



Estimation of stomatal conductance and stem water potential threshold values for water stress in olive trees (cv. Arbequina)

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Abstract

Many irrigation strategies have been proposed in olive orchards to overcome both increasing water scarcity and competition for water with other sectors of society. However, threshold values of stomatal conductance (g_s) and stem water potential (Ψ_{stem}) for use in designing deficit irrigation strategies have not yet been adequately defined. Thus, an experiment was conducted to determine g_s and Ψ_{stem} thresholds for water stress in a super-intensive olive orchard (cv. Arbequina) located in Pencahue Valley (Maule Region, Chile) over three consecutive growing seasons. The experimental design was completely randomized with four irrigation treatments. The stem water potential (Ψ_{stem}) of the T_1 treatment was maintained between -1.4 and -2.2 MPa, while the T_2 , T_3 , and T_4 treatments did not receive irrigation from fruit set until they reached a Ψ_{stem} threshold of approximately -3.5 , -5.0 , and -6.0 MPa, respectively. Stomatal conductance (g_s), transpiration (T_l), net CO_2 assimilation (A_n), and stem water potential (Ψ_{stem}) were measured fortnightly at midday. A significant nonlinear correlation between A_n and g_s was used to establish different levels of water stress. Water stress was considered to be mild or absent when the g_s values were greater than $0.18 \text{ mol m}^{-2} \text{ s}^{-1}$, whereas water stress was estimated to increase from moderate to severe as g_s decreased significantly below $0.18 \text{ mol m}^{-2} \text{ s}^{-1}$. Similarly, water stress using Ψ_{stem} was determined to be mild or absent above -2.0 MPa. Such categorizations should provide valuable information for maintaining trees well-watered in critical phenological phases.

Introduction

An evaluation of several studies of modern olive orchards in Mediterranean climatic conditions has demonstrated that irrigation benefits fruit and oil yield (Gucci and Fereres

2012). Nevertheless, the water scarcity and competition for water with other sectors of society that occurs worldwide has generated pressure to reduce the water used in agriculture (Feres et al. 2003; Fernández and Torrecillas 2012). For this reason, several researchers have indicated that regulated deficit irrigation (RDI) is a viable management tool for improving leaf-level water-use efficiency (WUE, $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$) and overall crop water productivity (WP, kg/m^3) in fruit trees (Lampinen et al. 2001; Ortega-Farías et al. 2012; Fereres et al. 2014). For RDI to be a practicable solution, adequate water stress indicators are required to properly schedule the timing of water application. Both stomatal conductance (g_s) and plant water potential (Ψ) have been suggested as potential indicators for olive orchards (Moriana et al. 2002, 2012; Tognetti et al. 2009; Agüero Alcaras et al. 2016).

Stomatal conductance is controlled by soil water availability, osmotic adjustment, xylem hydraulic conductivity, and environmental factors such as vapor pressure deficit and involves complex interactions between internal and external leaf factors (Flexas and Medrano 2002; Medrano et al. 2002; Fernández 2014). According to Cifre et al. (2005), g_s has

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been identified as a very good indicator of water stress in vineyards, because a decrease in g_s is an early response to water deficits in grape leaves. In olive trees, leaves have been shown to close their stomata progressively when soil water availability decreases to reduce water loss by transpiration (T_i) (Fernández et al. 1997; Hernandez-Santana et al. 2016). Stomatal closure in olives also reduces CO_2 diffusion into the leaf, thereby affecting net assimilation (A_n) (Giorio et al. 1999; Fernandes-Silva et al. 2016).

