Gas exchange and water relations of young apricot plants under drought conditions

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SUMMARY

Potted 1.5-year-old apricot plants (Prunus armeniaca L.), growing under polycarbonate glasshouse conditions with a cooling system, were subjected to two successive water stress/recovery periods until pre-dawn leaf water potential (Ψ_{pd}) reached values between -2.0 and -2.5 MPa, during summer 1996. Control plants were irrigated daily to maintain the soil matric potential at c. -20 kPa. Water stress limited plant growth and induced a significant reduction in leaf area, caused by mature leaf abscission. The parallel behaviour of leaf turgor potential and epinasty in stressed plants indicated that these movements are turgor-dependent. Osmotic adjustments of 0.27 and 0.60 MPa were observed at the end of the first and second stress period, respectively. Relative apoplastic water content (RWC_a) values were high, ranging from 27 to 42%, and were not affected by water stress. The rapid decrease in leaf conductance (g_l) from the beginning of the stress periods, together with the delay in stomatal reopening after rewatering the plants, indicated that stomatal behaviour was not a simple passive response to water deficits. Net photosynthesis decreased only at the end of both stress periods and recovered quickly. These observations indicate that leaf productivity may be affected only slightly by short-term water stress. The results indicate that drought resistance in apricot is based mainly on avoidance mechanisms, such as stomatal control, epinasty and limitation of transpiration by reducing leaf area. However, some tolerance characteristics, including osmotic adjustment, high RWC_a and low leaf osmotic potential at turgor loss point (Ψ_{tlp}) values were observed.

INTRODUCTION

Apricot trees (*Prunus armeniaca* L.) are widely cultivated in Mediterranean countries, with the Murcia Region of Spain being the foremost growing region in Europe, producing 126 372 tonnes of apricots annually, from a cultivation area of 11 637 ha; these figures represent *c.* 60% of Spanish apricot production and 50% of the Spanish total cultivation area of apricots (Ministerio de Agricultura, Pesca y Alimentación 1995).

Water shortage is the main characteristic of agriculture on the Mediterranean coast, which induces plant water deficits during the dry spring-summer period. Fruit-trees survive these conditions either because they avoid drought due to morphological or physiological modifications that enable them to avoid or postpone desiccation, or because they can tolerate desiccation (Savé *et al.* 1995; Torrecillas *et al.* 1996).

The problem of assessing to what extent gas exchange and growth can resume and productivity may be maintained once water stress is relieved, is particularly relevant for perennial crops cultivated in the coastal Mediterranean region. Apricot is considered to be a drought-resistant crop because it exhibits some xeromorphic characteristics, such as the ability to endure water stress in the dry season and the loss of leaves in winter. For these reasons, it can be grown with marginal water supply. In the Murcia Region, plantations of apricots grafted onto almond rootstocks are found growing under semi-desert conditions (< 300 mm mean annual rainfall) (J. Egea, personal communication). Nevertheless, under these climatic conditions, the crop requires irrigation for commercial production.

Despite the economic importance of apricot and the water stress conditions in the Mediterranean region, its water relations are not well

understood. The aim of this study was to determine the drought resistance mechanisms of the apricot cultivar Búlida, when subjected to two short-term water stress periods. Leaf gas exchange, osmotic adjustment and leaf water potential components, as well as vegetative growth, were measured.

MATERIALS AND METHODS

Plant material and culture conditions

The experiment was carried out on 1.5-year-old apricot trees (*Prunus armeniaca* L.), cv. Búlida, on Real Fino apricot rootstock, growing in 35 litre pots (40 cm diameter) filled with a mixture of clay loam topsoil and peat, containing 4% organic matter. Plants were cultured in a polycarbonate glasshouse, equipped with a cooling system (made up humidified panels and fans). Irrigation was carried out by daily drip irrigation providing 4 litres h⁻¹ per plant, to maintain the soil matric potential at *c.* -20 kPa (monitored with tensiometers placed at 15 cm depth) over a period of 6 months. Routine fertilization was applied (65 g N, 48 g K₂O, 72 g P₂O₅ and 1.5 g Fe (Fe-EDDHA) per plant and year) through the drip irrigation system every 2 weeks.

On 19 July 1996, 16 trees of uniform appearance (c. 1.2 m high and 20 mm trunk diameter, 10 cm above bud union) were selected. Two treatments were imposed: control plants, which were irrigated daily, as indicated, and water stressed plants, which were exposed to two successive stress/recovery periods. In stressed plants, no water was applied until a predetermined predawn leaf water potential (Ψ_{pd} between -2.0 and -2.5 MPa) was reached. The plants were then rewatered to saturation before water was withheld again until

the same predetermined Ψ_{pd} value was reached. During the second recovery period, plants were rewatered and treated as control plants (irrigated daily) for 6 days.

