



Leaf gas exchange, water status, and oil yield responses to rewatering after irrigation cut-off periods in a superintensive drip-irrigated olive (cv. Arbequina) orchard

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Received: 12 December 2021 / Accepted: 18 July 2022 / Published online: 23 August 2022
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Abstract

Yield and oil quality responses to different degrees of water stress have often reported for olive trees, but few studies have addressed how midday stem water potential (Ψ_{stem}), stomatal conductance (g_s), net assimilation (A_n), and oil yield respond to rewatering after experiencing water deficit. The objective of this study was to evaluate the responses of Ψ_{stem} , g_s , and A_n in olive leaves to rewatering after irrigation cut-off (ICO) periods during 2011/2012, 2012/2013, and 2013/2014 growing seasons. The drip-irrigated olive trees were located in the Penciahue Valley (Maule Region, Chile) and trained to a superintensive hedgerow system with a spacing of 1.5 m within rows \times 5.0 m between rows. The experiment included a treatment irrigated to satisfy their water requirement based on a previous study ($\Psi_{\text{stem}} > -2.5$ MPa, T0) and two ICO treatments in a completely randomized design. For the ICO treatments, irrigation was cut-off from fruit set until reaching Ψ_{stem} thresholds between -3.0 and -3.5 MPa for T1 and -5.0 and -5.5 MPa for T2. Once these thresholds were reached, the irrigation was restored to that of the T0 treatment level. In the T1 treatment, Ψ_{stem} , A_n , and g_s were all fully recovered from moderate water stress, although the time needed for recovery varied between growing seasons. Except 2012/2013 season, the Ψ_{stem} values were fully recovered 14 days from rewatering after severe water stress in the T2 treatment. A_n and g_s values were, however, 19–36% and 33–41%, respectively, less than those observed in T0 treatment after even 14 days of rewatering. Finally, the total oil yield per plant was significantly reduced in most study seasons after severe water stress (T2). These results suggest that the evolution of plant water status must be carefully monitored when water deficits are imposed in superintensive olive orchards to avoid unwanted delays in the recovery of photosynthesis and potential reductions in oil yields.

Introduction

Olive (*Olea europaea* L.) is one of the most extensively grown tree crops in arid and semiarid zones worldwide (Torres et al. 2017; Fernández et al. 2018). In the last few decades, olive growing has experienced a shift from traditional orchards cultivated under rainfed conditions at low plant density to superintensive drip-irrigated orchards in order to increase olive oil production (Gómez-Rico et al. 2006; Fernandes-Silva et al. 2010; Connor et al. 2014; López-Olivari et al. 2016). Nevertheless, the expansion of olive orchards is likely to be limited by competition with non-agricultural industries for water resources, which may be exacerbated by the negative impacts of climatic change (Feres et al. 2003; Cabezas et al. 2020).

Although there exist studies that report a decrease in oil quality with irrigation, many researchers have demonstrated that with correct irrigation scheduling it is possible to increase yield while maintaining high oil quality

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(Chartzoulakis et al. 1999; Goldhamer, 1999; Moriana et al. 2003; Ben-Gal et al. 2009). Thus, several studies have been conducted in different regions to identify proper irrigation strategies (Fernández et al. 2006; Ahumada-Orellana et al. 2017, 2018; Ben-Gal et al. 2021). Regulated deficit irrigation (RDI) is one of the most implemented irrigation strategies to reduce water application in fruit orchards (Chalmers et al. 1981; Tognetti et al. 2005, 2007; Iniesta et al. 2009; Ortega-Farias et al. 2012). This strategy holds water replenishment below actual evapotranspiration (ETa) during specific phenological periods when the trees are less sensitive to water stress. The success of the irrigation scheduling using an RDI strategy depends on the length and severity of the water stress period. If the water stress is too severe or prolonged, the tree water status will not fully recover after irrigation (Boussadia et al. 2008; Trabelsi et al. 2019; Dayer et al. 2019).

Monitoring the level of water stress during RDI using plant-based measurements of water potential and gas exchange is recommended to avoid significant yield reductions (Fernández, 2014). Plant water status can be a useful tool for irrigation management because it integrates the effects of both soil water availability and climatic conditions on water stress (Meyer and Reicosky, 1985). Midday stem water potential (Ψ_{stem}) has been suggested for irrigation scheduling in olive orchards because it is often highly sensitive to soil water deficit and is positively correlated with net leaf photosynthetic assimilation (A_n) and stomatal conductance (g_s) (Tognetti et al. 2005, 2007; Ben-Gal et al. 2010; Ahumada-Orellana et al. 2019). Several authors have noted that g_s is one of the first physiological variables affected when plants are under mild-to-moderate water stress (Medrano et al. 2002; Cifre et al. 2005; Agüero Alcaras et al. 2016). Stomatal closure affects A_n by first reducing leaf CO_2 diffusion, which may occur even before any change in leaf water potential and/or leaf water content is detected (Angelopoulos et al. 1996; Medrano et al. 2002). If the drought period is lengthened and dehydration becomes more severe, stomatal limitation begins to affect processes, such as photophosphorylation, RuBP regeneration, rubisco activity, and irreversible reductions in leaf area, and fruit dry matter accumulation may occur (Díaz-Espejo et al. 2006; Jara-Rojas et al. 2015; Hernandez-Santana et al. 2017).

Water stress was considered to be mild or absent in olive leaves of a superintensive orchard (cv. Arbequina) when the Ψ_{stem} and g_s were greater than -2.0 MPa and $0.18 \text{ mol m}^{-2} \text{ s}^{-1}$, respectively (Ahumada-Orellana et al. 2019). Moderate water stress in this same study was suggested to be between -2.0 and -5.0 MPa for Ψ_{stem} and 0.18 and $0.09 \text{ mol m}^{-2} \text{ s}^{-1}$ for g_s . Moriana et al. (2002) proposed

that Ψ_{stem} values less than -4.0 MPa represent severe water stress in olive cv. Picual. Other authors have reported that Ψ_{stem} values between -2.5 and -3.5 MPa could be considered appropriate to maintain adequate olive oil yield and quality (Naor et al. 2013; Trentacoste et al. 2015; Marra et al. 2016; Ahumada-Orellana et al. 2017, 2018). In addition, Fernandez et al. (2011) and Trentacoste et al. (2019) indicated that Ψ_{stem} values < -1.7 MPa could produce negative effect during shoot growth and fruit oil filling periods.

