Leaf mechanisms involved in the response of *Cydonia oblonga* trees to water stress and recovery

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ABSTRACT

Quince tree (*Cydonia oblonga* Mill.) is known for bearing fruits that are rich in nutrients and health-promoting compounds while requiring low inputs of agrochemicals, and maintenance, but no information exists on the mechanisms developed at the level of leaf water relations to confront water stress and recovery. For this reason, the purpose of the present study was to identify the strategy (isohydric or anisohydric) by which quince plants cope with water stress and to further elucidate the resistance mechanisms developed in response to water stress and during recovery. In summer 2016, field-grown own rooted 17-years old quince trees (cv. BA-29) were subjected to two irrigation treatments. Control (T0) plants were drip irrigated (105% ETo) to ensure non-limiting soil water conditions, while T1 plants were irrigated at the same level as used in T0, except that irrigation was withheld for 42 days during the linear fruit growth phase, after which irrigation returned to the levels of T0 (recovery period). During the experimental period, T0 and T1 received a total of 374 and 143 mm water, respectively, including rain water. The quince trees exhibited extreme anisohydric behaviour under the experimental conditions. As water stress developed and during the recovery period, the plants exhibited high hydraulic conductivity, probably the result of resistance to cavitation. From the beginning of water stress to the time of maximum water stress, leaf turgor was maintained, possibly due to active osmotic adjustment (stress tolerance mechanism). This leaf turgor maintenance may have contributed to the high leaf conductance, and, therefore, good leaf productivity. The low quince leaf apoplastic water fraction under water stress could be considered as another drought tolerance characteristic because if the accumulation of water in the apoplasm is avoided a steeper gradient in water potential between the leaf and the soil can take place under water stress, thus favouring water absorption.

1. Introduction

Modern agricultural systems have promoted the cultivation of high-input and high-yielding crop species, leading to the intense cultivation of a restricted number of species and a decline in the cultivation of many traditional fruit crops, resulting in a worldwide reduction in crop diversity (Chivenge et al., 2015). However, many of these neglected or underutilized species are not only critical for the diversity of human diets, but can also contribute to increasing food production, providing a more sustainable and resilient agro- and horti-food system (Baldermann et al., 2016). In view of the likelihood that climate change will generate more frequent and severe drought periods, one effective measure to attain sustainable agriculture in arid and semiarid agrosystems might be to introduce underutilized crop species, cultivars and even rootstocks that require low inputs of both agrochemicals and water, while providing attractive fruits that are rich in nutrients and health-promoting compounds.

Quince (*Cydonia oblonga* Mill.) is one example of an underutilized crop species. A shrub or small deciduous tree, quince is a member of the genus *Cydonia* in the family Rosaceae, subfamily Spiraeoideae, tribe Pyreae and subtribe Pyrinae (Postdam, 2012), along with apple (*Malus* sp.) and pear (*Pyrus* sp.). It is thought to originate in the foothills of the trans-Caucasus region including Armenia, Azerbaijan, Iran, south-western Russia, and Turkmenistan. Many of the cultivars described over 100 years ago are still cultivated today (Postdam, 2012). Quince does not require intensive maintenance and can grow in many warm-temperate and temperate regions of the world. It has also become a key factor for other crop cultures, being, for instance, the most important rootstock for pear cultivation (Gur et al., 1978).

Quince fruit is a member of the pome fruit species. Its fruits are climacteric, with a pear or apple shape and attractive golden yellow colour. Quince fruits have excessive astringency, sourness and woodiness at harvest, but a pleasant, lasting, and powerful flavour when ripe (Szychowski et al., 2014). In many countries, quince-based products such as jam, jelly, cakes and liquors are much appreciated. The most distinguishing characteristics of quince fruit are its low fat content and very high content of organic acids, sugars, crude fibre, minerals and health-promoting constituents with antioxidant effects (Silva et al., 2004; Fattouch et al., 2007; Shinomiya et al., 2009). Quince fruits are also known for their hypoglycemic, anti-inflammatory, anticarcinogenic, antimicrobial, anti-allergic and antiulcerative properties and the ability to act as a tonic for heart and brain (Hamauzu et al., 2005; Shinomiya et al., 2009; Gur et al., 1978). Despite these many desirable characteristics, consumption of the fresh quince fruit or quince-based products is not widespread.

However, to date, despite the very important advantages to be had as a result of eating quince and the ever more frequent water shortages experienced in the most suitable regions for its growth, the leaf water relations of quince trees in response to drought are unclear. In this sense, Galindo et al. (2018) suggested that fruit trees present different mechanisms to confront water deficit, even though most of them at leaf level resist dehydration through drought avoidance and tolerance mechanisms (Torrecillas et al., 2018). For this, the research reported in this paper was conducted to test the hypothesis that i) quince trees at leaf level resist dehydration through drought avoidance and tolerance mechanisms, and that ii) quince plants are able to improve their water stress resistance by means of an anisohydric strategy.

