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Olive fruit growth, tissue development and composition as affected by irradiance received in different hedgerow positions and orientations

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ABSTRACT

Incident radiation strongly influences fruit development, but little is known regarding the specific responses to the radiation differences found at different canopy heights and orientations in the new intensive hedgerow orchards. We tested the effect of position-determined solar microenvironment on olive fruit size, composition, and cellular development among positions at successive heights along both faces of N–S and E–W oriented olive hedgerows (cv. Arbequina). Total incident irradiance over the fruit growth period at each canopy position was modeled, and the relationships of all fruit parameters to irradiance and amongst each other were tested. Fruit and mesocarp weight and oil increased from canopy base to top and were linearly related to irradiance, while water content showed the opposite pattern, suggesting that priorities for distribution among different sinks are strongly influenced by irradiance level. Similar patterns of fruit size and composition in relation to irradiance were also observed among hedgerow orientations. Endocarp weight and composition varied little among irradiance levels, reflecting the conservative nature of this tissue as an active sink. Greater fruit size, mesocarp weight, and oil in positions of higher irradiance, even when fruit number was higher, indicating that those yield components were primarily affected by source supply and not limited by sink competition. Fruit exposed to light developed larger mesocarp cells than shaded fruit but cell number was not affected, and mesocarp oil content was highly associated with mesocarp cell size.

1. Introduction

Olive fruit size and oil content depend on assimilate supply and competition among sinks for its use, in which irradiance plays a key role. First, radiation intercepted by the canopy leads to increased assimilate synthesis by the leaves (Larbi et al., 2015) and second, irradiance influences fruit number by affecting flower induction and flowering (Tombesi and Cartechini 1986; Fabbri and Benelli 2000). Previous studies indicate significant variation of olive fruit number, size and oil content in relation with the heterogeneous distribution of irradiance among canopy positions in both the new hedgerow systems (Gómez-del-Campo et al., 2009; Trentacoste et al., 2015a,b) and traditional orchards (Acebedo et al., 2000), as well as among different radiation levels in experimentally shaded olive trees (Tombesi et al., 1998; Cherbiy-Hoffmann et al., 2012).

A multi-level (fruit, tissue and cellular levels) approach can provide essential knowledge for understanding the complex response of fruit development and composition to different solar microenvironments within the olive canopy. Indeed, in fruit crops such as peach and nectarine (Lopresti et al., 2014), tomato (Liu et al., 2007; Fanwoua et al., 2013), mango (Léchaudel et al., 2007) and grape (Dai et al., 2009; Prudent et al., 2014), a hierarchical approach has been found useful for understanding and modeling the effects of genetic, management and environment conditions on fruit size and composition, incorporating fruit heterogeneity within the canopy as a consequence of plant architecture. The relationships between levels and processes explored and modeled by these authors, though, are limited to fruits crops where fruit size and sugar accumulation are the dominant developmental criteria (Génard et al., 2009) and could differ in an oil-storing fruit such as olive (Martre et al., 2011).

At the tissue level, olive fruit size and composition result from the combined contributions of the endocarp (pit) and mesocarp (pulp), which differ in their morphogenetic patterns and developmental timing (Gucci et al., 2009). Endocarp size increases rapidly from fruit set to approximately 2 months after bloom, following which dry weight accumulation continues in the form of cell sclerification, the metabolically demanding synthesis and deposition of lignin and related substances (Hammami et al., 2013; Rapoport

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et al., 2013). Mesocarp expansive growth also initiates at fruit set, but then continues long after endocarp expansion until shortly before ripening (Hammami et al., 2011). The mesocarp consists of parenchymatous cells in which oil biosynthesis and storage will take place, processes for which there is also high metabolic demand (Connor and Fereres, 2005). Although most of the oil accumulation in the mesocarp occurs later (Rondanini et al., 2014), initial oil biosynthesis is simultaneous with the completion of endocarp sclerification, and competition between the endocarp and mesocarp for assimilates has been suggested (Rapoport et al., 2004; Matteucci et al., 2011). Thus varied absolute and relative contributions of mesocarp and endocarp to fruit size, as well as related differences in fruit composition, are likely to occur in response to temporal and spatial irradiance patterns.

The mesocarp is the largest and economically most important tissue in the olive fruit, and its size will be determined by cell division and cell expansion. Both processes occur throughout fruit expansion, but differ noticeably in the timing of their activity. For a range of olive varieties differing in fruit size, Hammami et al. (2011) found that at 8 weeks after bloom 65% of final mesocarp cell number and 25% final cell size were reached, while the other 35% and 75% increase in cell number and size, respectively, occurred during the remainder of fruit development (8–32 weeks). Beyond the genetic control over cell processes, mesocarp cell number and size are also affected by water status (Rapoport et al., 2004; Gucci et al., 2009) and the availability of assimilates as a consequence of fruit load variations (Prudent et al., 2010; Fanwoua et al., 2012) and irradiance intercepted by the canopy (Jackson and Coombe, 1966; Okello et al., 2015). In addition to cell division and expansion, an integrated view of fruit tissue growth should also include cell differentiation and storage of metabolites (Sinnott, 1960). Nevertheless there is scant quantitative information available about the relationships among fruit cell size, number and composition, although Conde et al. (2008) showed that mesocarp cell oil content is determined throughout fruit development according to the supply of carbohydrate, metabolic transformations, and dilution owing to cell expansion.

