Agricultural Water Management

Jujube fruit water relations at fruit maturation in response to water deficits

A. Galindo , Z.N. Cruz , P. Rodríguez , J. Collado-González , M. Corell , H. Memmi ,
F. Moreno , A. Moriana , A. Torrecillas , D. Pérez-López

A B S T R A C T

The fruit maturation stage is considered the optimal phenological stage for implementing water deficit in jujube (*Zizyphus jujuba* Mill.), since a low, moderate or severe water deficit at this time has no effect on yield, fruit volume or eating quality. However, no information exists at fruit water relations level on the mechanisms developed by *Z. jujuba* to confront drought. The purpose of the present study was to increase our understanding of the relationship between leaf and fruit water relations of jujube plants under different irrigation conditions during fruit maturation, paying special attention to analysing whether fruit size depends on fruit turgor. For this, adult jujube trees (cv. Grande de Albaterra) were subjected to five irrigation treatments. Control plants (T0) were irrigated daily above their crop water requirements in order to attain non-limiting soil water conditions in 2012 and 2013. T1 plants were subjected to deficit irrigation throughout the 2012 season, according to the criteria frequently used by the growers in the area. T2 (2012), T3 and T4 (2013) were irrigated as T0 except during fruit maturation, in which irrigation was withheld for 32, 17 and 24 days, respectively. The results indicated that the jujube fruit maturation period was clearly sensitive to water deficit. During most of this stage water could enter the fruits via the phloem rather than via the xylem. From the beginning of water withholding to when maximum water stress levels were achieved, fruit and leaf turgor were maintained in plants under water deficit. However, a direct relation between turgor and fruit size was not found in jujube fruits, which could be due to an enhancement of a cell elasticity mechanism (elastic adjustment) which maintains fruit turgor by reducing fruit cells size or to the fact that jujube fruit growth depends on the fruit growth-effective turgor rather than just turgor pressure.

1. Introduction

Jujube tree (*Zizyphus jujuba* Mill.), is native to temperate Asia and is mostly cultivated in China, India, Central Asia and southwest Asia (Williams, 2006b). Although considered as a multipurpose plant, its fruits are the major focus of interest (Bowe, 2006). *Z. jujuba* is considered a minor crop, but is an integral part of the culture and way of life for millions of Asians and has also become so for large regions of Africa (Williams, 2006a). This growing interest on

jujube fruit is due to its presumed health-promoting effects, and it is now considered a functional food, since it has nutritional as well as medicinal uses (Heo et al., 2003; Huang et al., 2007; Li et al., 2007; Zhao et al., 2008; Mahajan and Chopda, 2009; Choi et al., 2011; Collado-González et al., 2013, 2014). For all this, the International Centre for Underutilized Crops has identified *Z. jujuba* as a crop with substantial growth potential (Williams et al., 2006c).

Jujube tree is admired for its multiple uses, easy management, early bearing and wide adaptations to environmental conditions. In this sense, it is tolerant to saline irrigation water, low winter temperatures during dormancy and severe drought during the growing season (Dahiya et al., 1981; Ming and Sun, 1986; Jain and Dass, 1988). In this last respect, Cruz et al. (2012) showed that *Z.*

jujuba is able to withstand severe water deficits, while maintaining leaf turgor, which allows good gas exchange rates and, as a consequence, good leaf productivity. This leaf turgor maintenance was mainly due to two simultaneous and complementary mechanisms: decreased leaf conductance and a shorter period of maximum stomatal opening in order to control water loss via transpiration (stress avoidance mechanisms). The gradual recovery of leaf conductance after rewatering can also be considered as a mechanism for promoting leaf rehydration. In addition, from the beginning of the stress period, active osmotic adjustment operated, which can contribute to the maintenance of leaf turgor (stress tolerance mechanism). The high relative apoplastic water content levels and the possibility of increasing the accumulation of water in the apoplast in response to water stress, supporting a steeper gradient in water potential between the leaf and the soil, which can be considered another drought tolerance characteristic in pear-jujube leaves.

According to Cui et al. (2008), the phenological periods of jujube tree can be divided into bud burst to leafing (stage I, early April–early May), flowering to fruit set (stage II, mid May–late June), fruit growth (stage III, late June–late July), fruit maturation (stage IV, early August–early September) and dormancy (stage V, this October–next March) stages. Also, these authors indicated that the fruit maturation stage is the optimal stage for implementing water deficit in jujube, because low, moderate and severe water deficits have no effect on the fruit weight and volume, the fruits taste sweeter and eating quality is improved. In addition, the fruit maturation period is shortened, raising the market price of the fruit, fruit firmness is enhanced and the percentage of rotten fruit after storage is reduced. Despite the importance of the maturation period on jujube fruit quality, to the best of our knowledge no information exists on jujube fruit water relations. For these reasons, the aim of this study was to increase our understanding of the relationship between leaf and fruit water relations of jujube plants under different irrigation conditions during fruit maturation, paying special attention to analysing whether fruit size depends on fruit turgor.