Plants were arranged in a randomized complete block design with 4 blocks. Two plants per treatment and block were used. Measurements were completed block by block so that the effect of time was confounded with location in the glasshouse.

The climatic conditions inside the glasshouse varied slightly day to day during the first stress/recovery period, with a maximum air temperature (t^a max) of 33 \pm 1 °C, a vapour pressure deficit of the atmosphere (VPD) at midday of 1.8 \pm 0.30 kPa (calculated from dry and wet-bulb temperature data of a psicrometer installed inside the glasshouse) and photosynthetically active radiation (PAR) at midday 676 \pm 21 μ mol m⁻² s⁻¹, measured at the canopy surface with a line quantum sensor (LI-COR, model 190S-1). During the second stress/recovery period, the climatic glasshouse conditions were: t^a max 27 ± 1.2 °C; VPD 1.1 \pm 0.18 kPa, and PAR 496 \pm 60 μ mol m⁻² s⁻¹.

Measurements

Soil and plant water status and leaf gas exchange were measured every 2 days. Volumetric soil water content was determined pre-dawn using time domain reflectometry (TDR) equipment (model 1502B, Tektronix). A pair of TDR probes was installed at a depth of 250 mm in one pot per block and treatment, midway between the tree trunk and pot border. Values were expressed as stock of water in the soil profile (SWS), multiplying the volumetric

soil water content data by the length of the probes.

Leaf water potential was measured pre-dawn (Ψ_{pd}) and at midday (12.00 h solar time) (Ψ_{md}) , for one mature leaf per plant and two plants per treatment and block, using a pressure chamber (Soil Moisture Equipment Co. model 3000), following the recommendations of Turner (1988). Leaves were fully expanded and were selected at random from the middle third of the shoots. After measuring Ψ_{pd} , leaves were frozen in liquid nitrogen and osmotic potential was measured after thawing the samples and expressing sap, using a Wescor 5500 vapour pressure osmometer. Leaf turgor potential (Ψ_p) was derived as the difference between leaf osmotic and water potentials.

Leaf conductance (g_i) was measured at midday for a similar number and type of leaves as for leaf water potential, using a steady-state porometer (LI-1600, LI-COR Inc.). In the same leaf, net photosynthesis (Pn) and internal CO_2 concentration (Ci) were measured using a field-portable, closed gas-exchange photosynthesis system (LI-6200, LI-COR Inc.) equipped with a ventilated one-litre chamber. The return flow rate of air circulating within the closed system was c. 280 μ mol s⁻¹, and the leaf to air vapour deficit was c. 1.8-2.4 kPa. The CO_2 analyser was calibrated daily with a series of standard CO_2 /air mixtures. Estimates of osmotic potential at full turgor (Ψ_{os}), osmotic potential at the turgor loss point (Ψ_{tp}), and relative apoplastic water content (RWC_a) were obtained from pressure-volume (PV) analysis of leaves (Tyree & Hammel 1972). On days 0, 6, 8, 14, 16 and 20 of the experimental period, leaves were excised pre-dawn, placed in plastic bags, and allowed to reach full turgor by dipping their petioles in distilled water for 24 h in darkness at 4 °C.

The resaturated leaves were weighed using an analytical balance (± 0.1 mg precision), placed into 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 appears through the cut petiole protruding from the chamber). Once depressurized, the leaf was allowed to transpire outside the pressure chamber on the laboratory bench. Leaves were repeatedly weighed and their balance pressures determined over the full range of the pressure gauge. An entire PV procedure took about 4-6 h. Leaves were finally oven dried at 80 °C for 24 h to determine their dry weights. One randomized leaf (of similar characteristics to leaf water potentials) per tree and two trees per treatment and block were used.

The curves were drawn using a type II transformation (Tyree & Richter 1982). The reciprocal of water potential (1/ Ψ_{l}) was plotted against relative water content (RWC) and the resultant relationships displayed both linear and non-linear regions. Extrapolation of the straight section of the line to the ordinate gave the reciprocal of the balance pressure equivalent to the osmotic potential at full turgor (Ψ_{os}) and to the abscissa gave relative apoplastic water content (RWC_a). Osmotic potential at the turgor loss point (Ψ_{ttp}) was estimated as the intersection between the linear and curvilinear portions of the pressure-volume curve.

At several points during the experiment, the angle between the petiole of leaf and the stem (leaf insertion angle, LIA) was measured with a transparent protractor to determine epinasty, the change in petiole angle. Ten randomized leaves per plant in all experimental plants were measured.

In order to evaluate the effect of water stress on plant growth, at the

end of the experimental period, three plants per treatment were harvested and separated into roots, stems and leaves, and the fresh and dry weights (oven-dried at 80 °C to constant weight) of each component were determined. Total and average leaf area were determined using an Image Analysis System (Delta-T Devices Ltd.).