Several studies have found significant linear correlations between g_s and A_n for olive trees (Angelopoulos et al. 1996; Moriana et al. 2002; Tognetti et al. 2007). However, some other studies have reported nonlinear correlations between g_s and A_n for olive trees (Sofa et al. 2009; Marino et al. 2018) and vineyards (Medrano et al. 2002; Cifre et al. 2005). In young, potted olive plants, Sofa et al. (2009) found that g_s decreased from an upper limit of approximately $0.20 \text{ mol m}^{-2} \text{ s}^{-1}$ in well-watered plants as water stress increased and that A_n was more sensitive to water stress in plants exposed to full sunlight than in shaded plants. This suggests that both stomatal limitations and photoinhibition were likely to be of importance in the response to water stress. In vineyards, Cifre et al. (2005) observed a nonlinear correlation between g_s vs. A_n . In this study, the threshold values of $g_s > 0.15$, between 0.15 and 0.05 and $< 0.05 \text{ mol m}^{-2} \text{ s}^{-1}$ indicated null-mild, moderate, and severe water stress, respectively. Under mild water stress conditions, water-use efficiency (WUE) increased, because g_s and transpiration (T_i) had a greater rate of decrease than that of A_n (Cifre et al. 2005). This occurred, because A_n remains relatively high under partial stomatal closure due to limited decreases in the substomatal CO_2 concentration (C_i) (Angelopoulos et al. 1996; Medrano et al. 2002; Cifre et al. 2005). However, under high levels of water stress, C_i further decreases and both stomatal and nonstomatal limitations, such as decreased electron transport rate and carboxylation efficiency, begin to be more important (Medrano et al. 2002). Despite some advances, there is little information about g_s thresholds that define different levels of water stress in olive orchards under field conditions. López-Bernal et al. (2017) recently cautioned against extrapolating g_s values from young potted olive plants to older field-grown plants due to significant stomatal oscillations in young plants under water stress conditions.

Using a pressure chamber to determine water potential (Ψ) has been suggested as a good method for monitoring irrigation scheduling in vineyards and orchards, because it integrates the effects of soil water content, atmospheric conditions, and cultivar on leaf water status (Scholander et al. 1965; Meyer and Reicosky 1985; Williams and Araujo 2002; Naor 2006; Ortega-Farías and López-Olivari 2012). The measurement of water potential can be carried out using three different measurements: (1) the predawn leaf water

potential (Ψ_{pd}); (2) midday leaf water potential (Ψ_{leaf}) in leaves exposed to the full sun; and (3) midday stem water potential (Ψ_{stem}) measured in leaves previously enclosed in plastic and aluminum foil to obtain equilibrium with the plant xylem (Ahumada-Orellana et al. 2017; Tognetti et al. 2005; Fulton et al. 2001). Several researchers have suggested that Ψ_{stem} can be used to evaluate water deficit, because it is very sensitive to water deficit, has low variability between measurements in a given tree, and is highly correlated with other physiological variables such as g_s and A_n (Williams and Trout 2005; Naor 2006; Tognetti et al. 2007; Ennajeh et al. 2008; Ben-Gal et al. 2010).

Recent studies have indicated that Ψ_{stem} values between -2.5 and -3.5 MPa are appropriate to maintain adequate olive oil yield and quality (cv. Arbequina) (Naor et al. 2013; Trentacoste et al. 2015; Marra et al. 2016; Ahumada-Orellana et al. 2017, 2018). Such values likely represent mild-to-moderate water stress when applied over extended portions of the growing season. Moriana et al. (2002) also proposed that Ψ_{stem} values < -4.0 MPa represent severe water stress in cv. Picual. Nevertheless, more information is still needed regarding Ψ_{stem} thresholds in order for effective application of RDI in olive trees (Marino et al. 2018). As one step in defining such Ψ_{stem} thresholds, it is necessary to understand the effects of different water deficit levels on leaf gas exchange. Defining the relationships among leaf gas exchange variables (A_n , g_s and T_i) and Ψ_{stem} can help to establish threshold values that affect oil quality and yield. Therefore, the objective of this study was to determine g_s and Ψ_{stem} threshold values for water stress in a super-intensive, drip-irrigated olive orchard (cv. Arbequina) in Mediterranean climatic conditions. Gas exchange relationships were developed for olive trees under different irrigation treatments, which generated different degrees of water stress.

