Water stress preconditioning to improve drought resistance in young apricot plants

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Abstract

The effect of water stress preconditioning was studied in one-year-old apricot plants (*Prunus armeniaca* L., cv. Búlida). Plants were submitted to different treatments: T-0 (control treatment) and T-1, drip irrigated daily; T-2 and T-3, irrigated daily at 50% and 25% of T-0, respectively; T-4 and T-5, irrigated to field capacity every 3 and 6 days, respectively. After 30 days, irrigation was withheld for 10 days, maintaining the T-0 treatment irrigated daily. After this period, the plants were re-irrigated to run-off and treated as control treatment. The stomatal closure and epinasty observed in response to

water stress represented adaptive mechanisms to drought, allowing the plants to regulate water loss more effectively and prevent leaf heating. A substantial reduction in the irrigation water supplied combined with a high frequency of application (T-3 treatment) promoted plant hardening; the plants enduring drought better, due to their greater osmotic adjustment (0.77 MPa), which prevented severe plant dehydration and leaf abscission. Such a preconditioning treatment may be valuable for young apricot plants in the nursery stage in order to improve their subsequent resistance to drought. A 50% reduction in daily irrigation (T-2 treatment) did not significantly affect either gas exchange rates or leaf turgor, which suggests that water should be applied frequently if deficit irrigation is to be implemented.

Keywords: Gas exchange; Osmotic adjustment; Plant hardening; *Prunus armeniaca*; Water relations; Water stress.

Abbreviations: g_l, leaf conductance LIA, leaf insertion angle; Pn, net photosynthesis; Tc-Ta, canopy to air temperature difference; TDR, time domain reflectometry; θ_v, volumetric soil water content; Ψ_m, soil matric potential; Ψ_{md}, mid-day leaf water potential; Ψ_o, leaf osmotic potential; Ψ_{os}, leaf osmotic potential at full turgor; Ψ_p, leaf turgor potential; Ψ_{pd}, pre-dawn leaf water potential.

1. Introduction

Apricot is one of the few temperate fruit trees not affected by overproduction. Most apricot trees are cultivated in Mediterranean countries, under where drought periods are increasingly common, a fact which makes irrigation water the most limiting factor for apricot productivity, since it affects the viability of the young plantations.

Plants have developed physiological responses as well as ecological strategies to cope with water shortages, either by stress avoidance or stress tolerance. These responses allow them to survive and even to maintain some growth under adverse conditions. Plant response depends on the nature of the water shortage inducing physiological responses to short-term changes [1], acclimation to a certain level of water availability [2] and adaptation to drought [3, 4].

A knowledge of drought resistance mechanisms makes it easier to plan deficit irrigation strategies designed to save water while minimising the negative impacts on yield or crop revenue [5].

Previous studies have indicated that apricot drought resistance is mainly based on avoidance mechanisms, together with some degree of osmotic adjustment, when plants are submitted to short-term water stress periods [6]. However, drought imposition rates can have a large effect on the results of studies on drought resistance [7].

For these reasons, the aim of this study was to determine the ability of young apricot plants to drought hardening by the application of different water stress preconditioning treatments, as well as to improve our understanding of

the physiological mechanisms involved in the response of apricot plants to water stress. Such information may be valuable in the nursery stage in order to improve the drought resistance of young apricot plantations.

2. Material and methods

2.1. Plant material and experimental conditions

The experiment was carried out on one-year-old apricot trees (*Prunus armeniaca* L.), cv. Búlida, on Pollizo prune (*P. domestica* L.) rootstock, growing under field conditions in 35 litre pots (40 cm diameter) containing a mixture of clay loam topsoil and peat, with 4% organic matter. Holed pots were buried in the soil in order to minimise increases in soil temperature. Plants were drip irrigated daily using one emitter of 4 l h^{-1} per tree, maintaining the soil matric potential at about -20 kPa (monitored with tensiometers placed at 15 cm depth). Routine fertilization was applied (65 g N, 48 g K_2O, 72 g P_2O_5 and 1.5 g Fe (Fe-EDDHA) per plant and year) through the drip irrigation system every 2 weeks. No root emergence from pots into the surrounding soil was observed.