2. Materials and methods

2.1. Experimental conditions, plant material and treatments

The experimental plot was located at the farm of the Miguel Hernández Polytechnic University of Elche, near the city of Orihuela (Spain) (38° 4'N, 0° 59'W). The soil was a clay loam Xerofluvent (Soil Survey Staff, 2006), which showed high active calcium carbonate and

Table 1
Soil characteristics of the experimental plot.

Parameters[*]	
pH	8.37
Electrical conductivity (dS m^{-1})	0.46
Sand (%)	26.2
Loam (%)	37.2
Clay (%)	36.6
Active CaCO$_3$ (%)	13.6
Oxidisable organic C (g kg^{-1})	9.67
Total Kjeldahl N (g kg^{-1})	1.44
Available P (mg kg^{-1})	64
Exchangeable K (g kg^{-1})	0.44
Exchangeable Ca (g kg^{-1})	3.67
Exchangeable Mg (g kg^{-1})	0.65

[*] Values on a dry matter basis.

low organic matter content, electrical conductivity, available phosphorus and potassium exchange levels (Table 1). The irrigation water had a Cl^- concentration of 71–84 mg L^{-1} and an electrical conductivity of between 1.4 and 1.6 dS m^{-1}. The plant material consisted of own rooted 17-year old quince trees (*C. oblonga* Mill.), cv. BA-29, planted at 4 m × 5 m. Pest control and fertilization practices were those typically used by local farmers; no weeds were allowed to develop within the orchard using herbicides. Air temperature, solar radiation, air relative humidity, wind speed (2 m above the soil surface) and rainfall were recorded every 15 min by an automatic micrometereological station located near the experimental site. Mean daily air vapour pressure deficit (VPDm, kPa) and ETo (mm) were calculated according to Allen et al. (1998).

The experiment had a randomized complete block design, with two treatments and four replications. Control plants (T0) were irrigated daily during the night using a drip irrigation system with one lateral line per tree row and six emitters (each delivering 3 l h^{-1}) per plant to ensure non-limiting soil water conditions (105% ETo). T1 plants were irrigated as T0, except that irrigation was withheld during the linear fruit growth phase (day of the 2016 year (DOY) 209–251), before restoring irrigation at the same level as used in T0 from DOY 251–266 (recovery period). During the experimental period, T0 and T1 received a total of 374 and 143 mm water, respectively, including rain water. Each experimental plot consisting of three adjacent tree rows, each with seven trees very similar in appearance (ground shaded area, height, leaf area, trunk cross sectional area, etc.). The inner plants of the central row of each replicate were used for measurements.

2.2. Measurements

Indicators of leaf water relations were measured at midday (12 h solar time) and hourly throughout DOY 224, 238 and 251, using fully expanded leaves from the south-facing side and middle third of the tree. Leaf conductance (g_{leaf}) was measured in two leaves per tree, using a porometer (Delta T AP4, Delta-T Devices, Cambridge, UK) on the abaxial surface. Leaf water potential (Ψ_{leaf}) was measured in two leaves per tree, using a pressure chamber (PMS 600-EXP, PMS Instruments Company, Albany, USA), as recommended by Turner (1988). Midday (12 h solar time) stem water potential (Ψ_{stem}) was measured in a similar number and type of leaves as those used for Ψ_{leaf}, enclosing leaves in a small black plastic bag covered with aluminium foil for at least 2 h before measurements in the pressure chamber (Fulton et al., 2001; Shackel, 2011). Ψ_{leaf}, Ψ_{stem} and g_{leaf} were measured in two leaves per replicate in order to improve the representativeness and accuracy of the data and to decrease statistical bias. The values for each replicate were averaged.

After measuring predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potentials, the leaves were frozen in liquid nitrogen and the osmotic potentials (Ψ_{spd} and Ψ_{smd}, respectively) were measured after thawing the

samples and expressing sap, using a vapour pressure osmometer (Wescor 5600, Logan, USA). Predawn (Ψ_{ppd}) and midday (Ψ_{pmd}) leaf turgor potentials were derived as the difference between osmotic and water potentials.