Materials and methods

Site description and experimental design

The experiment was conducted during three consecutive growing seasons (2011–2012 to 2013–2014) in a 6-year-old drip-irrigated olive orchard (*Olea europaea* L. cv. Arbequina) established in 2005 and located in the Péncahue Valley, Maule Region, Chile (35° , 232°L.S ; $71^\circ442'\text{W}$; 96 m altitude). The olive trees were trained under a hedge-row system with a planting framework of 1.5×5.0 m ($1333 \text{ tree ha}^{-1}$) and irrigated using two 2.0 L h^{-1} drippers per tree. The climate is Mediterranean with an annual rainfall of 620 mm that is concentrated in the winter period (Ortega-Farías and López-Olivari 2012).

The experimental design was described in detail by Ahumada-Orellana et al. (2017). Briefly, the control treatment

(T_1) was maintained by irrigation at Ψ_{stem} values between -1.4 and -2.2 MPa during the growing season, with the most negative values tending to occur in the summer when crop demand was greatest. Irrigation was cutoff in the other treatments from fruit set (20 days after full bloom) until reaching Ψ_{stem} thresholds of approximately -3.5 MPa for T_2 , -5.0 MPa for T_3 , and -6.0 MPa for T_4 . Upon reaching the specific thresholds, irrigation was reinitiated, so that Ψ_{stem} recovered to values close to those of T_1 . The seasonal irrigation amount for T_1 averaged approximately 245 mm over the three growing seasons, and was 200, 180, and 160 mm for the T_2 , T_3 , and T_4 treatments, respectively. There were four replicate plots per treatment with each plot consisting of five trees.

Plant water status measurements

To evaluate olive water status between 12:30 and 14:00 h, the midday stem water potential (Ψ_{stem}) was measured weekly during each growing season using a Scholander-type pressure chamber (Model 1000, PMS Instrument Company., Albany, Oregon, USA) (Moriani and Fereres 2002). Two apical stems per plot were used for this measurement. The stems were located in the center of the hedgerow with at least five leaf pairs per stem (Secchi et al. 2007; Rousseaux et al. 2008), and they were covered with plastic bags and aluminum foil for 1–2 h before measurement (Meyer and Reicosky 1985).

Leaf gas exchange measurements

Gas exchange was measured during each growing season, between 12:00 and 14:00 h every 7–14 days, from December to February. Measurements were performed on two mature, sun-exposed leaves per plot, located at chest height on the hedgerow exterior (Tognetti et al. 2007).

An infrared gas analyzer (Model LI-6400, Li-Cor, Inc., Lincoln, NE, USA) was used to estimate values of stomatal conductance (g_s), transpiration (T_1), substomatal CO_2 concentration (C_i), and net photosynthesis (A_n). Measurements were made on sunny days with PAR and CO_2 concentration ranging between 1100–1700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 380–400 $\mu\text{mol mol}^{-1}$, respectively. Moreover, the leaf chamber temperature was maintained between 25 and 35 °C, molar air flow rate was 400 $\mu\text{mol s}^{-1}$, and relative humidity was between 40 and 50%.

Data analysis

Relationships between g_s and the other gas exchange variables, including Ψ_{stem} , were evaluated. In addition, g_s threshold values were obtained by plotting the relationship between A_n and g_s using a piecewise linear regression, which

is an effective technique for modeling changes in slope (Toms and Lesperance 2003). In this analysis, g_s values were segmented and regression analyses were done separately for each segment (Malash and El-Khaiary 2010). Finally, Ψ_{stem} vs g_s relationship was used to obtain Ψ_{stem} and g_s thresholds that defined water stress.