However, there is limited information concerning the recovery of Ψ_{stem} , g_s , and A_n after a water deficit period in superintensive drip-irrigated olive orchards. In a traditional orchard under dry-farming conditions, leaf water potential and transpiration only partially recovered after watering at the end of the summer (Moreno et al. 1996). For three-year-old olive trees of several cultivars growing in pots, Trentacoste et al. (2018) reported that Ψ_{stem} and g_s tended to completely recover even after exposure to severe water stress (-6.0 MPa). Other studies in low-density orchards or potted plants have indicated that g_s recovery was less than that of Ψ_{stem} (Moriana et al. 2002; Pérez-López et al. 2008). Furthermore, the recovery of A_n depends on the degree of photosynthetic inhibition during a water shortage and the plant species (Flexas et al. 2009; Chaves et al. 2003). Similarly, a study from a high-density olive orchard has suggested that the potential recovery of Ψ_{stem} and leaf gas exchange will depend on the degree of water stress imposed and the amount of irrigation provided during rewatering (Fernández et al. 2013).

More knowledge of the physiological responses of olive trees to rewatering is essential for developing irrigation strategies in superintensive olive orchards. Therefore, the aim of this study was to evaluate the Ψ_{stem} , g_s , and A_n responses to rewatering after irrigation cut-off periods of different durations in a superintensive drip-irrigated olive orchard. As a reference, the effect of ICO on fruit and oil yields was included in this study.

Materials and methods

Site description and experimental design

This study was conducted during three growing seasons (2011/2012, 2012/2013, and 2013/2014) in a superintensive commercial olive orchard (*Olea europaea* L. cv. Arbequina) located in the Penco Valley, Maule Region, of Chile (35° , $232'$ L.S.; 71° $442'$ W; 96 m elevation). The olive trees were trained to a hedgerow system in rows oriented from west to east with a spacing of $1.5 \text{ m} \times 5.0 \text{ m}$ (1333 trees

ha⁻¹). The olive orchard was irrigated using two drippers (2.0 L h⁻¹) per tree. The climate is Mediterranean semi-arid, with dry summers and an annual rainfall of 600 mm being concentrated in the winter months. The experimental unit presented a clay loam texture soil and was classified as the Quepo series (Vertisol; fine, Thermic Xeric Apiaquerts) with approximately 31% clay, 29% sand, and 40% silt. The volumetric soil water contents at field capacity and wilting point were 0.31 and 0.16 cm³ cm⁻³, respectively. In addition, the soil profile presents a high percentage of stones that produced significant errors and uncertainties in the measurements of soil water content (Θ) during the experiments. For this reason, soil water content data were not used in this study. Finally, Table 1 indicates the date of fruit set (FS), beginning (BPH) and end (EPH) of pit hardening, and harvest (H) for the three growing seasons.

The experiment was established in a randomized design with three treatments and four replicate plots per treatment. Each replicate plot consisted of 5 consecutive trees in a row. The control treatment (T0) was irrigated to satisfy actual evapotranspiration (ETa) throughout the growing season using crop coefficients (Kc from 0.42 to 0.56) obtained from a previous study in the region (López-Olivari et al. 2016). Climate data for determining potential evapotranspiration (ETo) and scheduling irrigation (ETa = ETo × Kc) were obtained using an automatic meteorological station installed in a reference grass area located 2 km from the experimental site. Irrigation for the T0 treatment (100% ETa) maintained Ψ_{stem} values > -2.5 MPa during the study period. For the other treatments, the irrigation was cut-off from the fruit set (Table 1) until reaching Ψ_{stem} thresholds between -3.0 and -3.5 MPa for T1 and -5.0 and -5.4 MPa for T2 (Table 2). Once the thresholds were reached in the T1 and T2 treatments, irrigation was restored to the control treatment level (100% of ETa). The Ψ_{stem} , g_s , and A_n responses of olive leaves to rewatering were evaluated at the end of the ICO period (D0) as well as 7 (D7) and 14 (D14) days after

Table 2 Days without irrigation for the irrigation cut-off treatments and the mean midday stem water potential (Ψ_{stem}) immediately before rewatering

Season	Treatment	Days without irrigation	Ψ_{stem} (MPa)
2011/2012	T1	30	-3.5
	T2	58	-5.0
2012/2013	T1	49	-3.0
	T2	70	-5.1
2013/2014	T1	39	-3.5
	T2	53	-5.4

rewatering. The irrigation was cut-off on DOY 341, 339, and 340 for 2011/2012, 2012/2013, and 2013/2014 growing seasons, respectively (Table 1).

Plant water status and leaf gas exchange measurements

To evaluate tree water status, Ψ_{stem} was measured at midday (12:00–14:00; Coordinated Universal Time, UTC-3) with a pressure chamber (PMS Instrument Company, Model 1000 Pressure Chamber Instrument) (Scholander et al. 1965). These measurements were performed on two current season shoots per replicate located in the middle of the tree canopy (Secchi et al. 2007; Rousseaux et al. 2008). The shoots were covered with aluminized plastic bags for 1 to 2 h before measuring in the pressure chamber (Meyer and Reicosky, 1985; Ortega-Farías and López-Olivari, 2012).

Measurements of A_n and g_s were conducted between 12:00 and 14:00 using an infrared gas analyzer (Model Li-6400, Li-Cor, Inc., Lincoln, NE, USA). These measurements were performed on two sun-exposed leaves per replicate and were located at chest height on the hedgerow exterior (Ahumada-Orellana et al. 2019; Tognetti et al. 2007). The molar air flow rate inside the leaf chamber was

Table 1 Date of fruit set (FS), pit hardening (PH), and harvest (H) for a drip-irrigated olive orchard during the 2011/2012, 2012/2013, and 2013/2014 growing seasons

Growing seasons	Fruit set mm/dd/yy (DOY)	Pit hardening		Harvest mm/dd/yy (DOY)
		Beginning mm/dd/yy (DOY)	End mm/dd/yy (DOY)	
2011/2012	12/07/2011 (341)	12/28/2011 (362)	01/13/2012 (13)	05/11/2012 (131)
2012/2013	12/05/2012 (339)	01/09/2013 (9)	01/23/2013 (23)	05/14/2013 (134)
2013/2014	12/06/2013 (340)	01/07/2014 (7)	01/21/2014 (21)	05/06/2014 (127)

DOY day of the year

set to $500 \mu\text{mol mol}^{-1}$. All measurements were taken at a reference CO_2 concentration like that of the environment ($380\text{--}400 \mu\text{mol mol}^{-1}$) and with a saturating photosynthetic photon flux density (PPFD; $1100\text{--}1700 \mu\text{mol m}^{-2} \text{s}^{-1}$). The leaf angle at the time of measurement was maintained to preserve the natural PPFD under clear sky conditions. No external light source was used in this study.

Fruit and oil yields

Four olive trees for each replicate (16 trees per treatments) were manually harvested to estimate fruit yield (kg plant^{-1}) on DOY 131 (2012), 134 (2013), and 127 (2014) (Table 1). Also, randomized samples of 50 olives for each replicate were taken to measure equatorial diameter. The total oil content was obtained using the Soxhlet method (Martín-Vertedor et al. 2011) and was expressed on a dry weight basis (% dwb). In this case, a sample of 30 kg for each replicate was used to measure total oil content and fruit yield.