Estimates of predawn leaf osmotic potential at full turgor (Ψ_{os}), leaf water potential at turgor loss point (Ψ_{tlp}), leaf bulk modulus of elasticity (€), relative water content at turgor loss point (RWC_{tlp}) and relative apoplastic water content (RWC_a) were obtained from pressure-volume (PV) analyses of leaves (Tyree and Hammel, 1972; Tyree and Richter, 1981; Tyree and Richter, 1982. At the end of the stress period, 10 leaves per replicate were sealed in plastic bags immediately after excision and resaturated by dipping their petioles in distilled water for 24 h at 4 °C. The resaturated leaves were weighed using an analytical balance (± 0.1 mg precision), placed in the pressure chamber (lined with damp filter paper) and slowly pressurized (0.025 MPa s^{-1}) until the balance pressure was reached (when the leaf sap appeared through the cut petiole protruding from the chamber). After being depressurized, the leaf was allowed to transpire outside the pressure chamber on the laboratory bench at room temperature (22 ± 2 °C). Leaves were repeatedly weighed and their balance pressures determined over the full range of the pressure gauge (Kikuta and Richter, 1986). Data for initial saturated weight, intermediate fresh weight (corresponding to values for Ψ_{leaf}), and final dry weight (at 80 °C for 48 h) were used to calculate the relative water content (RWC) (Barrs and Weatherley, 1962).

The curves were drawn using a type II transformation (Tyree and Richter, 1982). When the reciprocal of water potential (Ψ_{leaf}) was plotted against RWC, the resultant relationships displayed both linear and non-linear regions. Extrapolation on the straight portion of the curve obtained for a value of RWC = 1 gave the reciprocal of the Ψ_{os} and extrapolation to the abscissa gave RWC_a. Ψ_{tlp} and RWC_{tlp} were estimated as the intersection between the linear and curvilinear portions of the PV curve. The bulk modulus of elasticity (€) of leaf tissue at 100% RWC (RWC_o) was estimated according to Patakas and Noitsakis (1999) as € (MPa) = (Ψ_{os} - Ψ_{stlp})(100 -RWC_a)/(100 - RWC_{tlp}), where Ψ_{stlp} is the osmotic potential at the turgor loss point and Ψ_{os} values correspond to those obtained from the analysis of the PV curves.

The methodology proposed by Martínez-Vilalta et al. (2014) was used to categorize the strategy (isohydric or anisohydric) by means of which quince plants cope with drought stress. The above authors assumed that, within biologically reasonable ranges of water potentials, the relationship between soil water potential (Ψ_s) and minimum leaf water potential (Ψ_L) becomes linear ($\Psi_L \approx \Lambda + \sigma \Psi_s$), assuming that soil and plant water potential equilibrate overnight so that Ψ_{pd} and Ψ_{md} are proxies of Ψ_s and Ψ_L, respectively. The slope (σ) indicates the rate of reduction in Ψ_L as Ψ_s declines. Specifically, (i) when Ψ_L remains constant as Ψ_s diminishes ($\sigma = 0$), plants show a strictly isohydric behaviour, (ii) when the difference between Ψ_L and Ψ_s remains constant ($\sigma = 1$), plants show a strictly anisohydric behaviour, (iii) when the difference between Ψ_L and Ψ_s is reduced as Ψ_s diminishes ($0 < \sigma < 1$), plants show a partial isohydric behaviour, and (iv) when the pressure drop increases through the plant as Ψ_s diminishes ($\sigma > 1$), plants show an extremely anisohydric behaviour.

2.3. Statistical analysis

Statistical analysis was performed by an analysis of variance (ANOVA) using the general linear model (GLM) of SPSS v. 12.0 (SPSS Inc., 2002), for which an independent variable (irrigation), having two different levels (T0 and T1), was considered. To check statistical hypothesis (linearity, homoscedasticity, normality and independency) Kolmogorov–Smirnov with the Liliefors correction was used. Shapiro–Wilk and Levene tests were used to evaluate normality and homoscedasticity on the typified residuals, respectively. Independency was assumed by the experimental desing. Regression analysis was made for Ψ_{pd} and Ψ_{md} values with average data of each treatment by date, and statistical hypothesis was checked as for ANOVA.
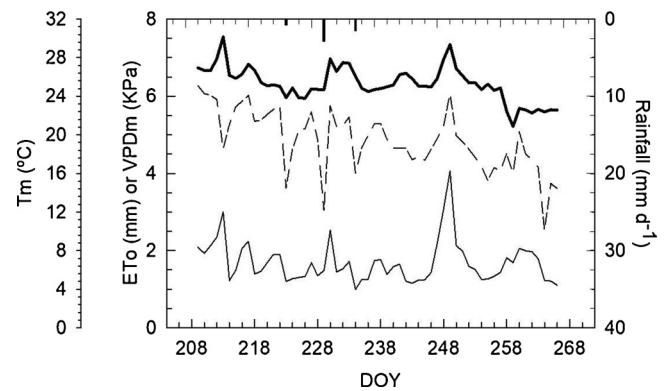

Fig. 1. Daily crop reference evapotranspiration (ETo, medium-medium line), daily mean air temperature (Tm, solid line), mean daily air vapour pressure deficit (VPDm) (thin line) and daily rainfall (vertical bars) during the experimental period.