Results

The overall relationship between A_n and g_s was curvilinear with a r^2 value = 0.88 (Fig. 1). Piecewise linear regression analysis indicated that there were three line segments of different slopes over the range of g_s values explored, which coincided with: $g_s > 0.18$ (Zone I), g_s between 0.18 and 0.09 (Zone II), and $g_s < 0.09$ $\text{mol m}^{-2} \text{s}^{-1}$ (Zone III). A change in slope at a g_s value of 0.18 $\text{mol m}^{-2} \text{s}^{-1}$ indicated an upper threshold above which water stress was mild or absent. This threshold value was consistent among seasons (Table 1). However, the point of inflection between the lower two line segments (Zones II, III) could not be determined the first season (2011–2012) and was different among seasons for 2012–2013 and 2013–2014. In Zone I, A_n was not significantly affected when $g_s > 0.18$ $\text{mol m}^{-2} \text{s}^{-1}$, presenting a clear plateau at 17.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Values of A_n for Zone II decreased linearly from 17.2 to 10.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ as g_s values declined from 0.18 to 0.09 $\text{mol m}^{-2} \text{s}^{-1}$, while A_n in Zone III decreased linearly from 10.5 to 1.00 $\mu\text{mol m}^{-2} \text{s}^{-1}$ as g_s decreased from 0.09 to nearly 0.01 $\text{mol m}^{-2} \text{s}^{-1}$. For Zones II and III, the ratios of A_n to g_s were 78.2 and 107.2 $\mu\text{mol m}^{-2} \text{s}^{-1}/\text{mol m}^{-2} \text{s}^{-1}$ with a r^2 of 0.55 and 0.63,

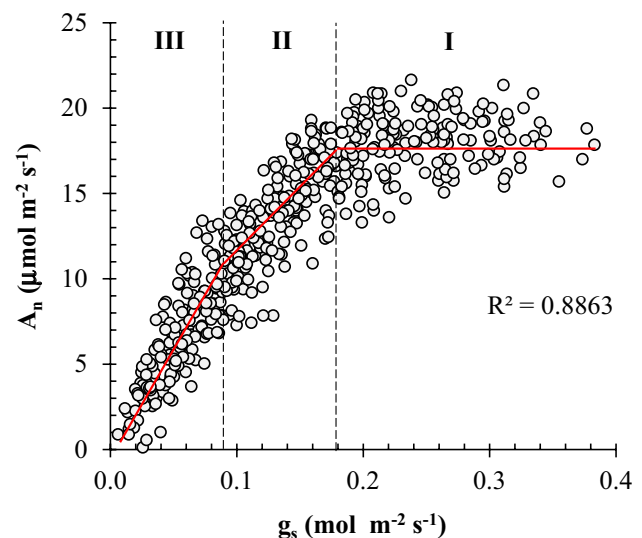


Fig. 1 Relationship between stomatal conductance (g_s) and net assimilation (A_n). Vertical dashed lines separate three line segments into zones (I, II, III) using piecewise regression