Statistical analysis

Analysis of variance (ANOVA) was performed using the statistical software Infostat (Universidad Nacional de Córdoba, Argentina). Significant differences among treatment means were evaluated with Tukey's multiple comparison tests using a significance level of $\alpha = 0.05$ (Di Rienzo et al. 2017).

Results

Weather conditions and irrigation

From October to March, the atmospheric conditions were usually hot and dry with a maximum season rainfall of 34 mm occurring in the 2012/2013 growing seasons (Fig. 1). The mean daily values of air temperature (T_a) and vapor pressure deficit ranged from 13.2 to $25.3 \text{ }^\circ\text{C}$ and 1.5 to 2.1 kPa , respectively, for the three seasons (Fig. 2). The maximum atmospheric vapor pressure deficits were observed in December and January with daily ETo ranging from 5.5 to 6.5 mm day^{-1} . The cumulative ETo was 1094, 1014, and 1099 mm for the 2011/2012, 2012/2013, and 2013/2014 growing seasons, respectively. Under these atmospheric demands, total seasonal irrigation for the three seasons ranged between 226 and 268, 183 and 223, and 155 and 198 mm for T0, T1, and T2, respectively (Table 3). In addition, the average water applications were 31 mm for

T0, 7 mm for T1, and 0 mm for T2 during the pit hardening period.

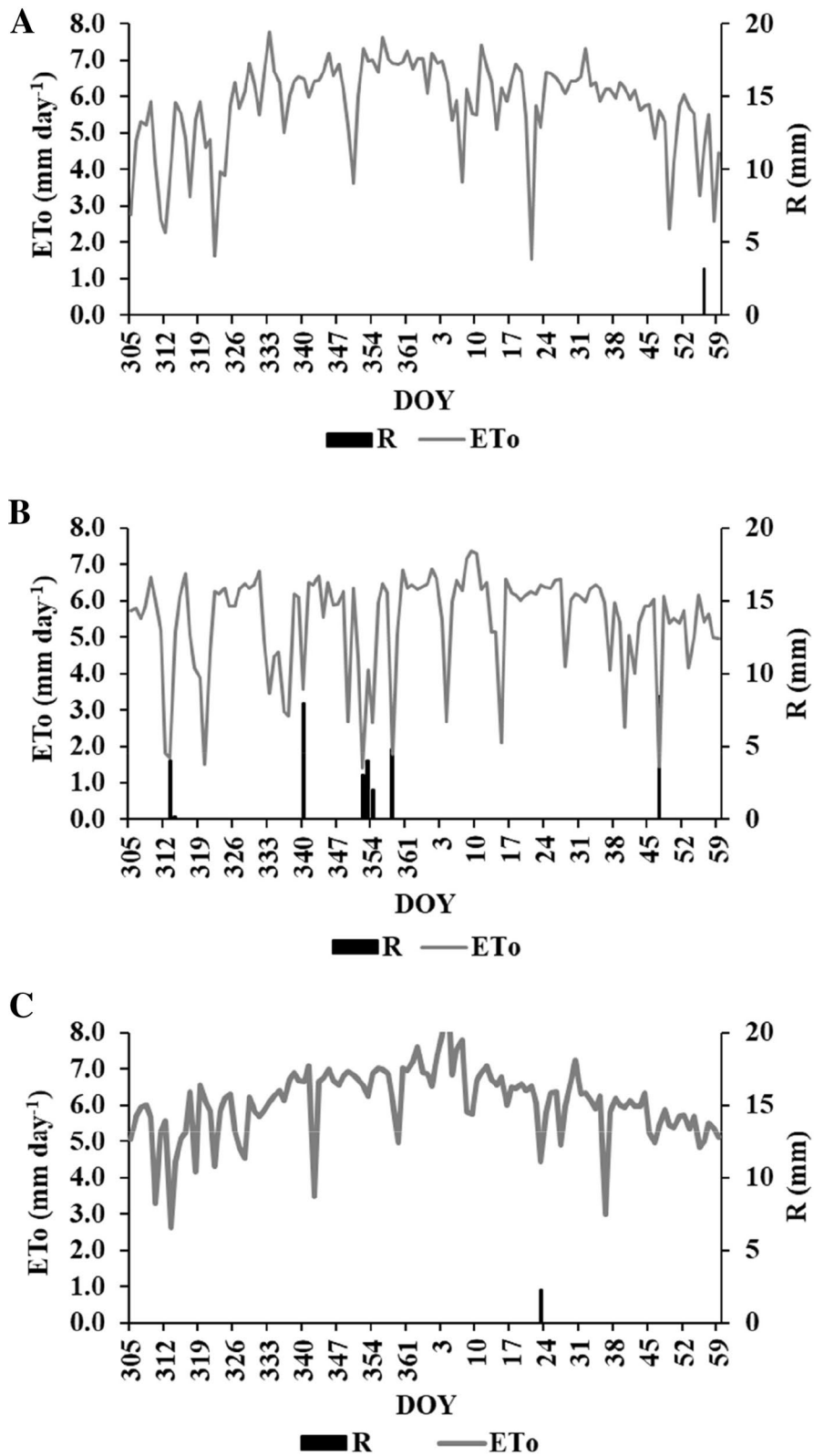
Stem water potential and leaf gas exchange in the ICO experiments

At beginning of the ICO there were no significant differences among treatments for Ψ_{stem} , A_n , and g_s (Table 4). For all treatments, the values of Ψ_{stem} , A_n , and g_s ranged from -1.34 to -1.55 MPa , 15.65 to $18.88 \mu\text{mol m}^{-2} \text{s}^{-1}$, and 0.16 to $0.24 \text{ mol m}^{-2} \text{s}^{-1}$, respectively, during the three-year study period. Under the experimental conditions, Ψ_{stem} values were mostly above -2.5 MPa in the T0 treatment in which irrigation was maintained throughout the season, although some lower values occurred at the end of January when ETo was the highest (Fig. 3). For T0 treatment, the A_n and g_s values ranged between 10.27 and $18.81 \mu\text{mol m}^{-2} \text{s}^{-1}$, and 0.11 and $0.29 \text{ mol m}^{-2} \text{s}^{-1}$, respectively, during the ICO periods (Figs. 4 and 5).

At the end of the ICO periods in T1 treatment (between 30 and 49 days without irrigation), the Ψ_{stem} , A_n , and g_s values ranged between -3.0 and -3.5 MPa , 10.38 and $11.67 \mu\text{mol m}^{-2} \text{s}^{-1}$, and 0.05 and $0.09 \text{ mol m}^{-2} \text{s}^{-1}$, respectively (Figs. 3, 4 and 5). At D0 in T1 treatment, the mean values of all three physiological variables in both the T1 and T2 treatments were significantly lower than those for the T0 treatment for the 2011/2012 and 2013/2014 seasons (Table 5). A full recovery of the physiological variables was observed in the 2011/2012 season with no significant differences between the T0 and T1 treatments after 7 or 14 days of the rewatering. Additionally, both treatments had higher values than those of the unwatered treatment (T2) as would be expected for these measurement dates. In contrast, Ψ_{stem} , A_n , and g_s values in the T1 treatment did not increase 7 or 14 days after rewatering in the last season (2013/2014), but Ψ_{stem} did show recovery the following week (i.e., 21 days after rewatering) by increasing from -3.6 to -2.7 MPa (Fig. 3c). The A_n and g_s values also increased soon after (Figs. 4c and 5c).