RESULTS

Water stress reduced shoot growth and affected total plant dry weight, as indicate the significant reduction (P < 0.05) on stem and leaf dry weights (Table 1). Total leaf area and leaf succulence were significantly lower (P < 0.01) in stressed plants. No significant changes (P > 0.05) in average leaf area and root growth were observed in stressed plants (Table 1).

Soil water stock (SWS) decreased significantly (P < 0.001) and progressively in the stressed plants during both water withholding periods, reaching similar values of c. 44 mm (a 65 % reduction from that of control plants) at the end of these two periods (data not shown).

Pre-dawn leaf water potential (Ψ_{pd}) values in control plants were high and fairly constant (c. -0.5 MPa) during the experimental period (Fig. 1), whereas Ψ_{pd} values for stressed plants were -2.3 and -2.5 MPa at the end of the first and the second stress periods, respectively. The significant decrease (P < 0.05) in Ψ_{pd} in stressed plants occurred from day 4 of the first stress period and from day 6 (12th of the experimental period) of the second one, coinciding with SWS decrease below 70 mm (data not shown). The recovery of Ψ_{pd} after rewatering occurred rapidly at the end of both stress

periods.

Two distinct phases were found in the relationship between SWS and Ψ_{pd} for stressed apricot plants (Fig. 2). In the first phase, below a SWS of 70 mm, a steep decrease in Ψ_{pd} occurred for a gradual decline in SWS. Above 70 mm, minimum Ψ_{pd} changes were caused by SWS changes.

Midday leaf water potential (Ψ_{md}) showed qualitatively similar responses to Ψ_{pd} (Fig. 1). The minimum Ψ_{md} values reached were -2.7 and -3.4 MPa at the end of first and the second water withholding periods, respectively.

In stressed plants, leaf turgor potential (Ψ_p) decreased significantly (P < 0.001) at the end of both water withholding periods (days 6 and 14 of the experimental period), reaching values near zero (0.06 and 0.26 MPa at the end of the first and second stress periods, respectively) (Table 2). The recovery of Ψ_p was rapid, reaching similar levels to control plants 2 days after rewatering. A decrease in leaf insertion angle (LIA), which was used to asses the extent of epinasty, was noted at the end of each stress period (Table 2). After rewatering, LIA recovered as quickly as Ψ_p .

No significant differences (P > 0.05) in leaf osmotic potential at the turgor loss point ($\Psi_{t|p}$) were found between the control and stress treatments (Table 3). Values of leaf osmotic potential at full turgor (Ψ_{os}) were significantly lower in stressed than in control plants at the end of each stress period, showing an osmotic adjustment of 0.27 and 0.60 MPa for the first and second stress periods, respectively (Table 3). Two days after rewatering (days 8 and 16 of the experiment) Ψ_{os} remained lower in stressed plants.

Relative apoplastic water content (RWC_a) was not affected by the water stress treatment, with values ranging from 27 to 42% (Table 3).

Midday leaf conductance (g_l) decreased more rapidly during both stress periods than Ψ_{md} (Figs 1 and 3). The recovery of g_l after each stress period was slower than that of Ψ_{md} , only reaching values close to control plants 4 days after rewatering (Fig. 3) although Ψ_{md} had fully recovered to control values 2 days after rewatering (Fig. 1).

Net photosynthesis (Pn) values did not decrease significantly due to water stress until the end of each stress period (Fig. 3). In the second stress period, the minimum Pn value (3.2 μ mol CO₂ m⁻² s⁻¹) was higher than during the first period (0.7 μ mol CO₂ m⁻² s⁻¹). After rewatering, Pn recovered as rapidly as leaf water potential (Fig. 1). From days 8 to 12, Pn values in stressed plants were lower but not statistically different (P > 0.05) from control plants. Daily irrigation after the second stress period induced a rapid recovery of Pn, which resulted in higher net photosynthesis values (non-significant, P> 0.05) than those of the control plants.

Values for internal CO_2 concentration (Ci) in stressed plants increased significantly (P < 0.05) only at the end of both stress periods (30 and 20% higher than the control values, for the first and the second stress periods, respectively) and recovered to control values after rewatering (Table 2).

The relationship between leaf conductance and net photosynthesis was similar during both stress periods, showing a curvilinear ($R^2 = 0.70$ cubic v. 0.53 for a linear model) relationship. The combined data for both stress periods indicate a steep slope at low g_l values (< 80 mmol m^{-2} s^{-1}), but

stabilizing at higher givalues (Fig. 4).

DISCUSSION

The imposition of water stress on apricot plants induced a limitation of plant growth and a significant reduction in total leaf area (Table 1), largely due to the abscission of mature (fully expanded) leaves. Leaf abscission under water stress is an avoidance mechanism, since it reduces the transpiration surface area (Nash & Graves 1993).