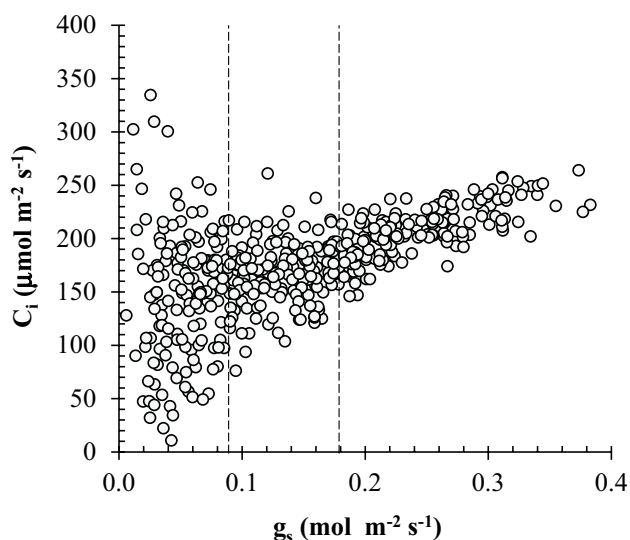
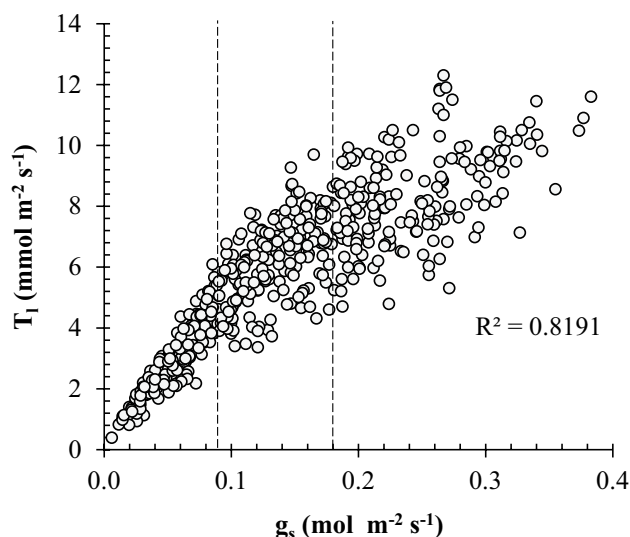
Table 1 Estimation of stomatal conductance (g_s) thresholds using piecewise linear regression

Water condition	Season	Threshold	Lower limit (95%)	Upper limit (95%)	Value p
Non water stress	2011–2012	0.19	0.18	0.21	0.00
	2012–2013	0.18	0.17	0.18	0.00
	2013–2014	0.18	0.17	0.19	0.00
	Overall	0.18	0.17	0.19	0.00
Water stress	2011–2012	n.f.	n.f.	n.f.	n.f.
	2012–2013	0.08	0.02	0.14	0.00
	2013–2014	0.06	0.04	0.08	0.00
	Overall	0.09	0.07	0.11	0.00

n.f. data were not fitted to the model

respectively. Therefore, Zones I, II, and III were used to interpret the behavior of the leaf gas exchange relationships (g_s vs C_i and T_1 vs g_s).

There were linear relationships between C_i and g_s for Zones I and II, with r^2 values equal to 0.79 and 0.48, respectively (Fig. 2). C_i values for Zone I increased linearly from 170 to 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for $g_s > 0.18 \text{ mol m}^{-2} \text{s}^{-1}$, while those for Zone II decreased linearly from 170 to 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ as g_s diminished from 0.18 to 0.09 $\text{mol m}^{-2} \text{s}^{-1}$. For Zone III, there was not a significant relationship between C_i and g_s , since the data were highly scattered. Finally, the relationship between T_1 and g_s was curvilinear ($r^2 = 0.82$) with highly scattered data for Zone I and low scattering for Zone III (Fig. 3). The r^2 values for Zones II and III were 0.25 and 0.81, respectively.

**Fig. 2** Relationship between stomatal conductance (g_s) and internal CO_2 concentration (C_i)**Fig. 3** Relationship between stomatal conductance (g_s) and leaf transpiration (T_1)

Significant nonlinear relationships were observed between A_n and Ψ_{stem} and g_s and Ψ_{stem} , with r^2 values of 0.65 and 0.67, respectively (Fig. 4). Values of g_s and A_n decreased rapidly at first and then more gradually as water status became more negative. The relationship between Ψ_{stem} and g_s was used to establish threshold values of Ψ_{stem} . This relationship was developed using values of Ψ_{stem} and g_s ranging from -0.9 to -6.5 MPa and 0.05 to nearly $0.395 \text{ mol m}^{-2} \text{s}^{-1}$, respectively. A piecewise linear regression indicated that a break point in the g_s - Ψ_{stem} relationship (i.e., a significant change in slope) occurred when g_s was $0.12 \text{ mol m}^{-2} \text{s}^{-1}$ and Ψ_{stem} was -2.3 MPa (Fig. 4b), and two linear equations were obtained ($\Psi_{\text{stem}} = -2.77 + 4.36g_s$ for $g_s > 0.12 \text{ mol m}^{-2} \text{s}^{-1}$ and $\Psi_{\text{stem}} = -5.29 + 25.54g_s$ for $g_s < 0.12 \text{ mol m}^{-2} \text{s}^{-1}$). A more detailed analysis of the g_s - Ψ_{stem} relationship indicated that crop load did not significantly affect the relationship for the range of crop load (6 – 10 kg tree^{-1}) evaluated (Fig. 5).