At the end of the ICO periods in T2 treatment (between 53 and 70 days without irrigation), the Ψ_{stem} , A_n and g_s values were very low ranging between -5.0 and -5.4 MPa , 2.74 and $4.45 \mu\text{mol m}^{-2} \text{s}^{-1}$, and 0.03 and $0.05 \text{ mol m}^{-2} \text{s}^{-1}$, respectively (Figs. 3, 4, and 5). At D0, the mean values of all physiological variables in the T2 treatment were significantly lower than those in the T0 and T1 treatments (Table 6). After 7 and 14 days of rewatering, there was no significant difference among the treatments for Ψ_{stem} in 2011/12 and

Fig. 1 Daily reference evapotranspiration (ET_o) and effective rainfall (R) during the study period for the 2011/2012 **A**, 2012/2013 **B**, and 2013/2014 **C** growing seasons. Effective rainfall (R) was calculated as $R = (\text{total rainfall} - 5) * 0.75$



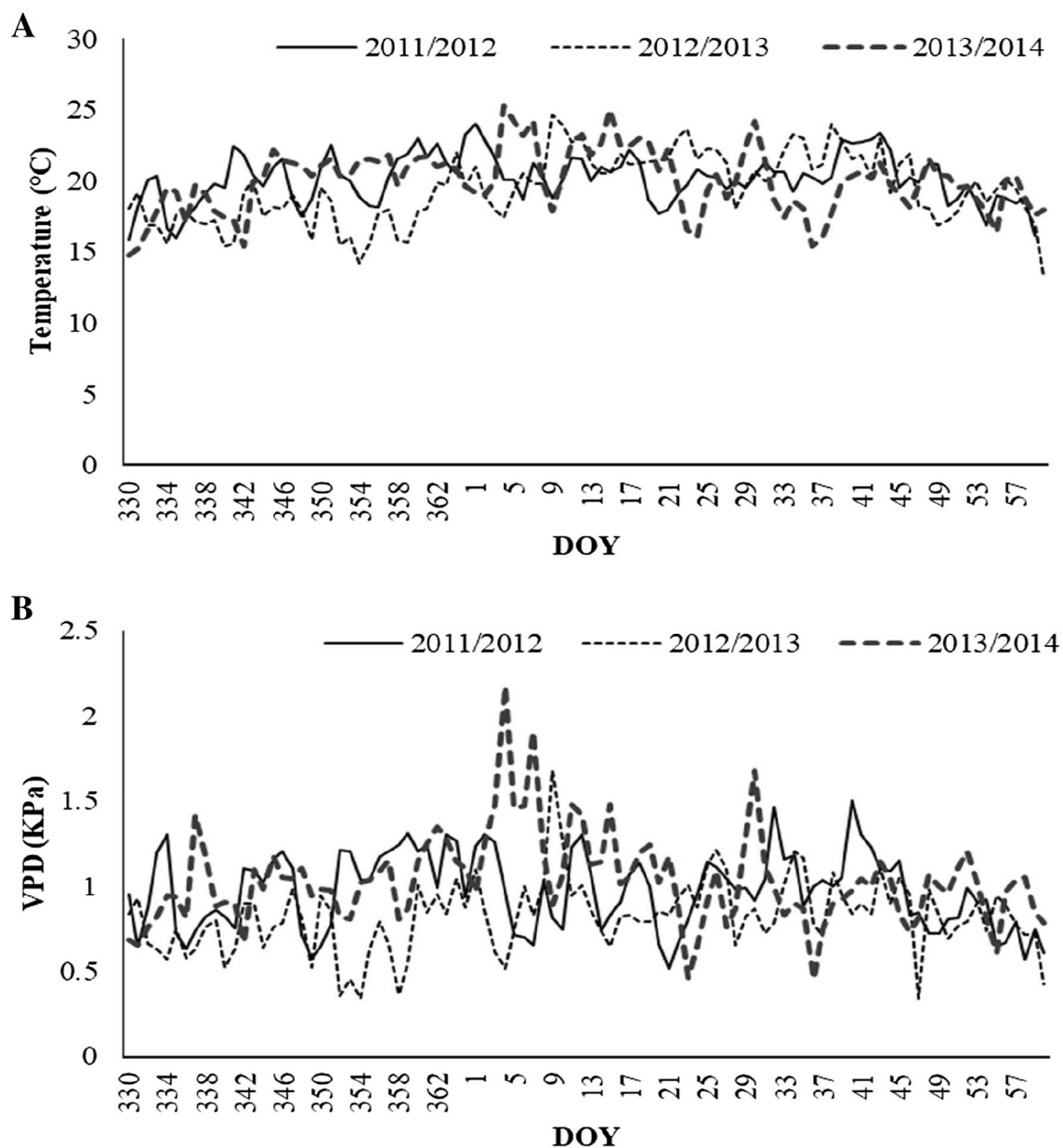


Fig. 2 Daily mean values of air temperature **A** and vapor pressure deficit **B** during the 2011/2012, 2012/2013, and 2013/2014 growing seasons

2013/14, indicating that tree water status had fully recovered after severe water stress. However, only a partial recovery occurred in 2012/13 with Ψ_{stem} still being significantly lower in T2 than that in T0 and T1 treatments after 14 days of the rewatering. In contrast to Ψ_{stem} , the A_n and g_s values in the T2 treatment remained significantly lower than those in the T0 treatment at D14 in all three seasons and were also lower than the values of the T1 treatment in most cases (Table 6). At D14, the A_n and g_s in the T2 treatment were between 19.2

and 36.3% and 33.3 and 41% less, respectively, than those in the T0 treatment.

Yield and oil components

Table 7 indicates significant effects of the ICO periods on fruit diameter, fruit yield, oil content, and total oil yield with higher values observed in the T0. In this treatment, fruit diameter, fruit yield, oil content, and total yield ranged

Table 3 Water application for the main phenological stages of a superintensive drip-irrigated olive (cv. Arbequina) orchard during the 2011/2012, 2012/2013, and 2013/2014 growing seasons

Growing seasons	Phenological stage	Water application (mm)		
		T0	T1	T2
2011/2012	FS-BPH	98	96	96
	BPH-EPH	52	9	0
	EPH-H	118	118	102
	Overall season	268	223	198
2012/2013	FS-BPH	95	75	75
	BPH-EPH	28	5	0
	EPH-H	103	103	80
	Overall season	226	183	155
2013/2014	FS-BPH	129	88	88
	BPH-EPH	12	6	0
	EPH-H	102	102	97
	Overall season	243	196	185

FS fruit set; BPH beginning of pit hardening (PH); EPH end of PH; H harvest

between 11.6 and 12.4 mm, 8.6 and 13.7 t ha⁻¹, 36.9% and 60.3%, and 1.8 and 3.2 t ha⁻¹, respectively. The lowest fruit and oil yields were observed in olive trees with ICO periods between 53 and 70 days without irrigation (T2 treatment). Under this water restriction period, fruit and oil yields were between 5.1 and 6.2 kg plant⁻¹ and 0.83–1.35 kg plant⁻¹, respectively. Finally, there was not a significant effect among seasons for fruit diameter and fruit yield, but oil content and total oil yield were significantly greater in 2011/2012 season than the other seasons.