At the end of July 1997, 30 trees of similar appearance were selected, and the following preconditioning treatments were imposed: T-0 (control treatment) and T-1, drip irrigated daily to field capacity; T-2, daily irrigated at 50% of the control treatment; T-3, daily irrigated at 25% of the control treatment; T-4, irrigated every 3 days to field capacity and T-5, irrigated every 6 days to field capacity. Plants were maintained for 30 days under these irrigation conditions (preconditioning period), after which irrigation was withheld for 10 days (stress

period) in all plants, except the control treatment (T-0), which continued to be irrigated daily. The pots were sealed with plastic film and covered with soil in order to decrease the rate at which water stress developed. Then, all the plants were re-irrigated to run-off and treated in the same way as the control treatment (recovery period).

The climatic conditions were typical of a Mediterranean climate. During the preconditioning period maximum air temperature was 34.7 ± 0.89 ºC, with a vapour pressure deficit (VPD) of the atmosphere at mid-day of 3.51 ± 0.31 kPa (calculated from dry and wet-bulb temperature data of the weather station, located in the orchard). During the stress/recovery period maximum air temperature was 26.9 ± 1.93 ºC and VPD 1.65 ± 0.97 kPa. Photosynthetically active radiation (PAR) at mid-day, measured at the canopy surface with a line quantum sensor (LI-COR, model 190 S-1), fluctuated around 1600 ± 50 μmol m^{-2} s^{-1} during the experimental period.

2.2. Measurements

Soil and plant water status, and leaf gas exchange were measured every 6 days during the preconditioning period and every 2 to 3 days during the stress/recovery period. Volumetric soil water content (θ_v) and soil matric potential (Ψ_m) were determined in 3 pots per treatment using time domain reflectometry (TDR) equipment [8] and tensiometers at 15 cm depth,

respectively. A pair of TDR probes was installed at a depth of 250 mm, midway between the tree trunk and pot border.

Leaf water potential was measured at pre-dawn (Ψ_{pd}) and at mid-day (12.00 h solar time) (Ψ_{md}) for one mature leaf per plant and 3 plants per treatment, using a pressure chamber, following the recommendations of Turner [9]. Leaves were fully expanded and were selected at random from the middle third of the shoots. After measuring Ψ_{pd}, the leaves were frozen in liquid nitrogen and osmotic potential (Ψ_o) was measured after thawing the samples and extracting the sap, using a Wescor 5500 vapour pressure osmometer. Pre-dawn leaf turgor potential (Ψ_p) was derived as the difference between leaf osmotic and water potentials.

Leaf osmotic potential at full turgor (Ψ_{os}) was measured on leaves adjacent to those used to measure leaf water potential. 3 leaves per treatment were taken at pre-dawn and rehydrated to full saturation, following the same methodology as for Ψ_o. Osmotic adjustment was estimated as the difference between the Ψ_{os} of stressed and control plants.

Leaf conductance (g_l) and net photosynthesis (Pn) were measured at mid-day for a similar number and type of leaves as for leaf water potential, using a field-portable, closed gas-exchange photosynthesis system (LI-6200) supplied with IRGA (LI-6250). Leaf was enclosed within a fan stirred one-litre chamber. The mean return flow rates of air circulating within the closed system and the leaf to air vapour deficit for all measurements were 280 μmol s^{-1}, and 1.8-2.4

kPa, respectively. The CO_2 analyser was calibrated daily with two standard CO_2/air mixtures.

The angle between leaf petiole and stem (leaf insertion angle, LIA) was measured with a transparent protractor to determine epinasty, the change in petiole angle. 10 randomised leaves per plant and 3 plants per treatment were measured.

Canopy temperature was measured using an infrared thermometer (Infrared Ag Multimeter de Everest Interscience Inc.) at mid-day. 4 measurements were taken in 3 plants per treatment. Simultaneously, air wet and dry bulb temperatures were monitored.

Defoliation was estimated by counting the number of leaves per plant at the beginning and at the end of the experimental period in 4 plants per treatment.

The design of the experiment was completely randomised with 5 replications. One plant per replicate was used. A one-way ANOVA was performed and means were separated by $LSD_{0.05}$ range test.

3. Results and discussion

3.1. Preconditioning period

During the preconditioning period (Table 1) a substantial depletion in soil water was observed in treatments T-3 (irrigated at 25% of control) and T-5

(irrigated every 6 days), with values of θ_v around 10.6%, and beyond the range of the tensiometer readings (< -80 kPa) (Table 1). Values of soil volumetric water content were slightly higher in pots from the T-2 treatment (irrigated at 50% of control) than those of the T-4 treatment (irrigated every 3 days). However, both promoted moderate plant water deficits, as indicated by the pre-dawn leaf water potential (Ψ_{pd}) values, which were around -0.7 MPa in these treatments (Fig. 1 and Table 1). In the T-3 and T-5 treatments a more severe plant water deficit (Ψ_{pd} around -1.1 MPa) was registered (Fig. 1). The values of leaf water potential at mid-day (Ψ_{md}) followed a similar behaviour to that of Ψ_{pd} (Table 1). Only the more severe water deficit situations (T-3 and T-5 treatments) induced decreases in leaf turgor potential (Ψ_p) values with respect to the control treatment (Table 1).