3. Results

The experimental period (DOY 209–266) was characterized by a VPDm ranging from 0.99 to 4.06 kPa, 282 mm of ETo, 5 mm of rainfall, which occurred mainly on DOY 229 (4 mm) (Fig. 1) and average daily maximum and minimum air temperatures of 32 and 19 °C respectively (data not shown). In other words, the climate of the area was typically Mediterranean, hot and dry during the summer with very scarce rainfall.

During the water stress period, the Ψ_{pd} values showed significant differences between treatments, the Ψ_{pd} values in T0 plants being significantly higher than those in T1 plants (Fig. 2A). The Ψ_{pd} values of the T0 plants were high and showed minimal fluctuations during the experimental period, with average values of -0.48 MPa, whereas the Ψ_{pd} values in T1 plants showed a tendency to decrease during the water withholding period, reaching minimum values at the end of this period (-1.27 MPa) and showing similar values to those of T0 plants at the end of the recovery period (Fig. 2A).

Ψ_{md} values in T0 and T1 plants tended to decrease during the water stress period, even though Ψ_{md} values in T0 plants were higher than those in T1 plants, except on DOY 217 and 238 (Fig. 2B). At the end of the water stress period, plants from both treatments had very low Ψ_{md} values of -3.15 and -3.75 MPa, respectively. When irrigation in T1 plants resumed, Ψ_{md} values recovered to reach similar values to those observed in T0 plants (Fig. 2B).

Ψ_{ppd} and Ψ_{pmd} values in T0 and T1 plants were always above zero, which indicates how turgor was maintained throughout the experimental period (Fig. 2C and D). Ψ_{ppd} values in T0 plants fluctuated moderately, showing average values of 1.49 MPa, whereas Ψ_{ppd} values in T1 plants decreased to reach values of 1.10 MPa at the end of the irrigation water withholding period but recovered when irrigation resumed. No differences between treatments were found in Ψ_{pmd} values, which fell in both plant treatments during the measurement period, reaching values of only 0.07 MPa and increasing slightly when irrigation was restarted in T1 plants.

Ψ_{stem} values in T0 and T1 plants showed a qualitative behaviour very similar to that shown by Ψ_{md} values during the experimental period, even though Ψ_{stem} values in both irrigation treatments were higher than the corresponding Ψ_{md} values Figs. 2B and 3 A). The Ψ_{stem} values of T1 plants had decreased by DOY 217, remaining lower than the corresponding values in T0 plants from that date onwards, except on DOY 224 and 231, reaching values of -2.35 MPa at the end of the stress period and recovering when irrigation resumed (Fig. 3A).

Midday leaf conductance (g_{lmd}) values in T0 plants were high and fairly constant throughout the experimental period, showing average values of 323 mmol m^{-2} s^{-1} (Fig. 3B). In contrast, water stress induced a gradual reduction in g_{lmd} values, before recovering when irrigation
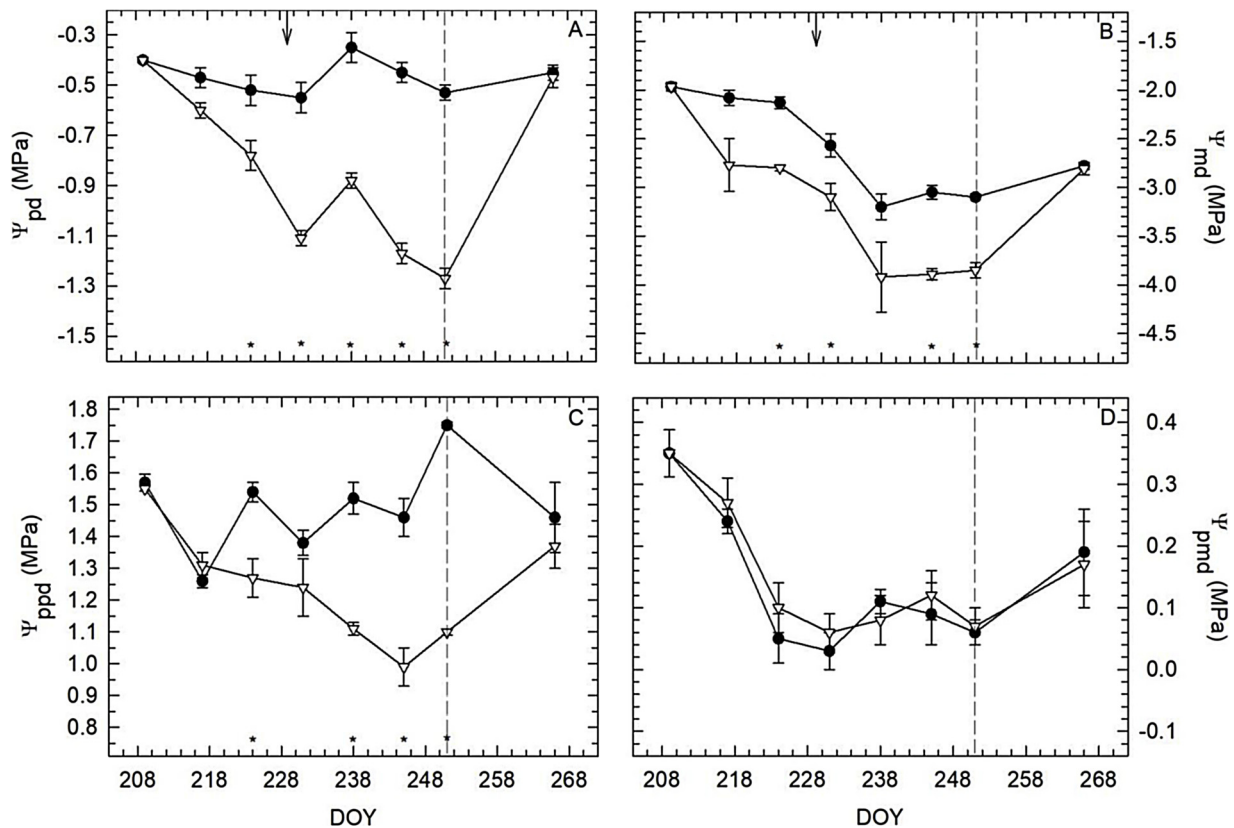
Fig. 2. Predawn (Ψ_{pd}, A) and midday (Ψ_{md} B) leaf water potential, and predawn (Ψ_{ppd}, C) and midday (Ψ_{pmd}, D) leaf turgor potential values (mean ± SE, not shown when smaller than symbols, n = 4) for quince plants in T0 (closed circles) and T1 (open triangles) treatments during the experimental period. Asterisks indicate significant differences between treatments at $P = 0.001$ (*). Vertical dashed line indicates the end of the water stress period. Arrows in A and B indicate daily rainfall events.