Discussion

This study provides an assessment of the ability of olive trees in a superintensive orchard to recover from different degrees of water stress after ICO periods. All olive trees

had Ψ_{stem} values > -1.5 MPa when the ICO periods started from fruit set (approximately 20 days after full bloom) for the three growing seasons. Such values are typical of unstressed trees in late Spring under Mediterranean conditions (Dell'Amico et al. 2012; Corell et al. 2016). Most of the measured Ψ_{stem} values in the T0 treatment were above -2.5 MPa during the ICO periods, although some lower values were observed when the atmospheric demand was high during summer. Values of approximately -2.5 MPa during the period between fruit set and pit hardening (mid-summer) were recently reported in well-watered trees of two cultivars in Israel (Ben-Gal et al. 2021), while values of -2.5 MPa were considered to be the threshold at which a water deficit treatment should be irrigated in central Argentina (Trentacoste et al. 2015). For well-irrigated olive trees, Ahumada-Orellana et al. (2019) reported that water stress was considered to be mild or absent when Ψ_{stem} , g_s , and A_n values were approximately -2.0 MPa, 0.18 mol m⁻² s⁻¹, and 17.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. In addition, several reports suggested that Ψ_{stem} values from -2.5 to -3.5 MPa are appropriated to maintain adequate olive oil yield and quality (Naor et al. 2013; Trentacoste et al. 2015; Marra et al. 2016; Ahumada-Orellana et al. 2017, 2018). However, Trentacoste et al. (2019) and Fernandez et al. 2011 suggested that Ψ_{stem} values < -1.7 MPa can produce adverse effects on shoot growth and fruit oil filling periods and generate reductions in vegetative growth and oil yield (Trentacoste et al., 2019; Fernandez et al. 2011). In this regard, further research is needed to evaluate the effect of water stress applied in flowering, shoot growth, and fruit oil filling periods on the oil yield for drip-irrigated olive trees growing under water scarcity conditions.

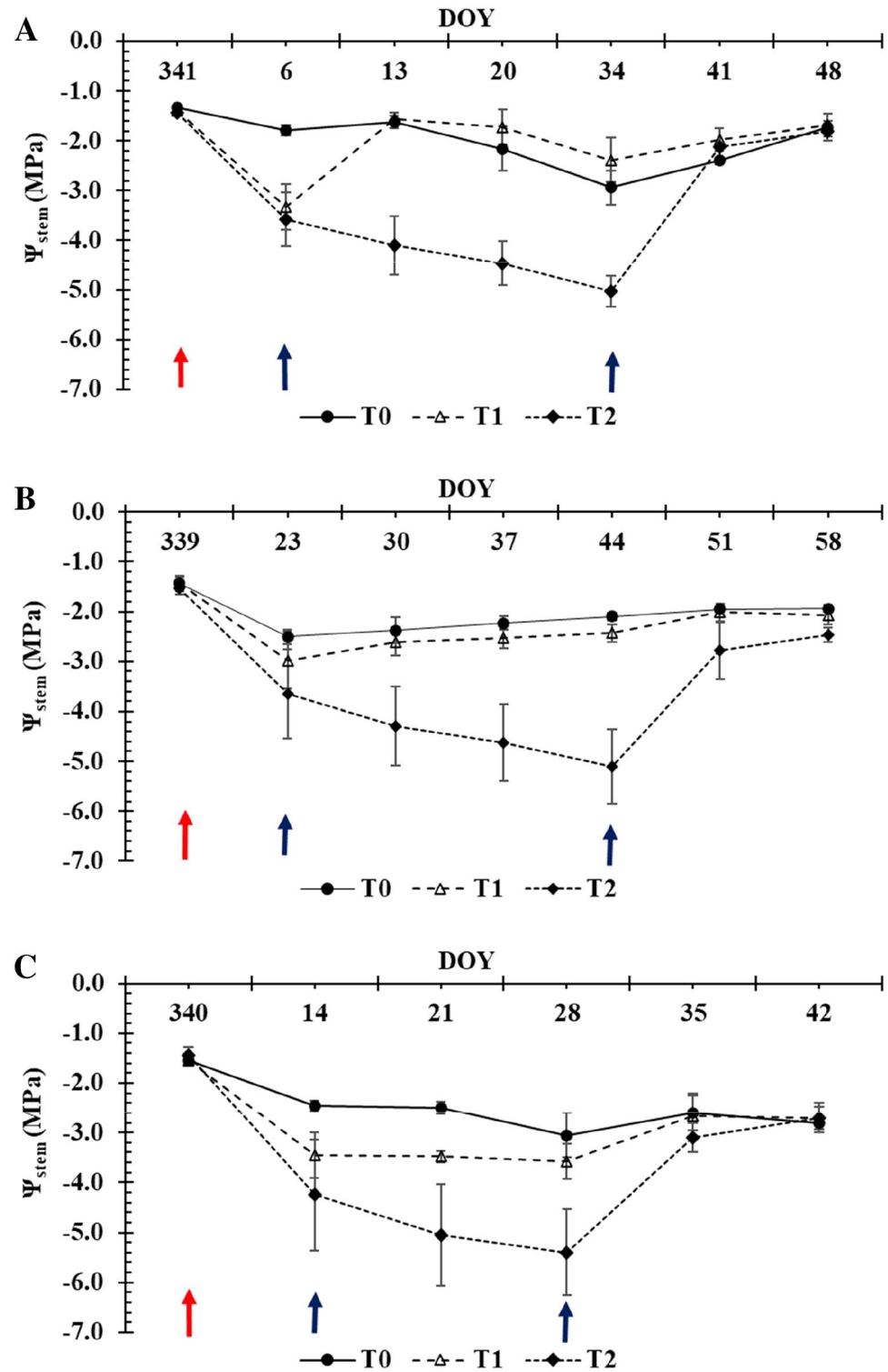
Moderate water stress was observed in the T1 treatment at the end of the ICO period (D0) with Ψ_{stem} values close to -3.0 MPa, and A_n and g_s values ranging between 11.22 – 12.31 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 0.08 – 0.15 mol m⁻² s⁻¹, respectively. A full recovery of Ψ_{stem} , A_n , and g_s was observed 7 days after rewatering in the first and second seasons, although the recovery was slower during the last