The high and constant Ψ_{pd} values in control plants during the experimental period (Fig. 1) indicates that adequate water supplies were present, as is confirmed by the values for soil water stock (c. 130 mm, which corresponds to field capacity) (data not shown). Torrecillas *et al.* (1988) indicated that pre-dawn leaf water potential depends mainly on soil moisture.

The existence of differences between Ψ_{pd} and Ψ_{md} values in stressed plants at the end of both water withholding periods suggested that some recovery in leaf water potential took place during the night (Fig. 1). At that time, very low SWS values were registered (c. 44 mm), suggesting that the capacity of the conducting system to transport water was sufficient to allow some rehydration of leaves at night. The rapid recovery of leaf water potential after rewatering the plants (Fig. 1) has been also observed when tomato, almond and lemon plants were subjected to severe water stress (Torrecillas *et al.* 1995, 1996; Ruiz-Sánchez *et al.* 1997).

Stressed apricot leaves showed epinasty (decrease in LIA values) (Table 2). At the end of both stress periods, the leaf insertion angle

decreased significantly (P < 0.05) in stressed plants, with a reduction of c. 15% respect to control values, coinciding with minimum Ψ_p values and stomatal closure (Table 2 and Fig. 3). Changes in leaf orientation have been associated with a mechanism of adaptive significance to reduce water loss and leaf heating (Sánchez-Blanco $et\ al.$ 1994). The parallel behaviour of Ψ_p and LIA in stressed plants could indicate that epinastic movement is turgor-dependent.

In fruit trees, the capacity for osmotic adjustment in response to water stress varies as a function of species as well as the cultivar considered (Lakso 1990; Torrecillas $et\ al.$ 1996). The observed Ψ_{os} reduction in stressed apricot plants (Table 3) can be considered to be a result of active accumulation of solutes (Wilson $et\ al.$ 1989) because of the observed osmotic adjustment (0.27 and 0.60 MPa for the first and second water stress periods, respectively). The greater osmotic adjustment during the second stress period could be ascribed to the accumulative effect of water stress.

Although it has been pointed out that Ψ_{os} affects Ψ_{tlp} in other crop species (Sánchez-Blanco *et al.* 1991; Torrecillas *et al.* 1996), a different pattern in Ψ_{os} and Ψ_{tlp} was observed for apricot plants under our experimental conditions (Table 3). This situation could indicate that the osmotic adjustment reached was not sufficient to modify the Ψ_{tlp} values.

The relative apoplastic water content (RWC_a) in apricot plants, ranging from 27 to 42% (Table 3), is relatively high compared with other tree species such as *Eucalyptus globulus* (14-27%) (Correia *et al.* 1989) and *Quercus alba* (26-31%) (Parker & Pallardi 1987), but lower than those found in *Pinus*

ponderosa (57-81%) (Hardegree 1989) and grapes (51-63%) (Rodrigues *et al.* 1993). The values obtained were similar to the lower limit of the range (30-70%) found for carob and almond trees (Nunes *et al.* 1989; Torrecillas *et al.* 1996). High RWC_a values are common in xeromorphic plants (Cutler *et al.* 1977). The existence of high RWC_a values in different plant species could be attributable to thicker cell walls or differences in cell wall structure (Hellkvist *et al.* 1974; Torrecillas *et al.* 1996).

The rapid decrease in leaf conductance from the beginning of the stress period, together with the delay in stomatal reopening after rewatering the plants (Fig. 3), with respect to the recovery of Ψ_{md} (Fig. 1), indicated that stomatal closure was not a simple passive response to water deficit; therefore, the pattern of g_l under water stress may be related to hormonal changes within the leaf, such as an increase in abscisic acid and/or a decrease in cytokinin content (Mansfield 1987; Davies & Zhang 1991). On the other hand, plants that delay stomatal opening following rewatering after drought might compete better on drier sites, since this would allow them to regain full turgor more effectively (Mansfield & Davies 1981).

Gradual closure of stomata over a wide range of leaf water potential may be of value in maintaining some photosynthesis during drought, as indicated by the relationship between g_l and Pn in stressed plants (Fig. 4). This curvilinear relationship suggests a stomatal limitation of leaf net photosynthesis below a g_l value of *c*. 80 mmol m⁻² s⁻¹ (Bethenod *et al*. 1989). Above this value, Pn levelled off (Fig. 4). The observed stomatal closure, together with leaf epinasty and partial defoliation, can be considered to be complementary mechanisms in regulating transpiration more effectively, and

have been recognised as important adaptive mechanisms to drought in crops (Tudela & Primo-Millo 1992).