resumed. This reduction during the stress period can be considered as moderate because average g_{lmd} values in T1 plants decreased by 31%, although at the end of water withholding period g_{lmd} values of 178 mmol m^{-2} s^{-1} were recorded (Fig. 3B).

During the water withholding period, Ψ_{leaf} values in T0 and T1 plants on DOY 224, 238 and 251 showed significant differences between treatments but a very similar daily time course, which was characterized by a gradual decrease in Ψ_{leaf} values during the early morning, reaching minimum values at around (13:00 - 15:00 h) and recovering in the afternoon (Fig. 4). On DOY 224, 238 and 251, these minimum Ψ_{leaf} values in T0 plants were -3.03, -3.20 and -3.15 MPa, respectively, and in T1 plants they were -3.32, -3.92 and -3.75 MPa, respectively. Differences between treatments in leaf

turgor values ($\Psi_{p\ leaf}$) were lower than those observed for Ψ_{leaf} values, and occurred mainly during the early morning and late afternoon (Fig. 4). $\Psi_{p\ leaf}$ values presented a diurnal time course very similar to that exhibited by Ψ_{leaf} values, even though daily minimum $\Psi_{p\ leaf}$ values, which stabilized from 13:00 to 15:00 h, were very low and ranged between 0.05 and 0.11 MPa (Fig. 4).