Table 4 Stem water potential (Ψ_{stem} , MPa), net assimilation (A_n , $\mu\text{mol m}^{-2} \text{s}^{-1}$), and stomatal conductance (g_s , mol m⁻² s⁻¹) for olive leaves at the beginning of the irrigation cut-off period

Treatments	Ψ_{stem}			A_n			g_s		
	2011–2012	2012–2013	2013–2014	2011–2012	2012–2013	2013–2014	2011–2012	2012–2013	2013–2014
T0	-1.34 a	-1.43 a	-1.55 a	18.23 a	18.61 a	17.81 a	0.24 a	0.20 a	0.19 a
T1	-1.40 a	-1.43 a	-1.55 a	17.75 a	18.88 a	16.54 a	0.22 a	0.20 a	0.18 a
T2	-1.44 a	-1.54 a	-1.45 a	17.50 a	18.83 a	15.65 a	0.22 a	0.20 a	0.16 a

Within each column, data followed by different letters are significantly different according to the Tukey multiple comparison test ($P < 0.05$)

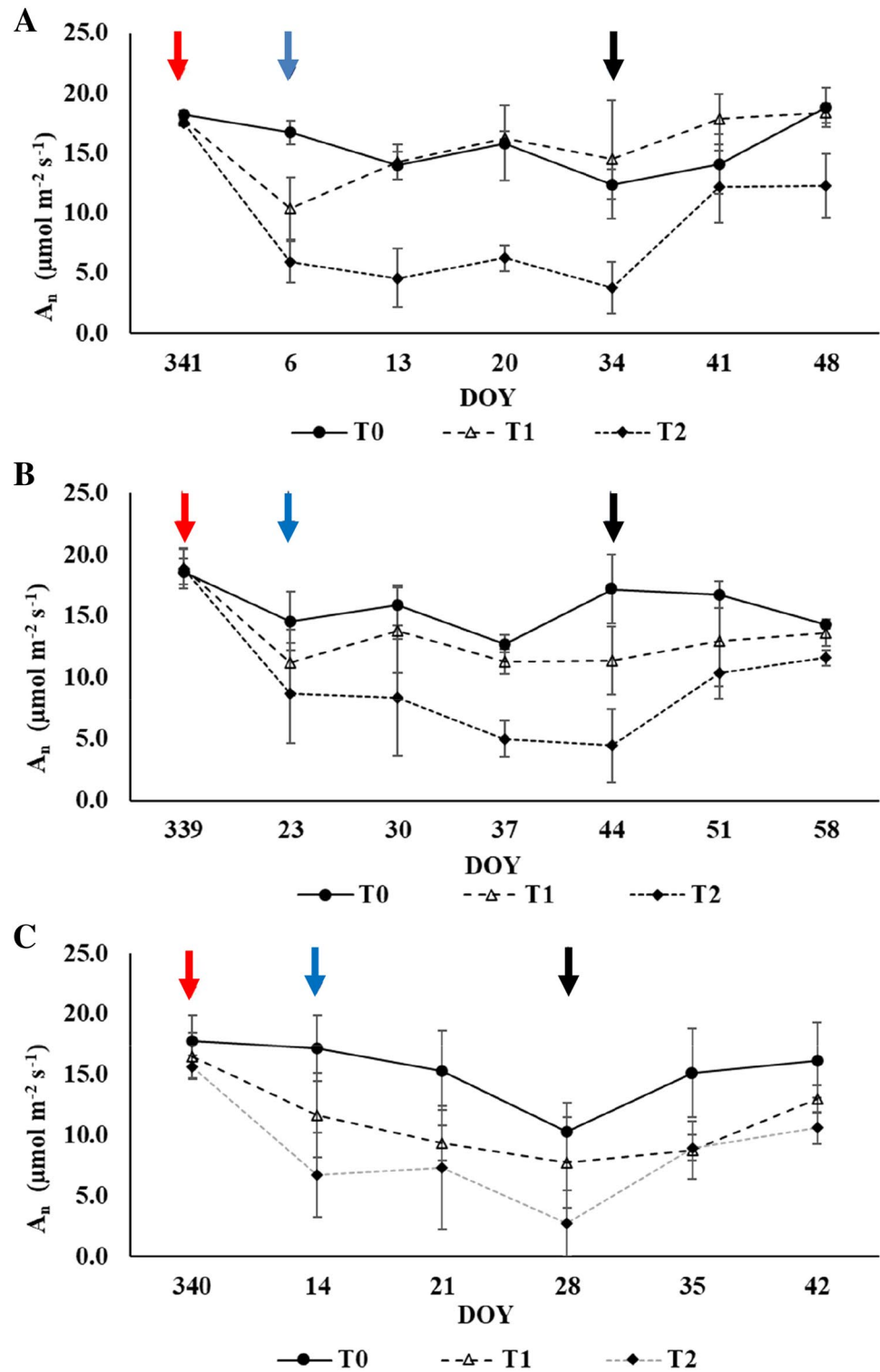
Fig. 3 Evolution of midday stem water potential (Ψ_{stem}) for each treatment during the 2011/2012 **A**, 2012/2013 **B**, and 2013/2014 **C** growing seasons. The red arrow indicates the beginning of the irrigation cut-off, while the blue and black arrows represent the beginning of rewatering for T1 and T2, respectively



season (2013/2014). For young olive trees under moderate water stress (-3.5 MPa) for a few days, Ben-Gal et al. (2010) reported that a full recovery of Ψ_{stem} and g_s was

observed within several days soon after water application was renewed, although Ψ_{stem} recovered faster (2 days) than g_s (4 days) (Ben-Gal et al. 2010). In a superintensive olive

Fig. 4 Evolution of net assimilation (A_n) for each treatment during the 2011/2012 **A**, 2012/2013 **B**, and 2013/2014 **C** growing seasons. The red arrow indicates the beginning of the irrigation cut-off, while the blue and black arrows represent the beginning of rewatering for T1 and T2, respectively



orchard (cv. Arbequina) in southern Spain, irrigation with 20–30% of water requirements during approximately two months during the summer led to moderately low values in

Ψ_{stem} between -2.5 to -3.5 MPa (Fernández et al. 2013). Upon rewatering with 100% of daily water needs, Ψ_{stem} partially recovered the first week and fully recovered within

Fig. 5 Evolution of stomatal conductance (g_s) for each treatment during the 2011/2012 **A**, 2012/2013 **B**, and 2013/2014 **C** growing seasons. The red arrow indicates the beginning of the irrigation cut-off, while the blue and black arrows represent the beginning of rewatering for T1 and T2, respectively