Discussion

In comparison with other agronomic species such as grapevines, there has been little emphasis on establishing water stress thresholds in olive trees using gas exchange measurements (Cifre et al. 2005; Medrano et al. 2002; Marino et al. 2018). Stomatal conductance values have been used successfully as an integrative parameter for determining the degree of water stress in vineyards (Zsófi et al. 2009). The water stress thresholds of 0.015 and $0.05 \text{ mol m}^{-2} \text{s}^{-1}$ for g_s , observed by Medrano et al. (2002) and Cifre et al. (2005) in grapevines, have also been proposed for other C_3 plants

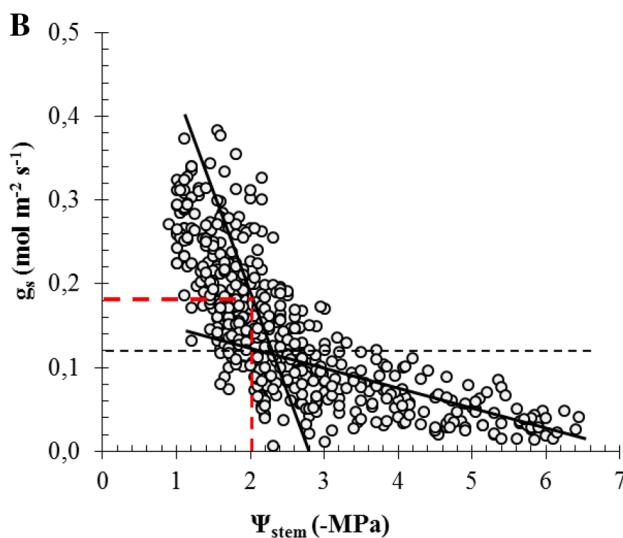
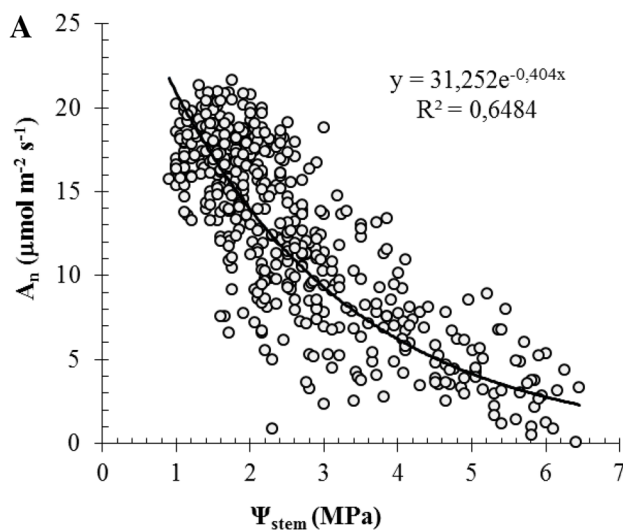


Fig. 4 Relationships between **a** net assimilation (A_n) and midday stem water potential (Ψ_{stem}) and **b** stomatal conductance (g_s) and midday stem water potential (Ψ_{stem}). The intersection of the black solid lines indicates a Ψ_{stem} threshold value (-2.3 MPa) at $g_s = 0.12$. The red dashed line indicates the Ψ_{stem} value (-2.0) that separates different zones in the g_s vs A_n relationship in Fig. 1

