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Photosynthetic limitations by water deficit: Effect on fruit and olive oil yield, leaf area and trunk diameter and its potential use to control vegetative growth of super-high density olive orchards

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ABSTRACT

Regulated deficit irrigation (RDI) reduces leaf area, which is advantageous for fruit tree orchards with high plant densities to increase their long-term productive life. However, RDI also decreases fruit yield. To establish an optimum irrigation level to control tree vegetative growth without severely penalizing fruit yield it is necessary to analyze the effect of the limited photosynthesis produced by RDI on the carbon allocation patterns between yield and tree vegetative growth, which are not fully established in olive. Thus, our main objective was to unravel the relationships between limited photosynthesis and tree growth as well as yield to establish an optimum level of deficit irrigation. We conducted the research during four irrigation seasons in a super-high density olive orchard using four irrigation treatments: a full irrigation treatment (control) and three RDI treatments with increasing levels of water reduction scaled to replacing 60%, 45% and 30% of the irrigation needs. The plant water stress produced by RDI reduced photosynthesis, which resulted in a significant decline of leaf area. In contrast, neither single fruit weight nor total fruit yield normalized by leaf area was adversely affected by RDI. We found significant and direct relationships between photosynthesis and leaf area ($r^2 = 0.90$, $p < 0.0001$) as well as between leaf area and yield ($r^2 = 0.55$, $p < 0.05$). Thus, we conclude that while leaf area is determined mainly by photosynthesis, fruit yield is largely determined by leaf area, and thus, photosynthesis and leaf area are the main variables to control tree growth without curtailing the yield. The lowest RDI levels (30% and 45%) lead to greater water savings than 60%, with a similar effect on leaf area and fruit yield, and thus, any of these lowest irrigation strategies is preferred to achieve the best balance between crop water consumption and fruit yield.

1. Introduction

One of the major causes of yield reduction in water-limited environments is stomatal limitation of photosynthesis controlled by water stress (Flexas and Medrano, 2002; Grassi and Magnani, 2005; Flexas et al., 2013). Indeed, the most immediate response of plants to water stress is to limit leaf transpiration by stomatal closure, which allows to avoid harmful hydraulic failure of the plant (Sperry and Tyree, 1988; McDowell et al., 2008). However, this also causes a decline in leaf intercellular CO_2 concentration, thereby limiting photosynthesis (Diaz-Espejo et al., 2007). These limitations can be produced either by low supply (soil water deficit) (Caruso et al., 2013; Rallo and Provenzano, 2013) or by high atmosphere demand (high vapor pressure deficit) (Fernández, 2014), being the effects of the interaction between both variables on photosynthesis not fully assessed (Giorio et al., 1999; Moriana et al., 2002; Perez-Martin et al., 2009). Water stress produced by soil water deficit can be ameliorated with irrigation which stabilizes the economic return and increases crop yield in comparison to rainfed yield crops (Ali and Talukder, 2008).

Uncontrolled tree vigor is a major problem in super-high density (SHD) orchards (Connor et al., 2014), as orchards with densities over 1500 trees ha^{-1} are usually named (Vossen et al., 2004), and in areas where local conditions can induce uncontrolled tree vigor (Correa-Tedesco et al., 2010). An excessive growth of the canopy produces difficult mechanical harvesting (León et al., 2007) and

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more importantly, a reduction of the long-term orchard productive life from mutual shading problems which conduct to an irregular distribution of the incident solar radiation into the canopy (Connor, 2006; Gómez-del-Campo and García, 2012; Connor et al., 2014). In dry areas where water is scarce, a deficit irrigation strategy (DI) is needed (Morison et al., 2008), specially under future climatic predictions (IPCC, 2014). Besides the substantial water saving that can be achieved using deficit irrigation (DI) strategies (Moriana et al., 2003; Caruso et al., 2013; Fernández et al., 2013; Padilla-Díaz et al., 2016), they could help to control excessive vegetative growth. This is the case of regulated deficit irrigation (RDI), one of the most effective DI strategies for SHD orchards (Fernández et al., 2013). RDI can help to reduce the problem of excessive growth because it consists of replacing the crop evapotranspiration (ET_c) in the phases of the growing cycle when the crop is most sensitive to water stress, specially vegetative growth, and reducing irrigation for the rest of the cycle (Chalmers et al., 1981). The irrigation periods coincide in olive partially with the periods of maximum rate of both vegetative growth and fruit growth and ripening, reducing the competition for resources at critical stages (Connor and Fereres, 2005).