The circadian rhythm of g_{leaf} values in T0 plants was characterized by an increase around sunrise because of the stomata opening, a peak at around 10:00 h, followed by a slight decreased and stable values until late afternoon. In response to the withholding of irrigation water, g_{leaf} values in T1 plants showed low diurnal time course changes, these values being significantly lower than those observed in T0 plants (Fig. 4).
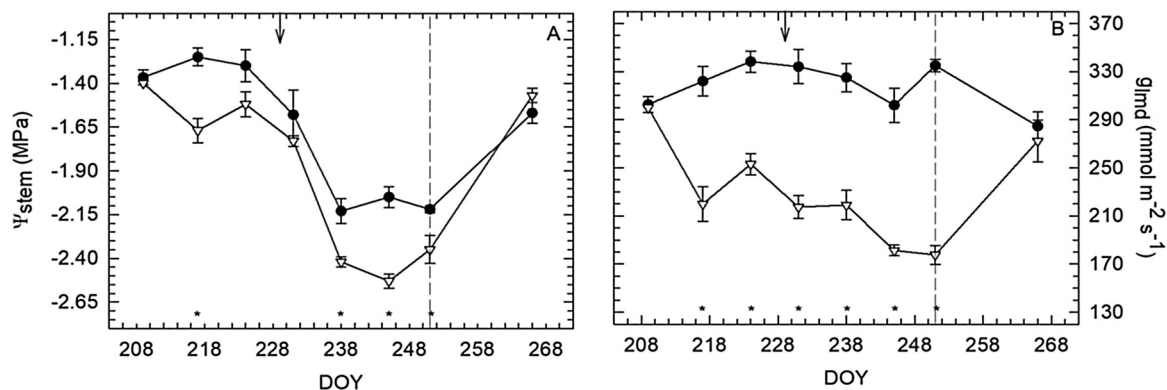
Fig. 3. Midday stem water potential (Ψ_{stem}, A) and midday leaf conductance (g_{lmd}, B) values for quince plants in T0 and T1 treatments during the experimental period. Symbols as in Fig. 2.
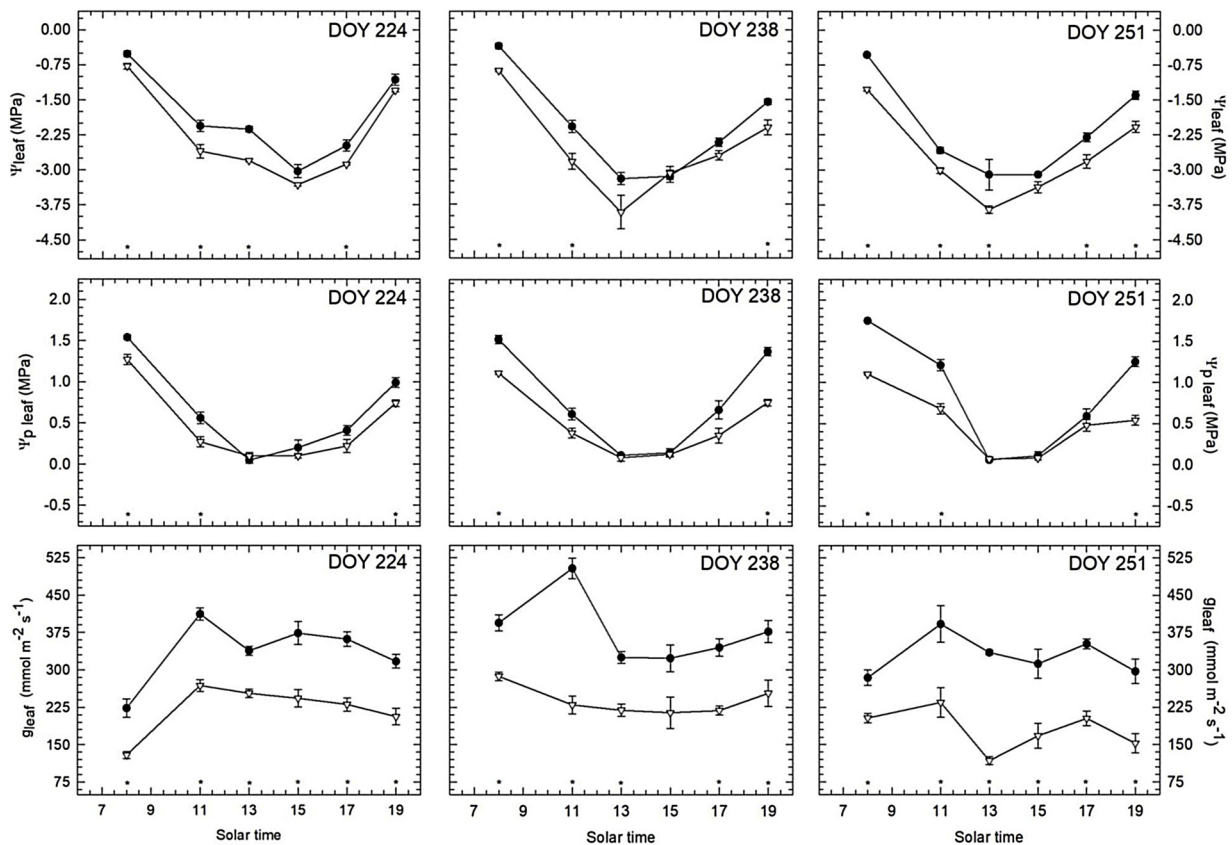
Fig. 4. Diurnal course of leaf water potential (Ψ_{leaf}), turgor potential ($\Psi_{p\ leaf}$) and leaf conductance (g_{leaf}) values for quince plants in T0 and T1 treatments at three different times during the stress period (DOY 224, 238, 251). Symbols as in Fig. 2.
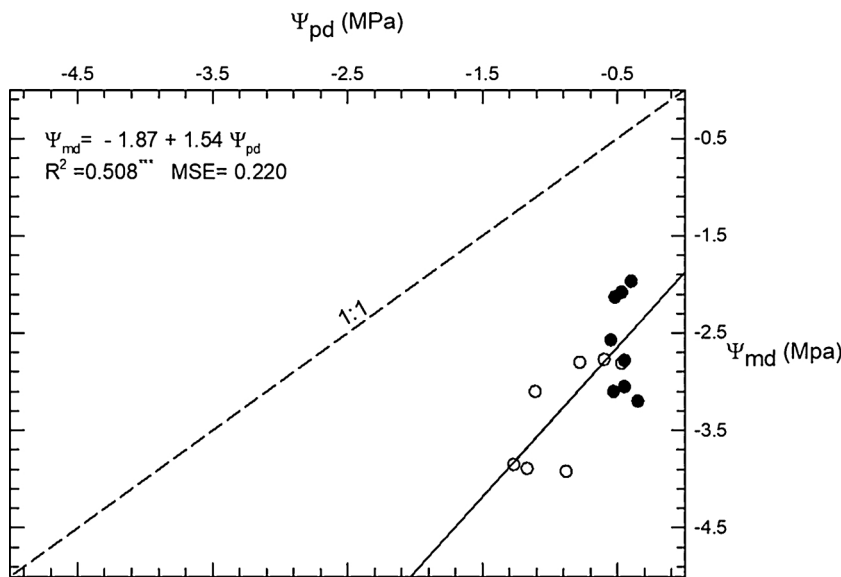