No significant differences in leaf osmotic potential at full turgor (Ψ_{os}) were found between treatments during the preconditioning period, with values of around -1.9 MPa in all the treatments (data not shown).

Similarly to that observed for leaf water potential, all the water-stressed treatments induced epinasty (a significant decrease in the leaf insertion angle values), particularly in the plants from the T-5 treatment (Table 2). A very strong relationship between LIA and Ψ_{md} was found (Fig. 2), confirming the view that epinastic movements in apricot plants are dependent on plant water status [6]. Changes in leaf orientation allow to a lower incidence of solar radiation and, as a consequence, a reduction in water loss and leaf heating [10].

Leaf conductance (g_l) was reduced by the water deficits applied, except in the T-2 treatment, which showed similar values to the control treatment. A 50% of reduction in g_l values occurred in plants from the T-3 and T-5 treatments (Table 2). However, net photosynthesis (Fn) only decreased significantly in the severe water deficit treatments (T-3 and T-5) (Table 2). Both parameters were linearly correlated (r = 0.87***, data not shown), which suggested a limitation in the photosynthetic capacity under water stress conditions [11]. Similar relationships between Pn and g_l have been reported for other *Prunus* species [12, 13], indicating an efficient co-ordination of stomatal behaviour and photosynthetic activity [14].

Within the range of mid-day leaf water potential values measured during the preconditioning period, a parallel decrease in leaf conductance and leaf water potential was found (Fig. 3). The linear relationship indicates that the regulation of water losses occurred early and regularly [15, 16]. The lack of a critical threshold Ψ_{md} to induce stomatal closure is similar to the findings of studies on almond [17], peach [18] and citrus [19], but contrast with those on apple [20] and senescent almond leaves [21].

Canopy temperature in control plants was around 31 ºC, whereas plants from the T-3 and T-5 showed the highest canopy temperatures (around 35 ºC) (data not shown). Canopy minus air temperature (Tc-Ta) values showed that well irrigated plants (T-1 treatment) keep their leaves 3ºC lower than air temperature (Table 2), which indicates the cooling effect of adequate transpiration levels [22, 23]. Stressed plants from the T-5 treatment presented a

positive value of canopy minus air temperature (Table 2). In this sense, Ehler [24] indicated that Tc-Ta values increase progressively when soil moisture is a limiting factor, for that reason it can be used as an index of plant water status [25].

3.2. Stress/recovery period

At the end of the withholding period, soil water content values were near permanent wilting point (around 9.5%, data not shown) in all the stressed treatments. Plants which had not been preconditioned (T-1 treatment) and those from the treatment irrigated every 6 days during the preconditioning period (T-5) reached the highest plant water deficits ($\Psi_{pd} \approx$ -4 MPa) (Fig. 4). Plants from the treatment irrigated daily at 25% of the control (T-3) presented the lowest plant water stress, with values of ≈ -1.6 MPa, compared to the -0.5 MPa measured in the control treatment (T-0) (Fig. 4).

Leaf turgor potential was close to zero in all the plants after 10 days of withholding irrigation. Plants from the T-3 treatment presented the lowest decrease, with values of Ψ_p = 0.7 MPa, compared with the 1.4 MPa of the T-0 treatment (data not shown). These plants also showed a smaller decrease in the leaf insertion angle (data not shown).

Water withholding induced a significant reduction in leaf osmotic potential at full turgor (Ψ_{os}) in all the preconditioned plants, with values of -2.16, -2.49, -2.04 and -2.22 MPa for T-2, T-3, T-4 and T-5 treatments, respectively.

No significant differences were found in Ψ_{os} values between the control (T-0) and the unpreconditioned (T-1 treatment) plants, with values of –1.72 and -1.84 MPa, respectively. A higher amount of osmotic adjustment occurred in plants from the T-3 treatment (0.77 MPa).