Stressed plants frequently display altered morphology which promotes plant survival by changing development including, for example, reduced growth, altered resource allocation between above-grown and below-grown tissues and a shift from vegetative to reproductive growth (Gifford and Evans, 1981; Allahverdiyeva et al., 2015). Actually, fruit competition for carbohydrates can subsequently lead to a reduced vegetative growth of shoots and roots (Génard et al., 2008) because fruit and seed growth dominate the growth of vegetative tissues (Wardlaw, 1990). In agricultural cultivars, the allocation partitioning patterns by which limited carbon is distributed from photosynthesizing leaves to heterotrophic plant organs and tissues have been largely modified through plant breeding and agricultural practices to increase productivity (Gifford and Evans, 1981; Génard et al., 2008). The effects of water deficit on photosynthesis is well described for olive (Angelopoulos et al., 1996; Giorio et al., 1999; Moriana et al., 2002), as it is also on fruit and olive oil yield (Moriana et al., 2003; Tognetti et al., 2006; Gucci et al., 2007; Fernández et al., 2013) and vegetative growth (Iniesta et al., 2009; Gomez-del-Campo, 2010). However, relationships between limited photosynthesis and plant growth patterns are not well established. The use of different irrigation levels to modify the growth patterns of aboveground organs such as leaves, trunks and fruits through the control of photosynthesis limitation may constitute a tool to avoid excessive vegetative biomass production and optimize reproductive growth (Connor et al., 2014) as well as saving a considerable amount of water, but more information is needed to unravel these relationships.

Thus, the main hypothesis we want to assess in this work is that there would be an optimum RDI level that would help to control excessive tree growth without severely penalizing crop production. Specifically, we hypothesize that the photosynthesis reduction caused by a RDI strategy would limit the increase of leaf area and trunk diameter (vegetative organs) to a greater extent than that of fruit weight (reproductive organs). We further hypothesize that for saturating light conditions, the photosynthesis limitation driven by stomatal closure would be mainly determined by soil water deficit but also by the effect of its interaction with high levels of vapor pressure deficit. Thus, the main objective of this work was to evaluate different RDI strategies as tools to control excessive vegetative growth of olive trees mediated by photosynthesis decline without penalizing yield. Our specific objectives were: (i) to assess the photosynthesis limitations produced by the interaction of different levels of soil water deficit and vapor pressure deficit and (ii) to determine the effect of limited photosynthesis on final leaf area, trunk diameter, fruit and virgin olive oil (VOO) yield and the effect of reduced photosynthesis on the increase rates of the former variables.

2. Materials and methods

2.1. Orchard and climate characteristics

The study was conducted from 2010 to 2015. From 2010 to 2012 we used a slightly different strategy in the timing and level of water stress than in the period 2013–2015 (explained in the following section). The data from 2010 and 2013 were not used in this work because the effects of the irrigation treatments of previous years could not be totally disregarded. The study plots were located in a commercial SHD olive orchard near Seville, southwest Spain (37°15′N, −5°48′W). Trees were 4-year-old in 2010. They were 'Arbequina' trees planted at 4 m × 1.5 m (1667 trees ha^{-1}), in rows oriented N-NE to S-SW. The trees, with a single trunk and branches from 0.6 to 0.7 m above ground, were manually pruned in December-January each year. The orchard soil (Arenic Albaqualf, USDA 2010) had a sandy loam top layer and a sandy clay layer downwards. The trees were planted at the top of 0.4 m high ridges. The amount of fertilizer was changed every month to match the crop needs (Troncoso et al., 2001). Further details on the orchard characteristics can be found in Fernández et al. (2013).

Climate in the area is Mediterranean, with mild rainy winters and hot, dry summers. Most of the annual rainfall occurs between late September and May. Average values in the area of potential evapotranspiration (ET_o) and precipitation (P) were 1528 mm and 540 mm, respectively, for the 2002–2014 period. For that period, average maximum and minimum air temperature were 24.9 °C and 10.7 °C, respectively. The hottest months are July and August.

2.2. The RDI strategy

In 2011 and 2012 we followed the RDI strategy described in Fernández et al. (2013), and in 2014 and 2015 we used a slightly different one described in Padilla-Díaz et al. (2016) (Fig. 1). Briefly, we considered three periods along the olive growing cycle on which the crop is highly sensitive to water stress and irrigation supplies must replace or be close to the crop water needs. Period 1 goes from the last stages of floral development to full bloom (DOY 118, 116, 111 and 115 for 2011, 2012, 2014 and 2015, respectively), period 2 occurs at the end of the first phase of fruit development (June) and period 3 refers to a period of ca. 3 weeks prior to ripening, after the midsummer period of high atmospheric demand (from late August to mid-September). Between periods 2 and 3 (late June-late August), the olive tree is highly resistant to drought and irrigation supplies can be reduced (Alegre et al., 2002; Moriana et al., 2003; Iniesta et al., 2009; Fernández et al., 2013; Padilla-Díaz et al., 2016). Indeed, if irrigation is enough on period 3, the olive tree shows an outstanding capacity for recovering from water stress (Lavee et al., 1990; Moriana et al., 2007; Fernández et al., 2013; Padilla-Díaz et al., 2016). In 2011 and 2012 we did not irrigate between periods 1 and 2. In 2014 and 2015 we decided to irrigate between periods 1 and 2, if rainfall supplies were far from replacing the crop water needs. According to Hammami et al. (2011), severe water stress between period 1 and 2 could limit fruit size.

In 2011 and 2012 we imposed three irrigation treatments, a control (100C) and two RDI treatments (30RDI and 60RDI). In the 100C treatment the trees were irrigated daily to replace 100% of the irrigation needs (IN). IN on a daily basis were calculated as $IN = ET_c - P_e$, being ET_c the maximum potential crop evapotranspiration calculated with the single crop coefficient approach (Allen et al., 1998) and P_e the effective precipitation which according to Orgaz and Fereres (2008), was calculated as 75% of the precipitation