Fig. 5. Relationship between predawn (Ψ_{pd}), and midday (Ψ_{md}) leaf water potentials, for quince plants in T0 (closed circles) and T1 (open circles), according to the theoretical model of Martínez-Vilalta et al. (2014), which assumes a linear relationship with four different behaviours, all sharing the same intercept: strictly isohydric (σ (slope) = 0), partially isohydric ($0 < \sigma < 1$), strictly anisohydric ($\sigma = 1$) and extremely anisohydric ($\sigma < 1$). Each value is the mean of four replicates.

The relation between Ψ_{pd} and Ψ_{md} (Fig. 5), which is used to define the ability of stomata to regulate the leaf water potential, or, in other words, the isohydric/anisohydric behaviour, showed a slope (σ) higher than unity. For this reason, under the studied experimental conditions, quince plants can be said to have exhibited an extreme anisohydric behaviour in response to drought stress.

On DOY 251, the last day of the irrigation water withholding period, Ψ_{os} values were lower in T1 than in T0 plants. However, no significant differences in Ψ_{tlp}, ε, RWC_{tlp} or RWC_a values were found between treatments (Table 2). In addition, it should be noted that Ψ_{tlp} values in

both treatments were very low (Table 2).

4. Discussion

The fact that Ψ_{pd} values, which depend on soil moisture levels (Elfving et al., 1972), in control plants (T0) were high and near constant during the experimental period (Fig. 2A) indicated that the irrigation applied to this treatment was sufficient to avoid any water deficit. In contrast, Ψ_{pd}, Ψ_{md} and Ψ_{stem} values in T1 plants decreased at a relatively low rate (0.02, 0.04 and 0.02 MPa d^{-1}, respectively) (Hale

Table 2

Effect of water stress on leaf osmotic potential at full turgor (Ψ_{os}), leaf osmotic potential at turgor loss point (Ψ_{tlp}), leaf bulk modulus of elasticity (Є), relative water content at turgor loss point (RWC_{tlp}) and relative apoplastic water content (RWC_a) of quince plants in T0 and T1 treatments at the end of the water withholding period. Means with different letter across each row differ significantly at $P = 0.05$ (n = 4).

Parameters	T0	T1
Ψ_{os} (MPa)	−1.66b	−1.88a
Ψ_{tlp} (MPa)	−4.76	−4.56
Є (MPa)	4.66	4.52
RWC_{tlp} (%)	45.33	44.91
RWC_a (%)	18.18	19.31

and Orcutt, 1987), achieving severe water stress levels (Figs. 2A, B and 3 A).

Under water stress conditions, the large differences between Ψ_{pd} and Ψ_{md} values in T1 plants (Fig. 2A and B) and the recovery of the low Ψ_{pd}, Ψ_{md} and Ψ_{stem} values when they were rewatered (Figs. 2A, B and 3 A) has also been observed in other crops subjected to severe water stress (Torrecillas et al., 1996; Ruiz-Sánchez et al., 1997; Rodríguez et al., 2012 and may be related with high hydraulic conductivity, probably as a result of the resistance to cavitation observed in anisohydric plants (Ewers et al., 2005; Alsina et al., 2007).