In our study, as water deficit progressed, values of g_s , A_n , C_i , and T_l decreased, but at different rates. In addition, the g_s – A_n relationship has been described in olives and other species, because the decrease in photosynthesis is greatly controlled by stomatal closure (Naor and Wample 1994; Angelopoulos et al. 1996; Medrano et al. 2002; Cifre et al. 2005; Galmés et al. 2007; Tognetti et al. 2007). Moriana et al. (2002) observed that the relationship between g_s and A_n was linear in olive trees. However, the relationship was nonlinear in our study (Fig. 1). This difference can likely be explained by the range of g_s values evaluated in the two studies. Moriana et al. (2002) evaluated the g_s vs A_n relationship up to maximum g_s values of about 0.2 mol m⁻² s⁻¹. In

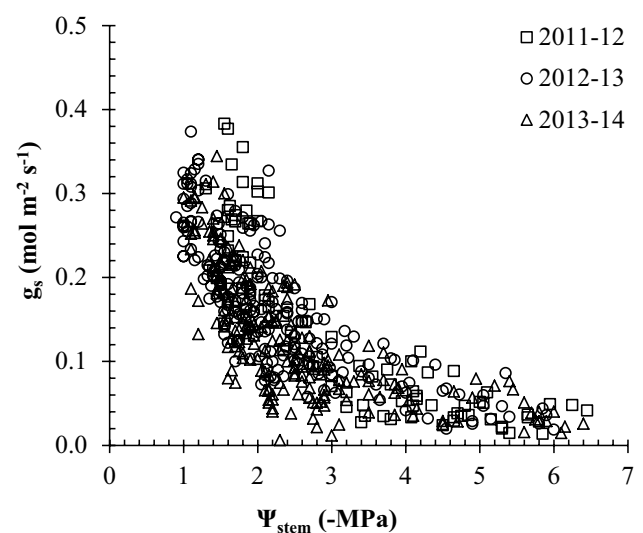


Fig. 5 Relationship between stomatal conductance (g_s) and midday stem water potential (Ψ_{stem}) for different growing seasons. Crop load was 8.3, 6.5, and 10.3 kg tree⁻¹ in 2011–2012, 2012–2013, and 2013–2014, respectively. The range of crop load evaluated did not affect the g_s vs. Ψ_{stem} relationship

contrast, g_s reached values of 0.4 mol m⁻² s⁻¹ under our field conditions, but A_n did not increase when g_s was greater than 0.18 mol m⁻² s⁻¹.

Based on the g_s – A_n relationship, two zones of water stress were identified with water stress being mild or absent in Zone I ($g_s > 0.18$ mol m⁻² s⁻¹) and water stress increasing from moderate to severe as g_s decreased significantly below 0.18 mol m⁻² s⁻¹ in Zone II. In Zone I, A_n presented a constant value of approximately 17.0 μmol m⁻² s⁻¹, which is similar to the maximum value obtained by Marino et al. (2018), although a higher g_s (> 0.25 mol m⁻² s⁻¹) was needed to reach the highest A_n rates. Fernández (2014) has reported that A_n values of C₃ plants usually do not exceed 25 μmol m⁻² s⁻¹. In contrast to A_n , C_i did not appear to reach maximum values within the measured range (i.e., up to g_s of 0.4 mol m⁻² s⁻¹). In Zone II, A_n decreased linearly to 10.5 μmol m⁻² s⁻¹ at g_s of 0.09 mol m⁻² s⁻¹. In this zone, stomatal closure is likely to limit photosynthesis due to diminishing C_i in the leaf mesophyll (Flexas and Medrano 2002). Finally, with g_s under 0.09 mol m⁻² s⁻¹, A_n decreased steeply, but C_i did not show any pattern as a result of highly scattered data. Nonstomatal limitations to photosynthesis become dominant in this range, as has been reported by several studies (Medrano et al. 2002; Cifre et al. 2005; Zsófi et al. 2009).

