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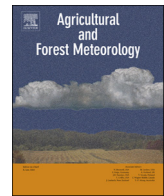
Relationships between fruit growth and oil accumulation with simulated seasonal dynamics of leaf gas exchange in the olive tree

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A B S T R A C T

Carbohydrates availability, which are directly related to photosynthesis (A_N), and turgor are the main determinants of fruit growth. Since stomatal conductance (g_s) is the main limiting factor of A_N in fruit trees in most environments, and is strongly regulated by turgor, its measurement is pivotal to understanding fruit growth dynamics. Despite its relevance, the use of g_s to estimate A_N faces the major limitation of being difficult to measure in an automated and continuous manner. Based on these observations, and considering the control that the stomata exert on transpiration, and thus on sap flux density (J_s) under conditions of high coupling to the atmosphere, we conducted a multi-faceted experiment in olive trees. The main objective was to assess the use of continuously modelled A_N, derived using a simulated g_s, as a tool to study fruit growth and oil accumulation and other components of vegetative above-ground growth (leaf area and number of shoot internodes) in a super-high-density olive orchard under different irrigation levels. Sixteen olive trees under four different irrigation treatments (two control and two deficit irrigated, with one and two drip lines each) were continuously monitored with J_s sensors from May to November 2016. Gas exchange, fruit growth, number of shoot internodes and leaf area were measured periodically. Stomatal conductance was empirically simulated through J_s, and A_N was modelled using previously simulated g_s and a biochemical model of photosynthesis. Results showed that A_N can be accurately modelled from simulated g_s, obtained in turn from J_s measurements divided by pressure deficit. Moreover, the approach was shown to be sensitive enough to infer the response of g_s and A_N to soil water content and vapour pressure deficit. Interestingly, accumulated A_N was significantly related to fruit growth and oil content for all the irrigation treatments which determine the slope of these relations. In contrast, the relationship with leaf area was only significant for the control irrigation treatments, where the number of shoot internodes increased significantly more than in the water-stressed trees. Our results show that under water stress conditions trees prioritize fruit growth and oil content accumulation over vegetative growth, suggesting a higher sink strength for reproductive growth than for vegetative growth. We conclude that the use of sap flow and the proposed approach provides reliable g_s and A_N data, and allows the modelling of the relations between carbon assimilation and allocation, which are helpful to estimate fruit growth.

1. Introduction

Water is an increasingly scarce resource, but central to achieve a more productive agricultural output to feed the growing world population (Foley et al., 2011; Mueller et al., 2012). Plants require water for growth and tissue expansion, with water absorbed by plants through their roots being lost through the stomata while CO_2 is taken up for photosynthesis. Stomatal opening is the main factor determining CO_2 uptake, and therefore, the synthesis of photoassimilates in the plant (Flexas and Medrano, 2002). Furthermore, stomatal closure is one of

the earliest responses to water deficit (Martin-StPaul et al., 2017), markedly affecting water uptake and water movement through the plant. Stomatal conductance (g_s) is, therefore, a sensitive water stress indicator, directly related to plant function, shoot and fruit growth and, eventually, to yield (Jones and Tardieu, 1998). In addition to affecting the amount of carbohydrate available for the fruit, stomatal regulation ultimately determines the fruit water status through its effect on both leaf and fruit water potential (Ho et al., 1987; Fishman and Génard, 1998; Lechaudel et al., 2007).

Despite it being important to know g_s for ecophysiological studies

and agricultural applications such as irrigation scheduling, its continuous and automated recording is not yet possible. However, new approaches have been recently proposed to conduct g_s estimations continuously, either by modifying the inverted equation of Penman-Monteith (Kucera et al., 2017), or by using its simplified version (McNaughton and Jarvis, 1983; Jarvis and McNaughton, 1986) as proposed by Hernandez-Santana et al. (2016a). Specifically, Hernandez-Santana et al. (2016a) proposed simulating g_s from sap flux density (J_s) values measured in the trunks of trees, divided by the air vapour pressure deficit (D). This avoids the uncertainty derived from upscaling from single point measurements of J_s in the trunk to the whole tree transpiration (Swanson, 1994; López-Bernal et al., 2010; Hernandez-Santana et al., 2015; Berdanier et al., 2016). The automated estimation of g_s opens the possibility of using it both as a reliable water stress indicator and as an input in photosynthesis models which, when applied to fruit tree orchards, could help to predict yield. The mechanistic model of photosynthesis by Farquhar et al. (1980) has proven to be robust and easily applicable to many species and environments (Farquhar et al., 2001; von Caemmerer, 2013). This model has been parameterised for many species of high agronomic interest (Diaz-Espejo et al., 2006; Egea et al., 2011; Greer and Weedon, 2012; Kattge and Knorr, 2007). After a correct parametrization, the main difficulty to its application rests in the estimation of g_s. However, once we have a value for g_s, A_N can be estimated from environmental variables, such that we can predict which region of the A_N-g_s relationship our crop is in at any given moment. Considering the close analogy between the A_N-g_s relationship and yield-transpiration (Flexas et al., 2010; Medrano et al., 2002; Morison et al. 2008; Parry et al., 2005), i.e., the two relations can be considered equivalent, the combination of sap flux density measurements and Farquhar et al.'s photosynthesis model may overcome the difficulty of applying a target level of water stress in deficit irrigated trees. For example, the known hyperbolic curve usually found between A_N and g_s justifies the maintenance of g_s values below the plateau region in which A_N hardly increases, but g_s, and thus tree water use, still grows significantly, thereby decreasing water use efficiency (Parry et al., 2005).