Osmotic adjustment may be responsible for maintaining of turgor in these plants [26]. In this sense, the obtained results confirmed that in apricot plants it is necessary to reach severe plant water deficits (Ψ_{pd} < -2 MPa) to trigger this tolerance mechanism [6]. Gebre and Kuhns [27] indicated that cottonwood plants submitted to water stress preconditioning using different irrigation intervals developed a limited osmotic adjustment of 0.2 MPa, although this mechanism was not observed after severe water stress (10 days of withholding irrigation).

Canopy temperature increased significantly in all the studied treatments, with values 3-4 ºC above the air temperature (data not shown).

Leaf conductance and net photosynthesis values were severely reduced by withholding irrigation in all the studied treatments (Fig. 5). However, a smaller reduction in g_l and Pn was observed in plants from the T-3 treatment, which showed a 55% reduction with respect to the control treatment (T-0) values, compared with the 75% reduction observed in the rest of the stressed treatments (Fig. 5).

Three days after irrigation was restored, pre-dawn leaf water potential reached similar values to those of the control treatment (Fig. 4). Leaf

conductance recovery was rapid in plants from the T-5 treatment (3 days), whereas in T-2, T-3 and T-4, total recovery occurred 5 days after re-irrigation of plants, and two days later in plants from the unpreconditioned treatment (T-1) (Fig. 5). Net photosynthesis recovered more rapidly than g_l, reaching values close to those of control plants in all the stressed treatments on day 5 of the recovery period (Fig. 5).

The faster recovery in leaf conductance values after re-irrigation in plants of the T-5 treatment can be explained by the greater defoliation suffered by these plants (data not shown). Most of the remaining leaves in these plants were young and have higher leaf conductance levels that mature leaves [18, 28, 29]

The relative delay in stomatal opening following rewatering (Fig. 5) compared with the rapid recovery shown by Ψ (Fig. 4) may be considered as a safety mechanism, which allows plants to regain full turgor more effectively [30].

4. Conclusions

Young apricot plants exposed to slight-moderate water stress conditions developed avoidance mechanisms based on stomatal closure, accompanied by leaf epinasty, which can be considered as a complementary mechanism for regulating transpiration, and both have been recognised as important adaptive mechanisms to drought. Under more severe water stress conditions (Ψ_{pd} < -1.75 MPa) partial defoliation occurred and osmotic adjustment was triggered as a tolerance mechanism.

Water stress induced by daily irrigation at 25% of the control (T-3 treatment) promoted plant hardening. When these plants were submitted to severe water stress conditions, they showed a lower reduction in leaf water potential and gas-exchange parameters, as well as lower epinasty, mainly due to their greater osmotic adjustment, which prevented severe plant dehydration and leaf abscission. This preconditioning treatment may be valuable in the nursery stage, since it hardens the plants against drought and so improve the survivability of the young apricot plantations.

Also, from a comparative study of the tested treatments, we can conclude that, when deficit irrigation is to be applied, it is advisable to use a high frequency with reduced amounts of water than longer irrigation intervals, since neither gas exchange nor leaf turgor was reduced by this.

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Table 1

Volumetric soil water content (θ_v), soil matric potential (Ψ_m), leaf water potential at pre-dawn (Ψ_{pd}) and at mid-day (Ψ_{md}) and leaf turgor potential (Ψ_p) in the different water stress treatments during the preconditioning period[a]

Treatment	θ_v (%)	Ψ_m (kPa)	Ψ_{pd} (MPa)	Ψ_{md} (MPa)	Ψ_p (MPa)
T-0 (control)	28.46 d	- 9.33 a	- 0.46 c	- 1.81 d	1.90 c
T-2 (50% T-0)	18.28 c	- 39.60 b	- 0.68 b	- 2.44 c	1.78 bc
T-3 (25% T-0)	10.70 a	*	- 1.08 a	- 2.89 ab	1.44 ab
T-4 (every 3 d)	14.47 b	- 55.25 c	- 0.69 b	- 2.62 bc	1.56 abc
T-5 (every 6 d)	10.40 a	*	- 1.14 a	- 3.18 a	1.23 a

[a]Data are the average of 5 measurements taken every 6 days. Values followed by a different letter indicate the existence of significant differences according to $LSD_{0.05}$ test.

*Beyond the range of the tensiometer.