The observation that significant decreases in leaf net photosynthesis occurred only at the end of the stress periods, together with the rapid recovery after rewatering the plants (Fig. 3), could indicate that productivity of the remaining leaves may only be slightly affected by short-term water stress. The higher (non-significant) net photosynthesis in stressed plants after rewatering relative to control plants (Fig. 3) may have been due to increased root activity after rehydration (Ceulemans *et al.* 1983) and/or stress-induced enhancement of photosynthetic capacity (Gebre & Kuhns 1993). An alternative explanation was suggested out by Ludlow (1975), who indicated that stressed leaves might be physiologically younger than leaves of the same chronological age, assuming that water stress suspends ageing.

The increase in internal CO₂ concentration observed in apricot plants at the end of both stress periods (Table 2) was consistent with the view that stomatal closure occurs as Ci increases (Hall *et al.* 1976). Eckstein & Robinson (1996) indicated that limitation of leaf photosynthesis under water stress conditions was caused by a combination of stomatal restriction and disruption of the mechanisms of photosynthetic carbon metabolism, leading to high Ci concentrations (Castrillo & Calcagno 1989).

It has been observed that leaf conductance in stressed apricot plants declined prior to changes in net photosynthesis, and that the recovery of Pn was faster than that of g_I (Fig. 3). This observation implies that the main role of stomata under water stress is to optimize the balance between CO₂ uptake and water loss via transpiration (Farquhar & Sharkey 1982). Similar

behaviour has been observed in lupin (Rodrigues *et al.* 1989), cottonwood (Gebre & Kuhns 1993), and various sclerophyllous species (Schulze 1986).

The above results indicate that apricot plants exposed to short-term water stress depended primarily on avoidance mechanisms, together with osmotic adjustment. These avoidance mechanisms were complementary and took place progressively. Early in each stress period, leaf conductance decreased in order to control water loss via transpiration and avoid decreases in leaf water potential. When, at the end of each stress period, severe water stress developed, other avoidance mechanisms are triggered, such as epinasty (change in leaf insertion angle), low leaf conductance and reduced net photosynthesis, and a degree of leaf shedding. The rapid recovery of Pn, as well as the progressive recovery of g_l after rewatering the plants, can also be considered as mechanisms for maintaining leaf productivity and promoting leaf rehydration.

Some drought tolerance characteristics were also observed in apricot. These were mainly based on the existence of high relative apoplastic water content and low leaf osmotic potentials at the turgor loss point. In addition, the observed osmotic adjustment could contribute to the maintenance of leaf turgor during stress.

The observation that increased osmotic adjustment and smaller Pn reductions occurred at the end of the second stress period might suggest an acclimation capacity in apricot. However, in our opinion, this cannot be definitively concluded from the results obtained, and further research is necessary to compare different water stress hardening (preconditioning) treatments, as well as more than two water stress cycles.

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REFERENCES

- BETHENOD, O., PILARSKI, J. & QUETIN, P. (1989). *In situ* measurement of leaf water use efficiency of lilac (*Syringa vulgaris*): comparison with crop plants. *Annales des Sciences Forestières* **46**, 421-425.
- CASTRILLO, M. & CALCAGNO, A.M. (1989). Effects of water stress and rewatering on ribulose-1.5-biphosphate carboxylase activity, chlorophyll and protein contents in two cultivars of tomato. *Journal of Horticultural Science* **64**, 717-724.
- CEULEMANS, R., IMPENS, Y. & NG, A.P. (1983). Photosynthesis, stomatal conductance and leaf water potential during water stress situations in young rubber tree (*Hevea brasiliensis*) under tropical conditions. In *Effects of Stress on Photosynthesis* (Eds R. Marcelle, H. Clijsters & M. van Poncke), pp. 11-119. The Hague: Martinus Nijhoff/Dr. W. Junk Publishers.
- CORREIA, M.J., TORRES, F. & PEREIRA, J.S. (1989). Water and nutrient supply regimes and the water relations of juvenile leaves of *Eucalyptus globulus*. *Tree Physiology* **5**, 459-471.
- CUTLER, J.M., RAINS, D.W. & LOOMIS, R.S. (1977). The importance of cell size in the water relations of plants. *Physiologia Plantarum* **40**, 255-260.
- DAVIES, W.J. & ZHANG, J. (1991). Root signals and regulation of growth and development of plants in drying soils. *Annual Review of Plant Physiology* and Plant Molecular Biology **42**, 55-76.
- ECKSTEIN, K. & ROBINSON, J.C. (1996). Physiological responses of banana (*Musa* AAA; Cavendish sub-group) in the subtropics. VI.