2. Materials and methods

2.1. Plant material, experimental conditions, and treatments

Two different but complementary experiments were performed with the common goal of investigating if jujube fruit maturation period was clearly sensitive to water deficit. In the first experiment (2012) control plants were compared with plants subjected to moderate water deficit and with plants under severe water deficit. In order to verify the results obtained in the first experiment, in the second experiment (2013) control plants were compared with other plants subjected to different water stress conditions.

Both experiments were carried out at a farm near the city of Albufera (Alicante, Spain) (38°12'N, 0°51'W). The plant material consisted of 8-year-old jujube trees (*Zizyphus jujuba* Mill), cv. Grande de Albufera, planted at 2 m × 6 m. The soil of the orchard is a Torrifluent with a sandy loam texture, very low electrical conductivity (109 µS/cm, 1:10 w:v), high lime content (570 g/kg), very low organic matter content (3 g/kg), low exchangeable potassium (40 mg/kg) and available phosphorus (20 mg/kg) levels. The irrigation water had an electrical conductivity of between 1.7 and 2.2 dS/m and a Cl⁻ concentration ranging from 36 to 48 mg l⁻¹. Pest control and fertilization practices were those usually used by the growers, and no weeds were allowed to develop within the orchard.

Jujube plants were drip-irrigated every night, using one lateral pipe parallel to the tree row and 2 emitters per tree, each delivering 8 l h⁻¹. In-line water meters were used to measure the water supplied to each experimental unit.

2.1.1. Experiment 1 (2012)

During the 2012 experimental period (DOY 93–230), control plants (treatment T0) were irrigated in order to guarantee non-limiting soil water conditions (41% daily crop reference evapotranspiration (ET₀) during bud burst and leafing (DOY 93–121), 52% ET₀ during flowering and fruit set (stage I, DOY 122–167), 69% ET₀ during fruit growth (stage II, DOY 168–197) and 106% ET₀ during fruit maturation (stage III, DOY 198–230). Such percentages were applied according to the water needs obtained in previous results. T1 plants were subjected to deficit irrigation throughout the season, according to the criteria frequently used by the growers in the area (23% ET₀ during bud burst and leafing (DOY 93–121), 30% ET₀ during flowering and fruit set (stage I, DOY 122–167), 40% ET₀ during fruit growth (stage II, DOY 168–197) and 61% ET₀ during fruit maturation (stage III, DOY 198–230). T2 treatment was irrigated as T0 except during 32 days before harvest, in which irrigation was withheld (from day of the year (DOY) 198 to 230). Total seasonal water amounts applied were 440, 252 and 274 mm for T0, T1 and T2 treatments, respectively.

2.1.2. Experiment 2 (2013)

During the 2013 experimental period (DOY 101–242), control plants (treatment T0) were irrigated with a similar criterion to that used in 2012 (42% ET₀ during bud burst and leafing (DOY 101–126), 53% ET₀ during flowering and fruit set (stage I, DOY 127–169), 76% ET₀ during fruit growth (stage II, DOY 170–198) and 110% ET₀ during fruit maturation (stage III, DOY 199–242). T3 and T4 plants were irrigated as T0 except during the last 17 and 24 days before harvest in which irrigation was withheld (from day of the year (DOY) 225 (T3) and 218 (T4) to 242), respectively. Total seasonal water amounts applied were 441, 360 and 322 mm for T0, T3 and T4 treatments, respectively.

2.2. Measurements

Meteorological data, namely air relative humidity, air temperature, solar radiation, rainfall and wind speed 2 m above the soil surface, were collected by an automatic weather station located near the experimental site. Mean daily air vapour pressure deficit (VPD_m) and daily crop reference evapotranspiration (ET₀) were calculated according to Allen et al. (1998).

The water relations of the leaves and fruits were measured at midday (12 h solar time). Fruits and fully expanded leaves from the south facing side and middle third of the tree of four trees per treatment were selected for measurements. Leaf conductance (g_{leaf}) was measured with a porometer (Delta T AP4, Delta-T Devices, Cambridge, UK) on the abaxial surface of two leaves per tree. Leaf water potential (Ψ_{leaf}), and stem water potential (Ψ_{stem}) were measured in a similar number and type of leaves as used for g_{leaf} using a pressure chamber (PMS 600-EXP, PMS Instruments Company, Albany, USA) (Greenspan et al., 1994; Nobel and de la Barrera, 2000). Leaves for Ψ_{stem} measurements were enclosed in a small black plastic bag covered with aluminium foil for at least 2 h before measurements. Fruit water potential (Ψ_{fruit}) was measured with the pressure chamber (PMS 600-EXP, PMS Instruments Company, Albany, USA) in two fruits per tree as described by McFadyen et al. (1996) and Gelly et al. (2004).

