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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 m^2 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 cm^2 $fruit^{-1}$) 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. Secondarily, 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 × 8 m between rows (208 trees ha^{-1}), east-west row orientation, and an initial canopy volume of 13 ± 3 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 °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