- Seasonal responses of leaf gas exchange to short-term water stress. Journal of Horticultural Science **71**, 679-692.
- FARQUHAR, G.D. & SHARKEY, T.D. (1982). Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology* **33**, 317-345.
- GEBRE, G.M. & KUHNS, M.R. (1993). Effects of water stress preconditioning on gas exchange and water relations of *Populus deltoides* clones. *Canadian Journal of Forest Research* **23**, 1291-1297.
- HALL, A.E., SCHULZE, E.D. & LANGE, O.L. (1976). Current perspectives of steady-state stomatal responses to environment. In *Water and Plant Life. Ecological Studies* 19 (Eds O.L. Lange, L. Kappen & E.D. Schulze), pp. 169-188. New York: Springer-Verlag.
- HARDEGREE, S.P. (1989). Discrepancies between water potential isotherm measurements on *Pinus ponderosa* seedling shoots: xylem hysteresis and apoplasmic potentials. *Plant, Cell and Environment* **12**, 57-62.
- HELLKVIST, J., RICHARDS, G.P. & JARVIS, P.G. (1974). Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. *Journal of Applied Ecology* **11**, 637-667.
- LAKSO, A.N. (1990). Interactions of physiology with multiple environmental stresses in horticultural crops. *HortScience* **25**, 1365-1369.
- LUDLOW, M.M. (1975). Effects of water stress on the decline of leaf net photosynthesis with age. In *Environmental and Biological Control of Photosynthesis* (Ed R. Marcelle), pp. 123-134. The Hague: Dr. W. Junk Publishers.
- MANSFIELD, T. A. (1987). Hormones as regulators of water balance. In *Plant*

- Hormones and their Role in Plant Growth and Development (Ed. W.J. Davies), pp. 411-430. Dordrecht: Martinus Nijhoff Publishers.
- MANSFIELD, T.A. & DAVIES, W.J. (1981). Stomata and stomatal mechanisms. In *The Physiology and Biochemistry of Drought Resistance* in *Plants* (Eds L.G. Paleg & D. Aspinall), pp. 315-346. New York: Academic Press.
- MINISTERIO DE AGRICULTURA, PESCA Y ALIMENTACIÓN (1995).

 Anuario de Estadística Agraria 1993, Madrid.
- NASH, L.J. & GRAVES, W.R. (1993). Drought and flood stress effects on plant development and leaf water relations of five taxa of trees native to bottomland habitats. *Journal of American Society for Horticultural Science* **118**, 845-850.
- NUNES, M.A., CATARINO, F. & PINTO, E. (1989). Strategies for acclimation to seasonal drought in *Ceratonia siliqua* leaves. *Physiologia Plantarum* **77**, 150-156.
- PARKER, W.C. & PALLARDI, S.G. (1987). The influence of resaturation method and tissue type on pressure-volume analysis of *Quercus alba*L. seedlings. *Journal of Experimental Botany* **38**, 535-549.
- RODRIGUES, M. L., CHAVES, M.M. & MARTINS, J.M.N. (1989). Carbon and water economy of two lupin lines under induced water stress. In *Structural and Functional Responses to Environmental Stresses* (Eds K.H. Kreeb, H. Richter & T.M. Hinckley), pp. 219-226. The Hague: SPB Academic Publishing.
- RODRIGUES, M.L., CHAVES, M.M., WENDLER, R., DAVIS, M.M., QUICK, W.P., LEEGOOD, R.C., STITT, M. & PEREIRA, J.S. (1993). Osmotic

- adjustment in water stressed grapevine leaves in relation to carbon assimilation. *Australian Journal of Plant Physiology* **20**, 309-321.
- RUIZ-SÁNCHEZ, M.C., DOMINGO, R., SAVÉ, R., BIEL, C. & TORRECILLAS, A. (1997). Effects of water deficit and rewatering on leaf water relations of Fino lemon plants. *Biologia Plantarum* **39**, 623-631.
- SÁNCHEZ-BLANCO, M.J., BOLARÍN, M.C., ALARCÓN, J.J. & TORRECILLAS, A. (1991). Salinity effects on water relations in *Lycopersicon esculentum* and its wild salt-tolerant relative species *L. pennellii. Physiologia Plantarum* **83**, 269-274.
- SÁNCHEZ-BLANCO, M.J., ALARCÓN, J. J., PLANES, J. & TORRECILLAS, A. (1994). Differential flood stress resistance of two almond cultivars based on survival, growth and water relations as stress indicators.

 Journal of Horticultural Science 69, 947-953.
- SAVÉ, R., BIEL, C., DOMINGO, R., RUIZ-SÁNCHEZ, M.C. & TORRECILLAS, A. (1995). Some physiological and morphological characteristics of citrus plants for drought resistance. *Plant Science* **110**, 167-172.
- SCHULZE, E.D. (1986) Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. *Annual Review of Plant Physiology* **37**, 247-274.
- TORRECILLAS, A., RUIZ-SÁNCHEZ, M.C., DEL AMOR, F. & LEÓN, A. (1988). Seasonal variations on water relations of *Amygdalus communis*L. under drip irrigated and non-irrigated conditions. *Plant and Soil* **106**, 215-220.
- TORRECILLAS, A., GUILLAUME, C., ALARCÓN, J.J. & RUIZ-SÁNCHEZ, M.C. (1995). Water relations of two tomato species under water stress