Midday leaf ($\Psi_{\pi \text{ leaf}}$) and fruit ($\Psi_{\pi \text{ fruit}}$) osmotic potentials were determined in the same leaves and fruits as used for Ψ_{leaf} and Ψ_{fruit} measurements, respectively. Leaves and fruits were covered with aluminium foil and immediately frozen in liquid nitrogen and stored at -80°C. The osmotic potential was measured after thawing the samples and expressing the sap, using a vapour pressure osmometer (Wescor 5600, Logan, USA). Estimated midday leaf ($\Psi_{\text{p leaf}}$) and fruit ($\Psi_{\text{p fruit}}$) turgor potentials were derived as the dif-

ference between osmotic and water potentials (Milad and Shackel, 1992; Mills et al., 1997; Yamada et al., 2004; Galindo et al., 2014).

Marketable jujube fruits were harvested on 18 August 2012 (DOY 230) and 30 August 2013 (DOY 242). The mean weight of jujube fruit was determined according to the weight and number of fruits per box in randomly selected boxes per replicate.

2.3. Statistical design and analysis

The design of the experiment was completely randomized with four replications, each replication consisting of three adjacent tree rows, each with eleven trees. Measurements were taken on the inner tree of the central row of each replicate, which were very similar in appearance (leaf area, trunk cross sectional area, height, ground shaded area, etc.), while the other trees served as border trees. Statistical analysis was performed by an analysis of variance using the general linear model (GLM) of SPSS v. 12.0 (SPSS Inc., 2002).

To check the regression model hypothesis (linearity, homoscedasticity, normality and independency) Kolmogorov-Smirnov with the Lilliefors correction was used. Normality and homoscedasticity on the typified residuals were evaluated using Shapiro-Wilk and Levene tests, respectively. Linearity was observed in the graphics and independency was assumed due to the way data were obtained.

All the measurements were taken on the same tree in each replicate. Values for each replicate were averaged before the mean and the standard error of each treatment were calculated.

3. Results

3.1. Meteorological conditions and leaf and fruit water relations

During the 2012 and 2013 experimental periods, meteorological conditions were very similar. In this sense, average daily maximum and minimum air temperatures were 29.7 and 15.1 °C and 29.2 and 14.9 °C, respectively. VPD_m ranged from 0.39 to 2.35 kPa in 2012 and from 0.22 to 2.27 kPa in 2013, and accumulated ETo were 654 mm and 643 mm in 2012 and 2013, respectively (Fig. 1). In the 2012 and 2013 experimental periods total rainfall were 30 and 63 mm, respectively, which took place mainly on DOY 95 (18 mm) and 103 (9 mm) in 2012 season and on DOY 115 (15 mm), DOY 117 (5 mm), DOY 118 (23 mm), DOY 240 (8 mm) and DOY 241 (9 mm) in 2013 season (Fig. 1).

The Ψ_{leaf} and Ψ_{stem} values in T0 plants were high and almost constant throughout both experimental periods (Fig. 2A–D). During 2012 season, Ψ_{leaf} values in T1 plants showed lower values but a similar seasonal course to those in T0 plants (Fig. 2A). Ψ_{stem} values in T0 and T1 plants showed a similar seasonal course until DOY 198, from which time Ψ_{stem} values in T1 plants were lower than in T0 plants (2012 season, Fig. 2C). Ψ_{leaf} and Ψ_{stem} values in T2, T3 and T4 plants decreased from the beginning of the water withholding periods, reaching minimum values of –3.69 and –2.91 MPa, –3.15 and –2.85 MPa and –3.30 and –3.90 MPa, respectively, on DOY 229 (T2) and 239 (T3 and T4) (Fig. 2A–D).

The values of Ψ_{fruit} in T0 plants were significantly higher than those observed in T1, T2, T3 and T4 plants, which decreased reaching minimum values at the end of both experimental periods (Fig. 2E and F). g_{leaf} values in T0 plants were nearly constant and higher than those in the other treatments (Fig. 2G and H). g_{leaf} values in T1 plants were also nearly constant and relatively high and throughout the measurement period of the 2012 season (Fig. 2G). In contrast, g_{leaf} values in water withheld plants (T2, T3 and T4) decreased during the stress period, reaching minimum values of

Table 1

Effect of irrigation treatments on total marketable jujube yield (kg tree^{–1}), number of fruits per tree (NF) and average fruit weight (FW, g), during the 2012 and 2013 seasons. Different letters indicate significant differences between treatments in the same year according to LSD_{0.05} test.