However, there is no straightforward relationship between A_N and yield. Indeed, the fraction of photoassimilates going to each organ of the plant depends on a series of complex rules. Carbon allocation partitioning links source and sink plant organs through various regulations and interactions among different plant processes related to carbon metabolism (Génard et al., 2008). When A_N is limited by low soil water availability, the allocation partitioning patterns can change based on priority rules. These allocation patterns have been widely studied (Le Roux et al., 2001), although they are not easy to implement in agriculture because the mechanisms by which dry matter is distributed among organs are not fully understood (Marcelis, 1996). Nevertheless, biomass allocation patterns have been manipulated in agricultural species for years to achieve a gain in productivity by increasing the plant harvest index (the ratio of grain/fruit weight to total plant weight), which reflects the partitioning of photoassimilates between the grain/fruit and the rest of the plant (Sinclair, 1998; Morison et al., 2008). Indeed, the plant harvest index can be increased by using deficit irrigation strategies (Morison et al., 2008). In addition to saving water, deficit irrigation strategies can reduce vegetative growth without decreasing yield, i.e., they are effective in decreasing the carbon spent on vegetative growth without decreasing fruit growth as shown previously in olive (Iniesta et al., 2009; Dag et al., 2010; Hernandez-Santana et al., 2017). Thus, under limited available water, fruits augment their already strong carbohydrate sink capacity and have higher priority for assimilates than vegetative organs, leading to a reduced vegetative growth of roots, stem and leaves (Génard et al., 2008; Hacket-Pain et al., 2017). Therefore, knowing the irrigation strategy that can modify the growth patterns of a plant to enhance the biomass allocation to fruits rather than to vegetative organs, would allow us to control excessive vegetative growth with a reduced impact on fruit growth. In

addition, this would lead to a net water saving in agriculture. Recent results indicate that 30–45% of the irrigation needs of a super-high-density olive orchard could be useful for this purpose (Hernandez-Santana et al., 2017). However, these results were based on values obtained at the end of the irrigation season of different years, and did not provide information about the dynamics during the fruit growth period.

In this work, we simulated the dynamics of g_s and A_N continuously over an irrigation season (late May to early November) in a hedgerow olive orchard with high plant density. Fruit size, oil content, leaf area and number of shoot internodes were frequently measured, to derive the correlation between accumulated A_N and fruit development. We followed the approach described in Hernandez-Santana et al. (2016a) to simulate g_s from continuous and automated J_s/D measurements, and then used the photosynthesis model by Farquhar et al. (Farquhar et al., 1980) to estimate A_N. Our hypothesis was that this approach would allow the estimation of the temporal dynamics of fruit size and oil content since g_s is highly sensitive to water stress, the main limiting factor of A_N and a major regulator of the incoming and outgoing water fluxes of the fruit. We further hypothesized that knowing the dynamics of accumulated A_N would allow the dynamics of fruit growth, oil accumulation, leaf area and the number of shoot internodes to be simulated over the course of the season. Finally, we hypothesized that vegetative growth would be more affected by deficit irrigation than fruit growth. Thus, our specific aims were (1) to calibrate and validate an approach to simulate g_s and A_N based on automated J_s measurements, and (2) to assess the use of continuously simulated A_N as a tool to study fruit growth, oil accumulation and other components of vegetative above-ground growth (leaf area and shoot length) in a super-high density olive orchard under different levels of irrigation.

2. Materials and methods

2.1. Orchard and climate characteristics

The experiment was conducted along the irrigation season (late May to early November) of 2016, in a commercial super-high-density orchard near Seville (Spain) (37° 15′ N, -5° 48′ W). At that time, the 'Arbequina' olive trees used were 10 year s old. They were planted in a 4 m × 1.5 m formation (1667 trees ha^{-1}), in rows oriented N-NE to S-SW. The trees, with a single trunk and shoots from 0.6 to 0.7 m above the ground, were pruned in December-January each year. The orchard soil (Arenic Albaqualf, USDA 2010) had a sandy loam top layer and a sandy clay layer underneath. 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).

The area has a Mediterranean climate with hot and dry weather from May to September, being mild and wet for the rest of the year. 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 1531 mm and 509 mm, respectively, for the 2002–2016 period. For that period, average maximum and minimum air temperature values were 25.3 °C and 10.9 °C, respectively. The hottest months are July and August.

We applied four irrigation treatments: two control treatments, in which irrigation fulfilled tree water demand, with one (100C-1L) or two (100C-2L) dripper lines, and two sustained deficit irrigation treatments (SDI) in which 45% of the water added to control was applied along the whole irrigation season, with one (45SDI-1L) or two (45SDI-2L) dripper lines. The objective of these sub-treatments is to alter the equilibrium between root and leaf area with localised irrigation by drippers which have an important effect on transpiration as shown preliminarily in Diaz-Espejo et al. (2012). However, this aim is beyond the scope of this work. Moreover, the dripper lines were doubled in 2016 and thus, no effect was observed between the treatments with one and two dripper