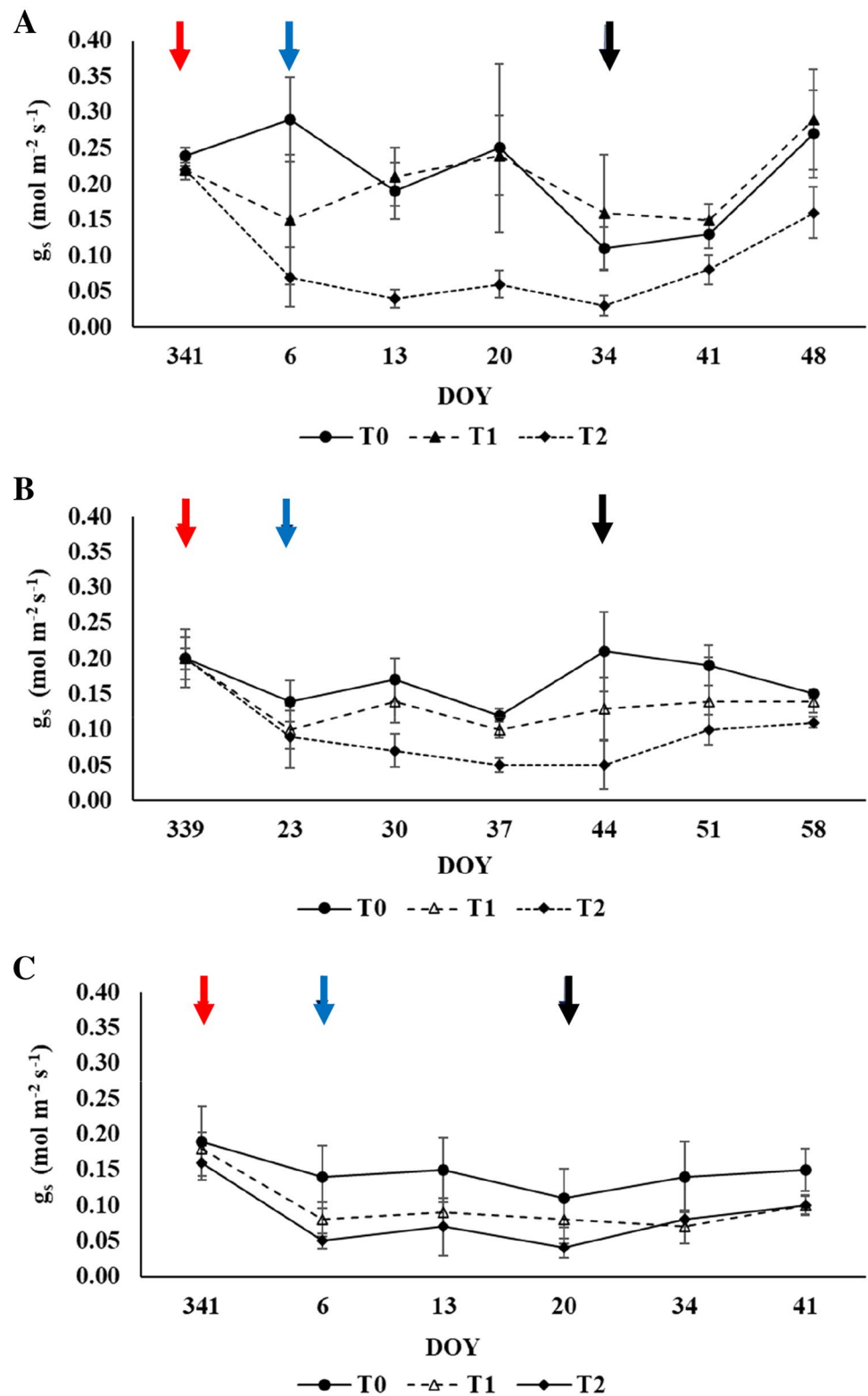


Table 5 Responses of stem water potential (Ψ_{stem} , MPa), net assimilation (A_n , $\mu\text{mol m}^{-2} \text{s}^{-1}$), and stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) in olive leaves at the end of the T1 treatment irrigation cut-off period (D0_T1) and 7 (D7_T1) and 14 (D14_T1) days after rewatering the T1 treatment. The T2 treatment remained without irrigation at this time

Ψ_{stem}	2011/2012			2012/2013			2013/2014		
	Treatment	D0_T1	D7_T1	D14_T1	D0_T1	D7_T1	D14_T1	D0_T1	D7_T1
T0	– 1.78 a	– 1.63 a	– 2.16 a	– 2.50 a	– 2.38 a	– 2.23 a	– 2.45 a	– 2.50 a	– 3.05 a
T1	– 3.33 b	– 1.55 a	– 1.73 a	– 2.98 b	– 2.60 a	– 2.52 a	– 3.45 b	– 3.48 a	– 3.58 a
T2	– 3.58 b	– 4.10 b	– 4.46 b	– 3.65 b	– 4.29 b	– 4.62 b	– 4.25 b	– 5.05 b	– 5.40 b
A_n									
Treatment									
T0	16.71 a	13.97 a	15.83 a	14.59 a	15.86 a	12.73 a	17.18 a	15.36 a	10.27 a
T1	10.38 b	14.25 a	16.23 a	11.22 b	13.82 a	11.30 a	11.67 b	9.37ab	7.75 a
T2	5.96 c	4.57 b	6.24 b	8.72 c	8.38 b	5.03 b	6.72 b	7.35 b	2.74 b
g_s									
Treatment									
T0	0.29 a	0.19 a	0.25 a	0.14 a	0.17 a	0.12 a	0.14 a	0.15 a	0.11 a
T1	0.15 b	0.21 a	0.24 a	0.10 b	0.14 a	0.10 a	0.08 b	0.09 ab	0.08 ab
T2	0.07 b	0.04 b	0.06 b	0.09 b	0.07 b	0.05 b	0.05 b	0.07 b	0.04 b

Within each column, data followed by different letters are significantly different according to the Tukey multiple comparison test ($P < 0.05$)

Table 6 Responses of stem water potential (Ψ_{stem} , MPa), net assimilation (A_n , $\mu\text{mol m}^{-2} \text{s}^{-1}$), and stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) in olive leaves at the end of the T2 treatment irrigation cut-off period (D0_T2) and 7 (D7_T2) and 14 (D14_T2) days after rewatering the T2 treatment. The T1 treatment was rewatered two weeks earlier