Season	Treatment	Yield	NF	FW
2012	T0	34.78a	1105.65a	31.46a
	T1	26.09b	899.98b	28.99a
	T2	10.89c	803.28b	13.54b
2013	T0	30.78a	946.00a	32.55a
	T3	18.91b	794.50b	23.81b
	T4	17.73b	797.75b	22.21b

81.22, 326.50 and 196.75 mmol m^{–2} s^{–1}, respectively, at the end of the measurement periods (Fig. 2G and H).

The differences between Ψ_{leaf} and Ψ_{fruit} ($\Delta\Psi$) values in all treatments were negative during both experimental periods (Fig. 3A and B). Significant differences between treatments were found on DOY 208, 211 and 229 (2012 season) (Fig. 3A) and on DOY 232 and 239 (2013 season) (Fig. 3B).

Ψ_{leaf} values in T0 plants were nearly constant during both measurement periods (Fig. 4A and B). Ψ_{leaf} values in T1 plants were also nearly constant but lower than those found in T0 plants (Fig. 4A). Ψ_{leaf} values in water withheld plants (T2, T3 and T4) tended to be lower than in T0 during the water withholding periods (Fig. 4A and B). Ψ_{leaf} values in T0 plants were nearly constant throughout both measurement periods (Fig. 4C and D), being very similar to those in T1 plants except on DOY 222 (Fig. 4C). Ψ_{leaf} values in T2, T3 and T4 plants decreased during the irrigation withholding periods, reaching minimum values of 0.18 MPa on DOY 229, 1.08 MPa on DOY 232 and 1.03 MPa on DOY 232, respectively (Fig. 4C and D).

Ψ_{fruit} values in T0 plants fell slightly during the 2012 measurement period, but were near constant during the 2013 measurement period (Fig. 5A and B). Ψ_{fruit} values in T1 were very similar to those in T0, showing significant differences between treatments only on DOY 205, 219 and 247 (Fig. 5A). In contrast, Ψ_{fruit} values in T2, T3 and T4 plants progressively decreased achieving lower values than T0 and T1 plants (Fig. 5A and B). Ψ_{fruit} values in T0 plants were almost constant throughout both measurement periods whereas Ψ_{fruit} values in T1, T2, T3 and T4 plants decreased below those in T0 reaching very low values, which frequently were slightly above the turgor loss point (values below zero) (Fig. 5C and D).

The effect of a reduction in Ψ_{fruit} on Ψ_{leaf} and Ψ_{fruit} values is shown in Fig. 6. Ψ_{fruit} showed a close and linear dependence of Ψ_{leaf} values (Fig. 6A), whereas the relation between Ψ_{fruit} and Ψ_{fruit} values showed a very low determination coefficient, which indicated that changes in Ψ_{fruit} values only explained a 3% of changes in Ψ_{fruit} values (Fig. 6B).

3.2. Yield and fruit characteristics

Both seasons, the irrigation treatments produced a significant effect in the quantity and quality of the total marketable fruit yield (Table 1). Total jujube yield was reduced significantly for the water restriction effect (Table 1). T1 plants showed a 25% fruit yield reduction, whereas yield decrease in T2, T3 and T4 plants was 69%, 39% and 42%, respectively (Table 1). The decrease in T1 fruit yield seemed to be due to the lower number of fruits, because the average fruit weight was similar to that in T0 plants (Table 1). The yield decrease in the treatments in which irrigation was withheld was mainly due to a significant decrease in both the average fruit weight and the number of fruits per tree (Table 1).

Fig. 1. Daily mean air temperature (T_m , solid thick line), daily crop reference evapotranspiration (ETo , thin line), mean daily air vapour pressure deficit (VPD_m) (dashed thick line) and daily rainfall (vertical bars) during both experimental periods.

4. Discussion

The fact that Ψ_{leaf} , Ψ_{stem} and g_{leaf} values in T0 plants were high and almost constant during both measurement periods (Fig. 2) suggested that the irrigation applied to this treatment was sufficient to avoid any water deficit during the measurement period. The differences in Ψ_{leaf} , Ψ_{stem} and g_{leaf} values between T0 and T1 plants clearly indicated a water deficit situation in T1 plants. However, the fact that at maximum stress the decrease in Ψ_{leaf} and Ψ_{stem} values in T1 plants with respect to T0 plants was only 0.65 and 0.63 MPa, respectively, together with the fact that g_{leaf} values in T1 plants, in spite of being lower than those in T0, were very high and nearly constant, indicated that water deficit in T1 can be considered as moderate. In this sense, the high g_{leaf} values under moderate water deficit could be a consequence of the leaf turgor maintenance (Fig. 4) due to the active osmotic adjustment developed under these conditions (Cruz et al., 2012).

