejong, T.M., 1993. Source- and sink-limited growth periods of developing peach fruits indicated by relative growth rate analysis. *J. Am. Soc. Hortic. Sci.* 118, 820–824.
- Penning de Vries, F.W., Brunsting, A.H., van Laar, H.H., 1974. Products, requirements and efficiency of biosynthesis: a quantitative approach. *J. Theor. Biol.* 45, 339–377.
- Proietti, P., Nasini, L., Famiani, F., 2006. Effect of different leaf-to-fruit ratios on photosynthesis and fruit growth in olive (*Olea europaea* L.). *Photosynthetica* 44, 275–285.
- Rangel, B., Platt, K.A., Thomson, W.W., 1997. Ultrastructural aspects of the cytoplasmic origin and accumulation of oil in olive fruit (*Olea europaea*). *Physiol. Plant.* 101, 109–114.
- Rapoport, H.F., 2008. OLEACEAE: *Olea europaea* (olive). In: Janick, J., Paull, R.E. (Eds.), *Encyclopedia of Fruits and Nuts.* CAB International, Cambridge, pp. 565–574.
- Rapoport, H.F., Costagli, G., Gucci, R., 2004. The effect of water deficit during early fruit development on olive fruit morphogenesis. *J. Am. Soc. Hortic. Sci.* 129, 121–127.
- Rodríguez, G., Lama, A., Rodríguez, R., Jiménez, A., Guillén, R., Fernández-Bolaños, J., 2008. Olive stone an attractive source of bioactive and valuable compounds. *Bioresour. Technol.* 99, 5261–5269.
- Rondanini, D.P., Castro, D.N., Searles, P.S., Rousseau, M.C., 2014. Contrasting patterns of fatty acid composition and oil accumulation during fruit growth in several olive varieties and locations in a non-Mediterranean region. *Eur. J. Agron.* 237–246.
- Rosati, A., Caporali, S., Paoletti, A., 2015. Fertilization with N and K increases oil and water content in olive (*Olea europaea* L.) fruit via increased proportion of pulp. *Sci. Hortic.* 192, 381–386.
- Rosati, A., Zipanic, M., Caporali, S., Paoletti, A., 2010. Fruit set is inversely related to flower and fruit weight in olive (*Olea europaea* L.). *Sci. Hortic.* 26, 200–204.
- Ruiz, R.D., Maddonni, A.G., 2006. Sunflower seed weight and oil concentration under different post-flowering source-sink ratios. *Crop Sci.* 46, 671–680.
- Samach, A., Smith, H.M., 2013. Constraints to obtaining consistent annual yields in perennials. II: environment and fruit load affect induction of flowering. *Plant Sci.* 207, 168–176.
- Searles, P.S., Agüero Alcaras, M., Rousseau, M.C., 2011. El consumo del agua por el cultivo de olivo (*Olea europaea* L.) en el noroeste de Argentina: una comparación con la Cuenca Mediterránea. *Ecol. Austral* 21, 15–28.
- Searles, P., Rousseau, M.C., Ladux, J., Trentacoste, E., Arjona, C., Cólica, J., Matias, C., Bueno, L., Vita Serman, F., 2012. Following olive footprints in Argentina. In: El-Kholy, M., Avanzato, D., Caballero, J., Chartzoulakis, K., Vita Serman, F., Perri, E. (Eds.), *Following Olive Footprints (Olea europaea L.)—Cultivation and Culture, Folk and History, Traditions and Uses.* International Society of Horticultural Science Scripta Series, Leuven, Belgium, pp. 13–23.
- Searles, P.S., Saravia, D.A., Rousseau, M.C., 2009. Root length density and soil water distribution in drip-irrigated olive orchards in Argentina under arid conditions. *Crop Pasture Sci.* 60, 280–288.
- Trentacoste, E.R., Puertas, C.M., Sadras, V.O., 2010. Effect of fruit load on oil yield components and dynamics of fruit growth and oil accumulation in olive (*Olea europaea* L.). *Eur. J. Agron.* 33, 132–138.
- Uceda, M., Hermoso, M., Aguilera, M.P., 2010. Olive oil quality. In: Barranco, D., Fernández-Escobar, R., Rallo, L. (Eds.), *Olive Growing.* Mundi-Prensa – Junta de Andalucía – Australian Olive Association. Rural Industries Research and Development Corporation; RIRDC, pp. 621–645.
- Villalobos, F.J., Testi, L., Orgaz, F., García-Tejera, O., López-Bernal, A., González-Dugo, M.V., Ballester-Lurbe, C., Castel, J.R., Alarcón-Cabañero, J.J., Nicolás-Nicolás, E., Girona, J., Marsal, J., Fereres, E., 2013. Modelling canopy conductance and transpiration of fruit trees in Mediterranean areas: a simplified approach. *Agric. For. Meteorol.* 171–172, 93–103.
- Villalobos, F.J., Testi, L., Hidalgo, J., Pastor, M., Orgaz, F., 2006. Modelling potential growth and yield of olive (*Olea europaea* L.) canopies. *Eur. J. Agron.* 24, 296–303.
- Walton, E.F., Wunsche, J.N., Palmer, J.W., 1999. Estimation of the bioenergetic costs of fruit and other organ synthesis in apple. *Physiol. Plant.* 106, 129–134.
- Whiting, M.D., Lang, G.A., 2004. 'Bing'sweet cherry on the dwarfing rootstock 'Gisela 5': thinning affects fruit quality and vegetative growth but not net CO₂ exchange. *J. Am. Soc. Hortic. Sci.* 129, 407–415.