In hedgerow orchard systems the irradiance microenvironment differs among canopy positions at different heights and with respect to row spacing and orientation (Connor et al., 2014; Trentacoste et al., 2015c), producing differences in vegetative growth, fruit characteristics and oil productivity (Trentacoste et al., 2015a,b). Fruit size and composition depend on growth capacity and the partitioning of development among tissues and processes in response to the irradiance microenvironment surrounding the fruit. Understanding that response is important for improving olive hedgerow design and subsequent canopy management, while the different positions provide different microenvironments for testing the effect of irradiance on fruit tissue development and elemental composition. In this context the aims of this work were to (1) determine olive mature fruit and tissue (mesocarp and endocarp) size and composition (oil, water and dry weight without water) variability of fruits located at different canopy heights and orientations in olive hedgerow orchards, (2) examine how fruit position in the canopy affects mesocarp cell size and number at fruit harvest and (3) explore the interaction of canopy-position-determined irradiance and fruit number with mesocarp size and composition.

2. Material and methods

2.1. Site and orchard

The study was carried out during 2012 and 2013 as part of an olive hedgerow spacing experiment (Trentacoste et al., 2015b) in an orchard (cv. Arbequina) planted in 2008 near La Puebla de Montalban (39°N), Spain. Briefly, two experimental plots, separated by approximately 100 m, were established, one with rows oriented N–S (north–south) and the other oriented E–W (east–west). Each plot consisted of 3 rows of 48 trees spaced at 2.5 × 1.3 m, in which the central row was studied. The hedgerow structural characteristics averaged over the fruit-growth season are shown in Table 1. Site, environment conditions and hedgerow management are described more fully in Trentacoste et al. (2015b).

Table 1
Canopy structure parameters of N–S and E–W hedgerows in 2012 and 2013.

Parameter	N–S	E–W
Top of hedgerow (m)	2.62 ± 0.30	2.50 ± 0.62
Base of canopy (m)	0.25 ± 0.06	0.23 ± 0.09
Hedgerow width (m)	1.02 ± 0.05	1.10 ± 0.09
Horizontal porosity (%)	18.3 ± 2.35	16.5 ± 1.86

Each value is the mean ± standard error of three observations (trees) in two years (6 repetitions).

2.2. Definition of canopy positions

Three individual olive trees in each experimental plot were chosen randomly among the 42 central trees in the row, after first excluding the trees with extremely different fruit loads. The canopy of each tree was divided into eleven positions based on height and orientation (see Fig. 1). Five heights were designated on both sides of the hedgerow: 0.0–0.4 m (Position 1), 0.4–0.8 m (Position 2), 0.8–1.2 m (Position 3), 1.2–1.6 m (Position 4), 1.6–2.0 m (Position 5) aboveground. An additional position consisted of the canopy top (≥2.0 m aboveground), incorporating both sides of the hedgerow. The same trees were evaluated in both years.

2.3. Irradiance values

The incident irradiance received at each canopy position was calculated using a model developed to evaluate radiation in porous olive hedgerow orchards (Connor et al., 2009) and validated in N–S and E–W oriented olive hedgerows by those authors. The model uses specific site and hedgerow parameters: latitude, day of year, hedge height, canopy width at base, row orientation, horizontal porosity and row spacing (Table 1). It operates daily at short (10–15 min) intervals to calculate solar position, beam irradiance, diffuse sky and reflected components, which it then uses to determine the irradiance. Correct model performance at the experimental site was confirmed by comparing predicted profiles of incident irradiance received at canopy positions with measurements made with a 1 m linear ceptometer (LI-191SA, LI-COR Inc., Lincoln, NE, USA) hourly during two clear-sky days (6 April and 20 June, 2013). Those measurements were taken at 4 heights (0.5, 1.2, 1.5 and 1.75 m height) on both sides of the hedgerows. To determine irradiance received in the fruit growth study, the model was used to calculate daily incident irradiance at each canopy position (Fig. 2A–C), then total irradiance from flowering to fruit harvest was obtained by summing all daily values for that period (Fig. 2D).

2.4. Fruit number, size, and tissue composition at harvest

All fruits were harvested on 28 October, 2012, and 2 November, 2013, a standard time in this region for 'Arbequina', which is highly sensitive to winter frosts. Harvest index, determined by a 0–7 scale using skin and pulp color, was 1.3 and 0.6 in 2012 and 2013, respectively. Total harvest fresh weight was obtained for each position. For each tree three subsamples of 20 fruits per position were weighed and then dried in a forced-air oven at 105 °C for 42 h to determine fruit fresh weight and then fruit water content. The fruit oil content