Moreover, the water relations of transpiring leaves in water withheld plants (T2, T3 and T4) indicated severe water deficit situations due to the very low minimum Ψ_{leaf} values (-3.69 , -2.91 and -3.15 MPa, respectively) and the important stomatal regulation respect to g_{leaf} values in T0 plants (81.22 , 326.50 and 196.75 $\text{mmol m}^{-2} \text{s}^{-1}$, respectively) (Fig. 2A, B, G and H). These water stress levels were more severe in T2 plants and less severe in T3 plants.

The maintenance of leaf turgor potential values in T1, T2, T3 and T4 plants above zero (Fig. 4C and D) even at maximum water stress levels, agrees with the results obtained in a previous paper by Cruz et al. (2012). These authors indicated that jujube plants are able to maintain leaf turgor under severe water deficit, essentially by developing two complementary mechanisms, leaf active osmoregulation and controlling water loss via transpiration, but allowing substantial gas exchange rates and, as a consequence, good leaf productivity.

The substantially higher Ψ_{fruit} values than Ψ_{leaf} values during both jujube fruit maturation periods studied (Figs. 2 A, B, E and F and 3 A and B) has been observed in other crops, such as Asian pear (Behboudian et al., 1994), apple (Lang, 1990; Mills et al., 1997; Ward and Marini, 1999), avocado (Blanke and Whaley, 1995), citrus (Syvertsen and Albrigo, 1980), cotton (Trolinder et al., 1993; Inglese et al., 1994), platyopuntias (Nobel and de la Barrera, 2000), pomegranate (Galindo et al., 2014) or tomato (Ho et al., 1987) and could be partially due to a high resistance to water movement from fruit to the rest of the tree, resulting in the maintenance of Ψ_{fruit} values at levels above Ψ_{leaf} values (Mills et al., 1997). Moreover, according to Nobel and de la Barrera (2000), from the energetic point of view, water can not flow from leaves to the fruits, since

the xylem is not the provider of water for the fruits (Nobel et al., 1994). So, in our experimental conditions, during jujube fruit maturation water might have entered the fruits via the phloem rather via the xylem. Nevertheless, other authors indicated that in fully irrigated prunes the relative importance of xylem and phloem in the water flow to the fruit may be reversible (Matthews and Shackel, 2005). Greenspan et al. (1994, 1996) suggested that the bulk vascular water flow changes from xylem in pre-veraison to phloem in post-veraison in fully irrigated grape berry. Also, Dell'Amico et al. (2012) showed that water flow in the olive fruit during pit hardening in fully irrigated conditions is via both xylem and phloem.

The fact that Ψ_{fruit} decreased by water deficit effect (Fig. 6A) could be related with previous results in which some authors showed that water deficit during jujube fruit maturation period induces important changes in most of fruit chemical characteristics which make up a more advanced degree of ripening (Collado-González et al., 2014). These chemical changes could be ascribed amongst others to a degradation of some of polymers (mucilage, proteins and starch) in order to enhance flesh sweetness during the final stages of fruit ripening (Ma et al., 2006; Cui et al., 2008; Collado-González et al., 2014).

The fact that Ψ_{pfruit} values were near constant and always above zero turgor when Ψ_{fruit} values decreased from -0.76 to -3.70 MPa indicated that jujube fruit turgor can be maintained in spite of very important changes in jujube fruit water status (Fig. 6B). To explain why fruit size was reduced in T2, T3 and T4 plants (Table 1) since fruit turgor was maintained ($\Psi_p \text{ fruit} > 0$) at maximum water stress levels (Fig. 5C and D and Fig. 6B) several hypothesis, which cannot be substantiated by our data, could be considered. Okello et al. (2015) showed that fruit size is strongly related to cell size instead cell number. Complementarily, a hypothesis to explain fruit size reduction and maintained fruit turgor is that elastic adjustment (increased elasticity of fruit cell walls) occurred. This passive mechanism allows a decrease in cell volume with dehydration, slowing the rate of turgor loss by decreasing Ψ_{fruit} . Other hypothesis is based in the idea that cell enlargement depends on the growth-effective turgor (difference between turgor pressure and wall yield threshold) rather than just turgor pressure (Van Volkenburg and Cleland, 1986; Hale and Orcutt, 1987). So, probably, Ψ_{pfruit} values in T2, T3 and T4 plants did not exceed the wall yield threshold. In addition, the fact that the levels of water deficit achieved in treated plants were able to affect yield and fruit size (Table 1) indicated that the jujube fruit maturation stage is a more critical period than indicated by Cui et al. (2008).