- and recovery. Plant Science 110, 167-172.
- TORRECILLAS, A. ALARCÓN, J.J. DOMINGO, R. PLANES J. & SÁNCHEZ-BLANCO, M.J. (1996). Strategies for drought resistance in leaves of two almond cultivars. *Plant Sci*ence **118**, 135-143.
- TUDELA, D. & PRIMO-MILLO, E. (1992). 1-Aminocyclopropano-1 carboxylic acid transported from roots to shoots promotes leaf abscission in Cleopatra mandarin (*Citrus reshni* Hort. ex Tan.) seedlings rehydrated after water stress. *Plant Physiology* **100**, 131-137.
- TURNER, N.C. (1988). Measurement of plant water status by the pressure chamber technique. *Irrigation Science* **9**, 289-308.
- TYREE, M. T. & HAMMEL, H.T. (1972). The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *Journal of Experimental Botany* **23**, 267-282.
- TYREE, M.T. & RICHTER, H. (1982). Alternative methods of analysing water potential isotherms: some cautions and clarifications. II. Curvilinearity in water potential isotherms. *Canadian Journal of Botany* **60**, 911-916.
- WILSON, J.R., LUDLOW, M.M., FISHER, M.J. & SCHULZE, E.D. (1989).

 Adaptation to water stress of the leaf water relations of four tropical forage species. *Australian Journal of Plant Physiology* **7**, 207-220.

Table 1. Growth parameters for apricot plants based on dry weight, total leaf area, leaf succulence and average leaf area in control and stress treatments at the end of the experimental period.

Variable	Control	Stress	S.E. (4 D.F.)
Stem DW (g plant ⁻¹)	421.9	387.5	10.08
Root DW (g plant ⁻¹)	189.6	187.6	14.70
Leaf DW (g plant ⁻¹)	135.9	117.0	3.47
Total leaf area (dm ² plant ⁻¹)	94.5	81.4	5.47
Leaf succulence (FW/DW)	0.21	0.15	0.015
Leaf area (cm ² leaf ⁻¹)	26.81	25.35	0.913

FW, fresh weight; DW, dry weight.

Table 2. Effect of water stress on leaf turgor potential (Ψ_p) , epinasty (LIA) and internal CO_2 concentration (Ci) of apricot plants in control and stress treatments. (\rightarrow indicates the end of the water withholding periods).

	Ψ _P (MPa)			LIA (°)			Ci (mg l ⁻¹)		
Days	Control	Stress	S.E. (6 D.F.)	Control	Stress	S.E. (6 D.F.)	Control	Stress	S.E. (6 D.F.)
0	1.46	-		79.2	-		229.1	-	
6 →	1.12	0.06	0.03	76.3	66.7	3.1	211.5	296.8	11.5
8	1.48	1.20	0.10	74.1	67.8	2.0	271.5	285.8	8.1
10	1.27	1.49	0.05	78.3	77.1	1.1	263.6	254.9	7.8
14 →	1.18	0.26	0.03	76.7	63.4	1.2	234.1	281.7	9.5
16	1.42	1.14	0.33	76.4	73.3	0.7	273.7	266.9	7.8
18	1.30	1.25	0.12	75.3	72.5	0.4	255.0	257.1	11.6
20	1.33	1.26	0.22	75.1	74.7	0.5	266.9	278.5	9.8

Table 3. Effect of water stress on leaf osmotic potential at full turgor (Ψ_{os}) , leaf osmotic potential at turgor loss point (Ψ_{tlp}) and relative apoplastic water content (RWC_a) of apricot plants in control and stress treatments. (\rightarrow indicates the end of the water withholding periods).

	Ψ _{os} (MPa)			Ψ _{tlp} (MPa)			RWC _a (%)		
Days	Control	Stress	S.E. (6 D.F.)		Stress	S.E. (6 D.F.)	Control	Stress	S.E. (6 D.F.)
0	-1.56	-		-2.86	-		39.10	-	
6 →	-1.82	-2.09	0.06	-2.66	-2.91	0.18	37.00	39.10	2.75
8	-1.36	-1.65	0.07	-2.52	-2.58	0.20	34.76	31.76	4.45
14 →	-1.52	-2.12	0.08	-2.82	-3.02	0.14	42.04	34.93	1.88
16	-1.89	-2.06	0.04	-3.50	-2.89	0.16	29.18	30.82	1.67
20	-1.59	-1.58	0.08	-3.17	-3.15	0.32	30.06	29.89	2.30

Legend to figures.

Fig. 1. Pre-dawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potential for apricot plants in control (\bullet) and stress (o) treatments. Asterisks indicate the end of the stress periods. Vertical bars are \pm S.E. of the mean (not shown when smaller than the symbols), D.F. = 6.