In T1 plants, the gradual reduction in g_{lmd} values from the beginning of the stress period (Fig. 3B) can be considered as a primary response to irrigation water withholding, which improves water use efficiency (Rodríguez et al., 2012; Rieger and Duemmel, 1992). The low level of stomatal regulation (Figs. 3B and 4), even when minimum Ψ_s levels (estimated as Ψ_{pd} values) were achieved (Figs. 2A, 3 B and 4), led to pronounced decreases in Ψ_{md} values in T1 plants. The Ψ_{md} values in T0 and T1 plants correlated with Ψ_{pd} values and showed a slope higher than unity (σ = 1.54) (Fig. 5). For this reason, and in agreement with Martínez-Vilalta et al. (2014), quince plants can be categorized as being extremely anisohydric, which improves the drought resistance of the crop (Sade et al., 2012). In this respect, in addition to the above mentioned advantage of being more resistant to cavitation, which permits anisohydric plants to recover rapidly following exposure to water stress, the low rate of stomatal regulation in such plants facilitates higher rates of leaf gas exchange than in isohydric plants (Franks et al., 2007).

Whatever the case, it is important to underline that, as Klein (2014) and Martínez-Vilalta et al. (2014) indicated, very few plant species conform strictly to the definitions of isohydric or anisohydric plants because plant species are ordered on a continuum, along which individual species can move in response not only of their physiological characteristics but also to those in which they grow and the conditions to which they are exposed at any given moment (Schultz, 2003; Domec and Johnson, 2012; Rogiers et al., 2012). Because of this, some plants can shift from being anisohydric to isohydric, depending on Ψ_s (Domec and Johnson, 2012).

The Ψ_{os} values decrease (0.22 MPa) in T1 quince leaves indicated an active accumulation of osmolytes and, consequently, an active osmotic adjustments (Table 2). Similar behaviours have been observed in other fruit trees such as apple (Wang et al., 1995), apricot (Torrecillas et al., 1999), cherry (Ranney et al., 1991), jujube (Cruz et al., 2012), peach (Steinberg et al., 1989; Arndt et al., 2000) and pomegranate (Rodríguez et al., 2012). In this sense, it is known that osmoregulation takes place mainly when water stress develops gradually over a prolonged period (Arndt et al., 2000), as in our experimental conditions, and it varies depending on the species and cultivar (Torrecillas et al., 1996; Lakso, 1990).

The maintenance of turgor in T1 plants even at maximum water deficit levels (Fig. 2C and D), when g_{lmd} values remained considerable (Figs. 3B and 4), suggested that active osmoregulation contributed to maintaining quince leaf turgor (Ψ_{ppd} and Ψ_{pmd} above zero) (Fig. 2C and

D). While the level of osmotic adjustment contributed to leaf turgor maintenance, it was not sufficient to modify the Ψ_{tlp} values (Table 2). Other authors observed no changes in Ψ_{tlp} values despite the fact that these woody crops developed osmoregulation (Rodríguez et al., 2012; Cruz et al., 2012; Mellisho et al., 2011).

Contrary to the behaviour observed in *Citrus* (Savé et al., 1995) and avocado (Sharon et al., 2001), quince plants were not able to develop elastic adjustment (decrease in Є) in T1 plants due to the effect of a water deficit (Table 2). Also, the similar behaviours observed for Є and RWC_{tlp} values agree with the results of Savé et al. (1995), who suggested that Є controlled RWC_{tlp}. Whatever the case, when plants are rehydrated after a water stress period, the maintenance of or an increase in cell wall rigidity may be necessary to maintain cell tissue integrity in species that show osmotic adjustment (Clifford et al., 1998; Álvarez et al., 2009).

The RWC_a values in quince plants of 18–19 % (Table 2), were lower than those found in other fruit trees (Rodrigues et al., 1993; Torrecillas et al., 1996, 1999; Mellisho et al., 2011; Cruz et al., 2012; Rodríguez et al., 2012) as a consequence of thinner cell walls or differences in cell wall structure (Hellkvist et al., 1974). In contrast with observations made in other woody crops (Cruz et al., 2012), the consistently low leaf apoplastic water fraction in quince exposed to water stress prevents the accumulation of water in the apoplasm, leading to lower leaf water potential values and, as a consequence, a steeper gradient in water potential between the leaf and the soil, thus favouring water absorption.

The above results indicated that under our experimental conditions quince trees were characterized by an extreme anisohydric behaviour. During the development of the severe water stress and recovery periods, the plants suggested high hydraulic conductivity, probably because of the resistance to cavitation. From the beginning of water stress to the time of maximum water stress, leaf turgor was maintained probably due to the contribution of the active osmotic adjustment (stress tolerance mechanism). This leaf turgor maintenance would allow substantial leaf conductance levels and, therefore, good leaf productivity. This constantly low quince leaf apoplastic water fraction under water stress could be considered as another drought tolerance characteristic because, if water is prevented from accumulating in the apoplasm, a steeper gradient in water potential between the leaf and the soil may occur during water stress, thus favouring water absorption.

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