In conclusion, this experiment clearly showed that the jujube fruit maturation period was sensitive to water deficit. During the jujube fruit maturation stage water could enter the fruits via

Fig. 2. Leaf water potential (Ψ_{leaf} , A, B), stem water potential (Ψ_{stem} , C, D), fruit water potential (Ψ_{fruit} , E, F) and leaf conductance (g_{leaf} , G, H) values (mean $\pm$ SE, not shown when smaller than symbols, $n=4$) at midday for jujube plants in T0 (closed circles and solid line), T1 (open triangles up and dotted line), T2 (open squares and short dash line), T3 (closed diamonds in grey and dash dot line) and T4 (closed triangles down in grey and long dash line) treatments during the experimental periods (2012 and 2013). Asterisks indicate significant differences between treatments according to LSD0.05 test.

Fig. 3. Differences between midday leaf water potential (Ψ_{leaf}) and fruit water potential (Ψ_{fruit}) values (mean $\pm$ SE, not shown when smaller than symbols, $n=4$) for jujube plants in T0 (closed circles and solid line), T1 (open triangles up and dotted line), T2 (open squares and short dash line), T3 (closed diamonds in grey and dash dot line) and T4 (closed triangles down in grey and long dash line) treatments during the experimental periods (2012 and 2013). Asterisks indicate significant differences between treatments according to LSD0.05 test.

phloem rather via xylem. In contrast with the axiom that expansive cell growth requires the presence of cell turgor, a direct relation between turgor and the rate of growth was not found in jujube fruits, which could be due to an enhancement of a cell elastic-

ity mechanism (elastic adjustment) which maintains fruit turgor by reducing fruit cells size or to the fact that jujube fruit growth depends on the fruit growth-effective turgor rather than just turgor pressure.

Fig. 4. Leaf osmotic potential ($\Psi_{\pi \text{ leaf}}$, A, B) and leaf turgor potential ($\Psi_{p \text{ leaf}}$, C, D) values (mean $\pm$ SE, not shown when smaller than symbols, $n=4$) at midday for jujube plants T0 (closed circles and solid line), T1 (open triangles up and dotted line), T2 (open squares and short dash line), T3 (closed diamonds in grey and dash dot line) and T4 (closed triangles down in grey and long dash line) treatments during the experimental periods (2012 and 2013). Asterisks indicate significant differences between treatments according to LSD0.05 test.

Fig. 5. Fruit osmotic potential ($\Psi_{\pi \text{ fruit}}$, A, B) and fruit turgor potential ($\Psi_{p \text{ fruit}}$, C, D) values (mean $\pm$ SE, not shown when smaller than symbols, $n=4$) at midday for jujube plants in T0 (closed circles and solid line), T1 (open triangles up and dotted line), T2 (open squares and short dash line), T3 (closed diamonds in grey and dash dot line) and T4 (closed triangles down in grey and long dash line) treatments during the experimental periods (2012 and 2013). Asterisks indicate significant differences between treatments according to LSD0.05 test.

Fig. 6. Relationships for jujube plants under T0 (closed circles), T1 (open triangles up), T2 (open squares), T3 (closed diamonds in grey) and T4 (closed triangles down in grey) conditions between midday fruit osmotic water potential ($\Psi_{\pi \text{ fruit}}$) and midday fruit turgor potential ($\Psi_{p \text{ fruit}}$) and midday fruit water potential (Ψ_{fruit}) using all data pooled.

Acknowledgements

This research was supported by Agencia Española de Cooperación Internacional para el Desarrollo (AECID) (A1/035430/11) and MICINN and MINECO (CICYT/FEDER AGL2010-19201-C04-01AGR and AGL2013-45922-C2-2-R) grants to the authors. AG, ZNC, JCG and HM were funded by a FPU, an AECID, a FPI an INIA grant from the Spanish Government, respectively.