Given the above discussion, the value of 0.18 mol m⁻² s⁻¹ could be used as a g_s threshold for determining water stress in olive trees (cv. Arbequina). With the decrease in Ψ_{stem} , the A_n and g_s values decreased rapidly at first; later, as Ψ_{stem} became more negative, the decreases

were more gradual (Fig. 4a, b). Such a nonlinear response coincides with the results reported by other studies with olive trees (Angelopoulos et al. 1996; Ennajeh et al. 2008; Marino et al. 2018). In addition, our results showed that g_s values were highly scattered when Ψ_{stem} was greater than -2 MPa. Similar results were observed by Marino et al. (2018), who suggested that a $\Psi_{\text{stem}}-g_s$ model for low-level stress ($\Psi_{\text{stem}} > -2$ MPa) is not reliable. This data scattering at high Ψ_{stem} values is caused by the sensitivity of g_s to other factors such as temperature, vapor pressure deficit, and radiation influx under well-watered conditions (Ennajeh et al. 2008; Marino et al. 2018). Later, as stress intensified ($\Psi_{\text{stem}} < -2$ MPa), g_s decreased more gradually. Based on these physiological responses, the -2.0 MPa value of Ψ_{stem} could be the break point between well-watered and water stress conditions. Therefore, -2.0 MPa of Ψ_{stem} is proposed as the threshold value for programming irrigation in super-intensive ‘Arbequina’ olive orchards.

These results complement the previous studies in the same orchard in Chile under Mediterranean climate conditions (Ahumada-Orellana et al. 2017, 2018). Fruit and oil yield were not affected in this orchard under 4 years of water deficit treatment when irrigation was cutoff after fruit set each year until reaching a Ψ_{stem} value of -3.5 MPa (Ahumada-Orellana et al. 2017). Moreover, the quality of the olive oil was not affected negatively by this level of water stress (Ahumada-Orellana et al. 2018). Similar results were observed by Marra et al. (2016) who suggested maintaining a Ψ_{stem} between -3.5 and -2.5 MPa for moderate, sustainable yields with good oil quality.

When interpreting Ψ_{stem} and g_s values in field situations, it should be recognized that crop load in a given year can influence such variables with Ψ_{stem} tending to decrease late in the season as crop load increases (Naor et al. 2013). This indicates that agronomic factors, as well as climatic conditions may influence target Ψ_{stem} and g_s values to some degree. In our study, crop load did not influence the $g_s-\Psi_{\text{stem}}$ relationship (Fig. 5) likely because the range of crop load was fairly narrow ($6.5-10.3$ kg tree⁻¹) in the three seasons evaluated. Ψ_{stem} of -2.0 MPa and g_s of 0.18 mol m⁻² s⁻¹ found in this study are proposed to provide a guideline as to when water stress occurs under moderate yields in Mediterranean climates. The empirical relationships obtained between these variables and photosynthetic rate could be of use in validating simulation models addressing different aspects of irrigation and global change such as OliveCan (López-Bernal et al. 2018). The obtained Ψ_{stem} and g_s thresholds also give valuable information for maintaining trees well-watered in critical phenological stages such as flowering, and could be used in baseline, reference plots when RDI is implemented in super-intensive ‘Arbequina’ olive orchards.

Conclusion

Results obtained in the present study over three growing seasons showed that there were significant nonlinear correlations between A_n vs g_s , A_n vs Ψ_{stem} , and g_s vs Ψ_{stem} with r^2 values ranging between 0.65 and 0.88. Water stress was considered to be mild or absent when g_s and Ψ_{stem} values were above 0.18 mol m⁻² s⁻¹ and above -2.0 MPa, respectively. These threshold values should provide valuable information for maintaining trees well-watered in critical phenological stages such as flowering, and could be used in establishing baseline or reference plots when regulated deficit irrigation is implemented in super-intensive ‘Arbequina’ olive orchards. Further research is necessary to establish threshold values of g_s and Ψ_{stem} for olive trees under severe water stress.

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