Fig. 2. Relationship between stock of water in the soil (SWS) and pre-dawn leaf water potential (Ψ_{pd}) in stressed apricot plants. Regression equation of fitted line: Ψ_{pd} = SWS / (92.48 - 2.75 SWS), (R 2 = 0.80).

Fig. 3. Leaf conductance (g_i) and net photosynthesis (Pn) of apricot plants in the control (\bullet) and stress (o) treatments. Asterisks indicate the end of the stress periods. Vertical bars are \pm S.E. of the mean (not shown when smaller than the symbols), D.F. = 6.

Fig. 4. Relationship between net photosynthesis (Pn) and stomatal conductance (g_i) in stressed apricot plants. The best fit equation for the whole data set was Pn = -1.99 + 0.19 g_i -1.35 g_i^2 + 3.25 g_i^3 (R 2 = 0.70).

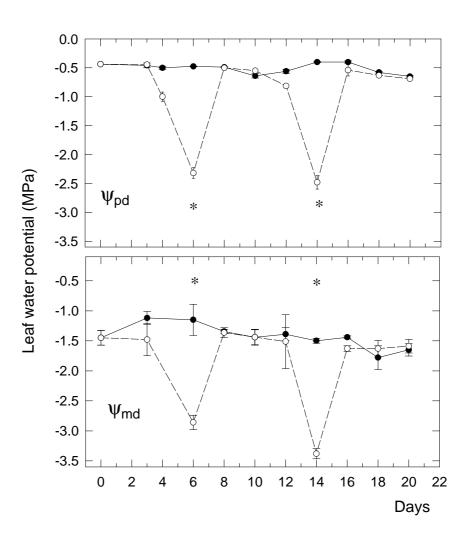


Figure 1
Ruiz-Sánchez et al. (1997)

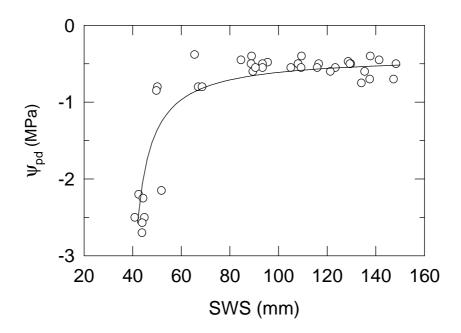


Figure 2 Ruiz-Sánchez *et al.* (1997)

Figure 3

Ruiz-Sánchez et al. (1997)

Figure 4

Ruiz-Sánchez et al. (1997)

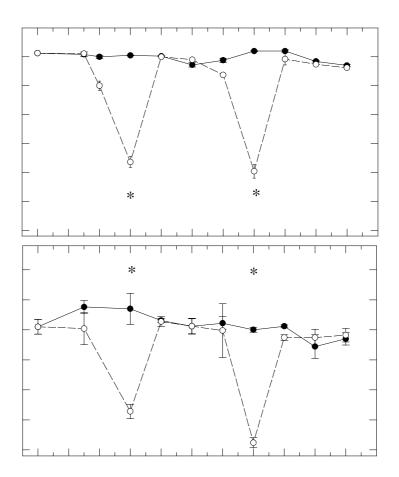


Figure 1
Ruiz-Sánchez *et al.* (1997)

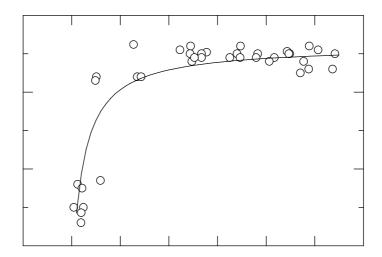


Figure 2 Ruiz-Sánchez *et al.* (1997)

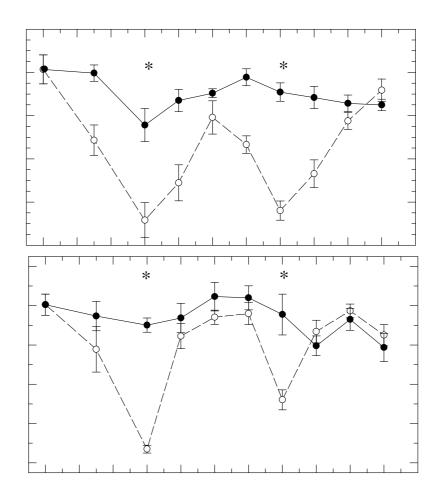


Figure 3 Ruiz-Sánchez *et al.* (1997)

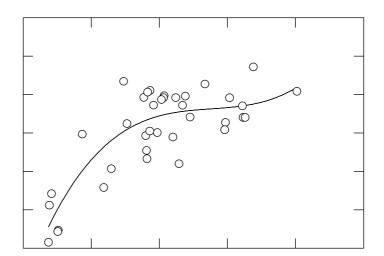


Figure 4
Ruiz-Sánchez *et al.* (1997)