References

- Allen, R.G., Pereira, R.S., Raes, D., Smith, M., 1998. Crop evapotranspiration. In: Guidelines for Computing Crop Water Requirements. Irrigation and Drainage Paper 56. FAO, Rome.
- Behboudian, M.H., Lawes, G.S., Griffiths, K.M., 1994. The influence of water deficit on water relations, photosynthesis and fruit growth in Asian pear (*Pyrus serotina* Rehd.). *Sci. Hortic.* 60, 89–99.
- Blanke, M.M., Whitley, A.W., 1995. Bioenergetics, respiration cost and water relations of developing avocado fruit. *J. Plant Physiol.* 145, 87–92.
- Bowe, C., 2006. Composition. In: Williams, J.T., Smith, R.W., Haq, N., Dunsiger, Z. (Eds.), *Ber and Other Jujubes*. International Centre for Underutilised Crops, Southampton, pp. 18–28.
- Choi, S.H., Ahn, J.B., Kozukue, N., Levin, C.E., Friedman, M., 2011. Distribution of free amino acids, flavonoids, total phenolics, and antioxidative activities of jujube (*Ziziphus jujuba*) fruits and seeds harvested from plants grown in Korea. *J. Agric. Food Chem.* 59, 6594–6604.
- Collado-González, J., Cruz, Z.N., Medina, S., Mellisho, C.D., Rodríguez, P., Galindo, A., Egea, I., Romojaro, F., Ferreres, F., Torrecillas, A., Gil-Izquierdo, A., 2014. Effects of water deficit during maturation on amino acids and jujube fruit eating quality. *Maced. J. Chem. Chem. Eng.* 33, 105–119.
- Collado-González, J., Cruz, Z.N., Rodríguez, P., Galindo, A., Díaz-Baños, F.G., García de la Torre, J., Ferreres, F., Medina, S., Torrecillas, A., Gil-Izquierdo, A., 2013. Effect of water deficit and domestic storage on the procyanidin content, size and aggregation process in pear-jujube (*Z. jujuba*) fruits. *J. Agric. Food Chem.* 61, 6187–6197.
- Cruz, Z.N., Rodríguez, P., Galindo, A., Torrecillas, E., Ondoño, S., Mellisho, C.D., Torrecillas, A., 2012. Leaf mechanisms for drought resistance in *Ziziphus jujuba* trees. *Plant Sci.* 197, 77–83.
- Cui, N., Du, T., Kang, S., Li, F., Zhang, J., Wang, M., Li, Z., 2008. Regulated deficit irrigation improved fruit quality and water use efficiency of jujube trees. *Agric. Water Manag.* 95, 489–497.
- Dahiya, S.S., Dhankar, O.P., Khera, A.P., 1981. Studies on the effect of soil salinity levels on seed germination of ber (*Ziziphus rotundifolia*). *Haryana J. Hortic. Sci.* 10, 20–23.
- Dell'Amico, J., Moriana, A., Corell, M., Girón, I.F., Morales, D., Torrecillas, A., Moreno, F., 2012. Low water stress conditions in table olive trees (*Olea europaea* L.) during pit hardening produced a different response of fruit and leaf water relations. *Agric. Water Manag.* 114, 11–17.
- Galindo, A., Rodríguez, P., Collado-González, J., Cruz, Z.N., Torrecillas, E., Ondoño, S., Corell, M., Moriana, A., Torrecillas, A., 2014. Rainfall intensifies fruit peel cracking in water stressed pomegranate trees. *Agric. Forest Meteorol.* 194, 29–35.
- Gelly, M., Marsal, J., Mata, M., Arbonès, J., Rufat, J., Girona, J., 2004. Fruit water potential: a comparative study with other water potential parameters. *Acta Hortic.* 646, 35–40.
- Greenspan, M.D., Schultz, H.R., Matthews, M.A., 1996. Field evaluation of water transport in grape during water deficits. *Physiol. Plant* 97, 55–62.
- Greenspan, M.D., Shackel, K.A., Matthews, M.A., 1994. Developmental changes in the diurnal water budget of the grape berry exposed to water deficits. *Plant Cell Environ.* 17, 811–820.
- Hale, M.G., Orcutt, D.M., 1987. *The Physiology of Plants under Stress*. Wiley & Sons, 206 pp.
- Heo, H.J., Park, Y.J., Suh, Y.M., Choi, S.J., Kim, M.J., Cho, H.Y., Chang, Y.J., Hong, B., Kim, H.K., Kim, E., Kim, C.J., Kim, B.G., Shin, D.H., 2003. Effects of oleamide on choline acetyltransferase and cognitive activities. *Biosci. Biotechnol. Biochem.* 67, 1284–1291.
- Ho, L.C., Grange, R.I., Picken, A.J., 1987. An analysis of the accumulation of water and dry matter in tomato fruit. *Plant Cell Environ.* 10, 157–162.
- Huang, X., Kojima-Yuasa, A., Norikura, T., Kennedy, D.O., Hasuma, T., Matsui-Yuasa, I., 2007. Mechanism of the anti-cancer activity of *Ziziphus jujuba* in HepG2 cells. *Am. J. Chin. Med.* 35, 517–532.