Ψ_{stem}	2011/2012			2012/2013			2013/2014		
	Treatments	D0_T2	D7_T2	D14_T2	D0_T2	D7_T2	D14_T2	D0_T2	D7_T2
T0	– 2.94 a	– 2.39 a	– 1.73 a	– 2.10 a	– 1.95 a	– 1.94 a	– 3.05 a	– 2.60 a	– 2.80 a
T1	– 2.38 a	– 1.98 a	– 1.69 a	– 2.43 a	– 2.01 a	– 2.07 a	– 3.58 a	– 2.67 a	– 2.70 a
T2	– 5.03 b	– 2.11 a	– 1.80 a	– 5.10 b	– 2.78 b	– 2.46 b	– 5.40 b	– 3.10 a	– 2.70 a
A_n									
Treatments									
T0	12.40 a	14.06 ab	18.81 a	17.19 a	16.71 a	14.33 a	10.27 a	15.14 a	16.19 a
T1	14.48 a	17.83 a	18.36 a	11.4 b	12.99 ab	13.63 a	7.75 ab	8.80 b	10.0 b
T2	3.78 b	12.18 b	12.28 b	4.45 c	10.40 b	11.58 b	2.74 b	8.98 b	10.63 b
g_s									
Treatments									
T0	0.11 ab	0.13 a	0.27 ab	0.21 a	0.19 a	0.15 a	0.11 a	0.14 a	0.15 a
T1	0.16 a	0.15 a	0.29 a	0.13 ab	0.14 ab	0.14 a	0.08 ab	0.07 b	0.10 b
T2	0.03 b	0.08 b	0.16 b	0.05 b	0.10 b	0.11 b	0.04 b	0.08 b	0.10 b

Within each column, data followed by different letters are significantly different according to the Tukey multiple comparison test ($P < 0.05$)

about 20 days. The g_s also recovered, but over a longer period in that study. Another field study with mature olive trees showed that Ψ_{stem} recovered at the end of the summer within a couple of weeks after experiencing an extended period of water stress with minimum Ψ_{stem} values of approximately -3.5 MPa (Corell et al. 2020). In that study, the recovery of g_s was difficult to evaluate because the g_s of all trees decreased toward the end of the season independent of the watering regime. Our results and other studies are largely consistent in showing that Ψ_{stem} and g_s of olive trees mostly

recover from moderate water stress. However, the dynamics of recovery appears to depend on the duration of the stress and other factors. In this regard, Pérez-López et al. (2008) indicated that the differences in the recovery of Ψ_{stem} and g_s were probably related to root flow suggesting that varying irrigation rates could provide a new means of controlling the length and intensity of water stress during the recovery period.

More severe water stress was observed at the end of the ICO periods for the T2 treatment with Ψ_{stem} ranging

Table 7 Responses of fruit diameter, fruit yield, oil content, and total oil yield in olive trees to irrigation cut-off period treatments for the 2011/2012, 2012/2013, and 2013/2014 growing seasons

Seasons	Treatments	Fruit diameter (mm)	Fruit yield (t ha ⁻¹)	Total oil content (dwb %)	Total oil yield (t ha ⁻¹)
2011/2012	T0	11.6 ab	11.1 a	60.3 a	3.2 a
	T1	11.8 a	11.3 a	57.4 a	2.7 a
	T2	11.1 b	8.3 b	52.7 b	1.8 b
2012/2013	T0	12.4 a	8.6 a	50.5 a	1.8 a
	T1	11.7 ^b	8.1 a	47.1 a	1.7 a
	T2	11.2 b	7.3 a	46.7 a	1.6 a
2013/2014	T0	12.2 a	13.7 a	36.9 a	2.2 a
	T1	11.5 b	9.8 b	38.9 a	1.7 a
	T2	11.1 b	6.8 b	37.3 a	1.1 b
Overall	2012/2013	11.8 a	8.0 a	48.10 b	1.7 b
	2013/2014	11.9 a	10.1 a	37.70 c	1.7 b

Within each column data followed by different letters are significantly different according to the Tukey multiple comparison test ($P < 0.05$)

between -5.0 and -5.4 MPa. For these low Ψ_{stem} values, A_n ranged from 2.74 to $4.45 \mu\text{mol m}^{-2} \text{s}^{-1}$ and g_s was from 0.03 to $0.05 \text{ mol m}^{-2} \text{s}^{-1}$. Several studies have indicated that severe water stress (Ψ_{stem} values between -4.0 and -5.0 MPa) in olive trees significantly reduces leaf gas exchange (Moriana et al. 2002; Trentacoste et al. 2018; Ahumada-Orellana et al. 2019). Under such conditions, Ahumada-Orellana et al. (2019) found that A_n in olive leaves decreased linearly with decreasing Ψ_{stem} . Although the Ψ_{stem} recovered fully with 7 days after rewatering in two of the three growing seasons, the gas exchange remained significantly lower after 14 days in all seasons than that in the T0 and T1 treatments. The A_n and g_s values in the T2 treatment were between 19 and 36% and 26 and 41% lower, respectively, than those in the T0 treatment. In a moderately high-density plantation ($625 \text{ trees ha}^{-1}$), Trabelsi et al. (2019) found that the A_n and g_s did not recover in mature olive leaves following a severe, summer water stress period with reductions in A_n of about 50%. However, young leaves showed a significant capacity to recover. Severe water stress could permanently damage leaf photosynthetic capacity and thus significantly reduce the response of A_n to rewatering or rainfall (Medrano et al. 2002; Boussadia et al. 2008). In our study, A_n and g_s in the T2 treatment did not completely recover after severe water stress at the end of ICO, which significantly reduced fruit and total oil yields for the three seasons. In this case, mean values of fruit yield in the T2 treatment were 30.4% and 22.7% lower than those in T0 and T1 treatments,

respectively. Also, the total oil yield in T2 treatment was between 25.2% and 34.0% lower than those for T0 and T1.

This study suggests that the T1 treatment allowed water savings (between 16.8% and 19.3%) due to the ICO period without negative effects on yields over three growing seasons. Marra et al. (2016) indicated that maintaining Ψ_{stem} values between -3.5 and -2.5 MPa is an optimal strategy for moderate yields with good oil quality. These authors also suggested that Ψ_{stem} values > -2.5 MPa were less effective at increasing productivity. In a 4-year study, Ahumada-Orellana et al. (2017, 2018) reported that an ICO strategy applied from fruit set until reaching a Ψ_{stem} threshold of approximately -3.5 MPa saved 20% of water without affecting yield or olive quality.

Conclusions

The results indicate that the responses of water status and gas exchange to rewatering after an ICO period depend on the severity of water stress prior to rewatering. When irrigation was cut-off for 30–49 days, all the measured physiological variables showed recovery from moderate water stress (Ψ_{stem} between -3.0 and -3.5 MPa), although the timing varied somewhat between growing seasons. With a longer ICO period (53–70 days) and more severe water stress (Ψ_{stem} between -5.0 and -5.4 MPa), the Ψ_{stem} fully recovered in most seasons after 14 days, but A_n and g_s always remained significantly lower than the control treatment which received irrigation the entire season. These results suggest that a Ψ_{stem} threshold between -3.0 and -3.5 MPa from fruit set to end of pit hardening in superintensive olive (cv. Arbequina) orchards allows for rapid recovery of photosynthesis, good oil yields, and an almost 20% water savings under Mediterranean climate conditions over several growing seasons. Further research should focus on whether such findings differ by cultivar and climatic conditions.

Acknowledgements This study was supported by the Chilean government through the projects CONICYT "Programa Formación de Capital Humano Avanzado" (21120443), FONDECYT (1130729), and FONDEF (N D10I1157).

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