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Olive floral development in different hedgerow positions and orientations as affected by irradiance

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ABSTRACT

Irradiance received within the olive hedgerow canopy varies with respect to row orientation, spacing and hedge dimensions. These orchard management criteria offer the opportunity for improving productivity based on understanding the responses of yield-determining processes to irradiance. How irradiance influences inflorescence and flower development, the initial steps in fruit formation, are fundamental components of these processes. In this study we evaluated flowering and fruiting parameters in 5 hedgerow positions (defined by hedgerow side and vertical layer above soil) for N–S (North-South) and E–W (East–West) olive hedgerows (cv. Arbequina). The canopy layers and orientations provided a wide gradient of irradiance received and the relationship of estimated mean daily irradiance for annual and for short periods during floral development and initial fruit set was explored. The numbers of inflorescences and fruits per layer increased from the less illuminated base to more illuminated upper canopy layers. Axillary bud number per shoot also increased toward more illuminated positions, while the proportion of floral buds was unresponsive to the irradiance microenvironment at different positions within the hedgerows. Inflorescence length, node and flower number per inflorescence, and perfect flower percentage increased with position illumination. Ovary quality, indicated by ovule differentiation, was consistently high, independent of position, but ovary size showed some slight significant increases with illumination, mainly in the endocarp. Flowers/inflorescence, fruits/fruiting inflorescence and inflorescence and fruit number per position correlated positively and significantly with estimated irradiance similarly for annual and short periods (*r* range from 0.49 to 0.86). Despite improved flowering parameters with greater irradiance, no consistent differences among positions were found for percentage of inflorescences bearing fruit and fruit number per inflorescence. Instead, our results indicated that different fruit numbers among canopy positions were primarily due to an irradiance effect on vegetative growth, causing more and longer fruiting shoots and therefore more total flowering sites (nodes) per layer, with only a small contribution by inflorescence structure and flower quality.

1. Introduction

Irradiance plays a key role in perennial fruit crop flower formation via directly or indirectly impacting photosynthesis, carbohydrate availability and resource partitioning, and also by modifying the internal chemical composition of the plant, particularly the balance of endogenous hormones, e.g. in apple (*Malus domestica* L.) (Jackson and Palmer, 1977; Lauri and Térouanne, 1999) and grape (*Vitis vinifera* L.) (Lebon et al., 2008; Petrie and Clingeleffer, 2005). Nevertheless, reported effects of irradiance on floral formation in the olive tree (*Olea europaea* L.) are scarce and seemingly inconsistent, with variable results in relation to the experimental method (artificial shadow and natural gradient) and the irradiance level used. Tombesi and Cartechini (1986), in adult trees, and Gregoriou et al. (2007), in young trees in containers, found that artificial shading up to 40% of daily incident photosynthetically active radiation (PAR) reduced inflorescence formation. Similarly, Acebedo et al. (2000), in a traditional olive orchard (density of 238 trees/ha), demonstrated that flower intensity and flower number

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per inflorescence increased in relation to more illuminated positions on the tree canopy. In contrast, Cherbiy-Hoffmann et al. (2015) observed that the intensity of artificial shadow (from 3 to 70% of daily incident PAR) and three shading periods during fruit set, pit hardening and oil synthesis did not affect the return flowering. Stutte and Martin (1986) did not find a relationship between various artificial irradiance levels and flowering in trees inside to growth chambers, mediated by inconsistent differences in carbohydrate levels between treatments.

Flower formation in the olive tree is complex, extending over two seasons. The interaction among the numerous micro- and macro-environmental conditions during this long period, previous fruiting behavior, genotype, and management practices give rise to considerable variation between seasons, trees in the same orchard and within the same tree (Acebedo et al., 2000; Cuevas et al., 1994). Flower development involves the formation of potential flowering buds in the leaf axils during spring-early autumn shoot growth, floral induction of those buds the following winter, and differentiation of the inflorescence and flower structures, which begins with bud break in late winter (i.e. 8–12 weeks before full bloom, WBFB) and finalizes by bloom (Cuevas et al., 1994; Reale et al., 2006). The period prior to bloom is critical for floral formation and thus fruit yield determination (Rapoport and Gómez-del-Campo, 2008). For example olive tree exposure to water stress from 10 weeks before full bloom to full bloom strongly affected different flowering parameters including inflorescence number, flower number, perfect flower number, and ovule development (Rapoport et al., 2012).