- Inglese, P., Israel, A.A., Nobel, P.S., 1994. Growth and CO₂ uptake for cladodes and fruit of the Crassulacean acid metabolism species *Opuntia ficus-indica* during fruit development. *Physiol. Plant* 91, 708–714.
- Jain, B.L., Dass, H.C., 1988. Effect of saline water on performance of saplings of jujube (*Ziziphus mauritiana*), Indian cherry (*Cordia dichotoma* var. wallichii) and pomegranate (*Punica granatum*) at nursery stage. *Indian J. Agric. Sci.* 58, 420–421.
- Lang, A., 1990. Xylem, phloem and transpiration flows in developing apple fruits. *J. Exp. Bot.* 41, 645–651.
- Li, J.W., Fan, L.P., Ding, S.D., Ding, X.L., 2007. Nutritional composition of five cultivars of Chinese jujube. *Food Chem.* 103, 454–460.
- Ma, F.S., Kang, S.Z., Li, F.S., Wang, M.X., Pang, X.M., Wang, J.F., Li, Z.J., 2006. Effect of regulated deficit irrigation on water use efficiency and fruit quality of pear jujube tree in greenhouse. *Trans. CSAE* 22, 37–43.
- Mahajan, R.T., Chopda, M.Z., 2009. Phyto-pharmacology of *Ziziphus jujuba* Mill—a plant review. *Pharmacogn. Rev.* 3, 320–329.
- Matthews, M.A., Shackel, K.A., 2005. Growth and water transport in fleshy fruit. In: Holbrook, N.M., Zwieniecki, M.A. (Eds.), *Vascular Transport in Plants*. Elsevier, Boston, pp. 181–197.
- McFadyen, L.M., Hutton, R.J., Barlow, E.W.R., 1996. Effects of crop load on fruit water relations and fruit growth in peach. *J. Hortic. Sci.* 71, 469–480.
- Milad, R.E., Shackel, K.A., 1992. Water relations of fruit end cracking in French prune (*Prunus domestica* L. cv. French). *J. Am. Soc. Hortic. Sci.* 117, 824–828.
- Mills, M.T., Behboudian, M.H., Clothier, B.E., 1997. The diurnal and seasonal water relations, and composition, of 'Braeburn' apple fruit under reduced plant water status. *Plant Sci.* 126, 145–154.
- Ming, W., Sun, Y., 1986. Fruit trees and vegetables for arid and semi-arid areas in northwest China. *J. Arid Environ.* 11, 3–16.
- Nobel, P.S., Andrade, J.L., Wang, N., North, G.B., 1994. Water potential for developing cladodes and fruits of a succulent plant, including xylem-versus-phloem implications for water movement. *J. Exp. Bot.* 45, 1801–1807.
- Nobel, P.S., de la Barrera, E., 2000. Carbon and water balances for young fruits of platyopuntias. *Physiol. Plant* 109, 160–166.
- Okello, R.C.O., Heuvelink, E., Visser, P.H.B., Strunk, P.C., Marcelis, L.F.M., 2015. What drives fruit growth? *Funct. Plant Biol.* 42, 817–827.
- SPSS Inc, 2002. *SPSS Professional Statistics*, 12. Business Intelligence Division, Chicago.
- Syvertsen, J.P., Albrigo, L.G., 1980. Seasonal and diurnal Citrus leaf and fruit water relations. *Bot. Gaz.* 141, 440–446.
- Trolinder, N.L., McMichael, B.L., Upchurch, D.R., 1993. Water relations of cotton flower petals and fruit. *Plant Cell Environ.* 16, 755–760.
- Van Volkenburg, E., Cleland, R.E., 1986. Wall yield threshold and effective turgor in growing bean leaves. *Planta* 167, 37–43.
- Ward, D., Marini, R.P., 1999. Growth and development of young apple fruits following applications of ethephon plus carbaryl for thinning. *HortScience* 34, 1057–1059.
- Williams, J.T., 2006a. Current situation and research needs. In: Williams, J.T., Smith, R.W., Haq, N., Dunsiger, Z. (Eds.), *Ber and Other Jujubes*. International Centre for Underutilised Crops, Southampton, pp. 160–166.
- Williams, J.T., 2006b. Introduction, taxonomy and history. In: Williams, J.T., Smith, R.W., Haq, N., Dunsiger, Z. (Eds.), *Ber and Other Jujubes*. International Centre for Underutilised Crops, Southampton, pp. 1–17.
- Williams, J.T., Smith, R.W., Haq, N., Dunsiger, Z., 2006c. Preface. In: Williams, J.T., Smith, R.W., Haq, N., Dunsiger, Z. (Eds.), *Ber and Other Jujubes*. International Centre for Underutilised Crops, Southampton, pp. iii.
- Yamada, H., Takechi, K., Hoshi, A., Amano, S., 2004. Comparison of water relations in watercored and non-watercored apples induced by fruit temperature treatment. *Sci. Hort.* 99, 309–318.
- Zhao, Z.H., Liu, M.J., Tu, P.F., 2008. Characterization of water soluble polysaccharides from organs of Chinese jujube (*Ziziphus jujuba* Mill. cv. Dongzao). *Eur. Food Res. Technol.* 985–989.