From the perspective of olive production, total flower number per olive tree represents an upper limit for olive orchard potential yield. However satisfactory production requires not only a sufficient number of inflorescences per tree and flowers per inflorescence, but these flowers must have good quality. Based on Williams (1965) characterization of floral structure and processes in apple, the term "floral quality" refers to any morphological or developmental characteristics of the flower that affect its ability to set and form a good quality fruit. Martins et al. (2006) extended this concept to olive and, in addition to the traditionally considered development of perfect (hermaphrodite) flowers in contrast to imperfect (staminate) flowers caused by varying degrees of pistil abortion (Cuevas and Polito, 2004; Reale et al., 2009), included additional parameters such as ovary size, which could influence fruit size, and ovule development, which affects potential fertilization and fruit set. Olive ovule development is often incomplete and an embryo sac is not formed, thus representing a possible limitation to fruit set. While usually only one ovule is fertilized for fruit set to occur, the lack of full differentiation of more than one of the four ovules present in the ovary is considered to reduce fruit-set capacity (Moreno-Alías et al., 2012). Consequently, potential fruit number in a particular canopy position can be represented by the product of the number of inflorescences x number of flowers per inflorescence x proportion of flowers of good quality (i.e. hermaphrodite with three or more developed ovules). Potential fruit size is related to floral attributes including ovary mesocarp and endocarp size, cell size and cell number (Rosati et al., 2012). Furthermore, developmental modifications in olive tree flowering due to total flower number (Cuevas et al., 1994) or water status (Rapoport et al., 2012) may lead to partial compensations among different flowering components, which could likely occur as well in relation to irradiance.

In recent decades, intensive hedgerow olive orchards have been established to facilitate mechanical harvesting which reduces the costs of manual labour and allows more rapid and timely management intervention (Connor et al., 2014). Hedgerow orchards planted at super-high density (more than 1000 trees/ha) are known to produce very high yield in early years after planting. This early yield advantage can, however, be lost with time if the growing canopy is not well illuminated (Trentacoste et al., 2015). Adequate hedgerow design and subsequent canopy management are required to avoid potential yield reduction in the mature olive hedgerows.

Irradiance effects on assimilate availability, oil synthesis and partitioning during fruit development, have recently been characterized in olive hedgerows (Castillo-Ruiz et al., 2015; Trentacoste et al., 2016). Knowledge of how inflorescence and flower development, the crucial first steps for fruit formation, respond to varied irradiance received at different positions on the hedgerow is also essential for improving hedgerow design, management and modeling. In this context the aims of this work were to (i) determine quantity and quality parameters of inflorescence, flower and ovary development at different canopy heights and orientations in olive hedgerow orchards and (ii) explore the relationships between the irradiance received in different periods and canopy positions, determined by simulation, and inflorescence and floral characteristics. We have also included closely related developmental events immediately prior and subsequent to flowering, in particular bud formation and fruit set, respectively.

2. Material and methods

2.1. Site and orchard

The study was carried out during 2013 in an olive hedgerow spacing experiment (Trentacoste et al., 2015) in an orchard (cv. Arbequina) planted in 2008 in La Puebla de Montalbán (39° N), Toledo, Spain. Two experimental plots, separated by approximately 100 m, were established, one with rows oriented N–S (North-South) and the other 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. Both hedgerow orientations had similar dimensions, i.e. canopy height 2.37 m and 2.27 m and canopy width 1.02 m and 1.10 m in N–S and E–W oriented hedgerows, respectively. Site, environment conditions and hedgerow management are fully described in Trentacoste et al. (2015).

2.2. Definition of canopy positions

Six individual olive trees were chosen randomly in each experimental plot (N–S and E–W hedgerows) among the 42 central trees in the central row (three for continuous evaluation of flower and fruit development and three for sampling of inflorescences and fruits). The canopy of each tree was divided into ten positions based on five vertical layers (heights) and two canopy sides or faces (Fig. 1 in Trentacoste et al., 2016). The designated layers for each side of the hedgerow were 0.0–0.4 m (layer 1), 0.4–0.8 m (layer 2), 0.8–1.2 m (layer 3), 1.2–1.6 m (layer 4) and 1.6–2.0 m (layer 5) above the soil surface.

2.3. Inflorescence and fruit formation

In winter, before budburst, three one-year-old shoots were selected at random for each position and tree, on which shoot length measured and bud number (node number x 2) counted. The number of inflorescences per shoot was recorded in the weeks prior to flowering (FB was June 4) and at 30 days after full bloom the number of fruits per shoot and inflorescences bearing at least one fruit (fruiting inflorescences). The measurements of the selected shoots were used to calculate the number of total buds which formed inflorescences on each one-year-old shoot, the percentage of buds forming inflorescences (floral buds), the percentage of inflorescence bearing at least one fruit (fruiting inflorescences), and the mean number of fruits per fruiting inflorescence. At harvest (29 October), total fruits of each layer and side were collected and counted. The shoot data were used along with the number of fruits per position in order to calculate the total inflorescence number per position as follows:

$$\textit{Total inflorescence per position} = \frac{\textit{fruit number per position}}{(\textit{fruit/fruiting inflorescence}) \times (\%\textit{fruiting inflorescence}/100)}$$