Table 2

Leaf insertion angle (LIA), leaf conductance (g_l), net photosynthesis (Pn), and canopy to air temperature difference (Tc-Ta), in the different water stress treatments during the preconditioning period[a]

Treatment	LIA (º)	g_l (mmol m^{-2} s^{-1})	Pn (μmol CO_2 m^{-2} s^{-1})	Tc-Ta (ºC)
T-0 (control)	82.43 d	135.63 c	8.52 b	-2.75 a
T-2 (50% T-0)	62.50 c	109.02 bc	7.26 ab	-1.13 b
T-3 (25% T-0)	45.95 b	67.21 a	4.54 a	-0.40 bc
T-4 (every 3 d)	41.44 b	94.61 ab	6.57 ab	-1.20 b
T-5 (every 6 d)	31.40 a	63.86 a	4.36 a	0.35 c

[a]Data are the average of 5 measurements taken every 6 days. Values followed by a different letter indicate the existence of significant differences according to $LSD_{0.05}$ test.

Legend to Figures

Fig. 1. Pre-dawn leaf water potential (Ψ_{pd}, MPa) during the preconditioning period in the different water stress treatments. Each point is the average of three replicates. Vertical bars on data points are ± S.E. of the mean (not shown when smaller than the symbols).

Fig. 2. Relationship between leaf insertion angle (LIA, º) and mid-day leaf water potential (Ψ_{md}, MPa) during the preconditioning period, in the different water stress treatments. ($LIA = 121.57 + 25.51 \cdot \Psi_{md}$, $r = 0.84$***).

Fig. 3. Relationship between leaf conductance (g_l, mmol m^{-2} s^{-1}) and mid-day leaf water potential (Ψ_{md}, MPa) during the preconditioning period, in the different water stress treatments ($g_l = 220.78 + 47.36 \cdot \Psi_{md}$, $r = 0.72$***).

Fig. 4. Pre-dawn leaf water potential (Ψ_{pd}, MPa) at the end of the stress period (day 0) and during the recovery period in the different water stress treatments. Each point is the average of three replicates. Vertical bars on data points are ± S.E. of the mean (not shown when smaller than the symbols).

Fig. 5. Leaf conductance (g_l, mmol m^{-2} s^{-1}) and net photosynthesis (Pn, μmol CO_2 m^{-2} s^{-1}) in the different water stress treatments at the end of the withholding period (day 0) and during the recovery period. Each point is the average of three replicates. Vertical bars on data points are ± S.E. of the mean (not shown when smaller than the symbols).

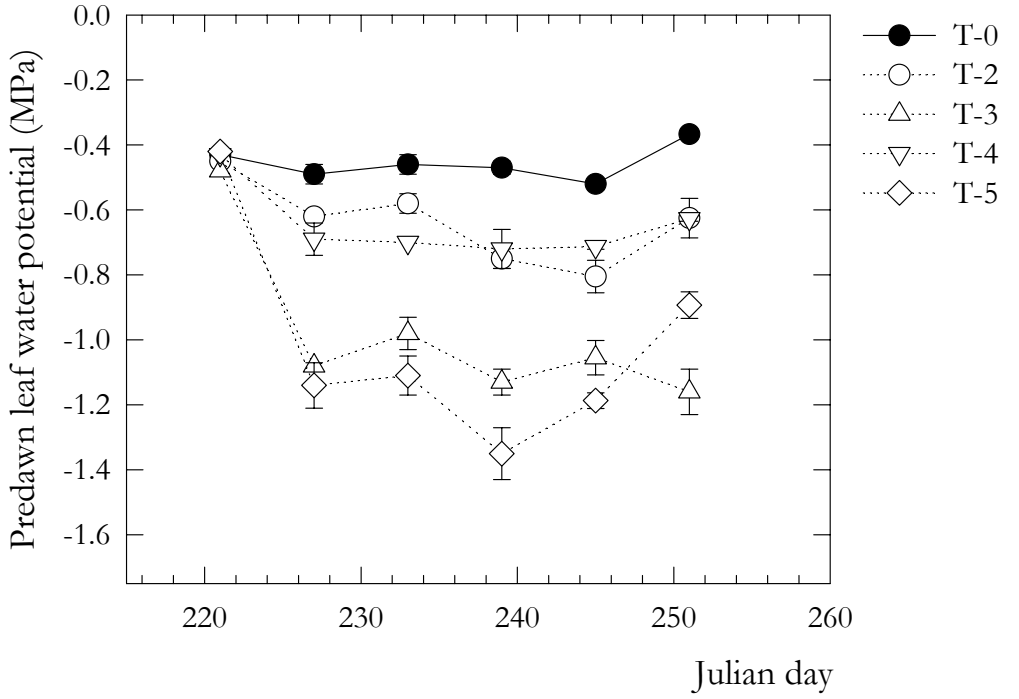
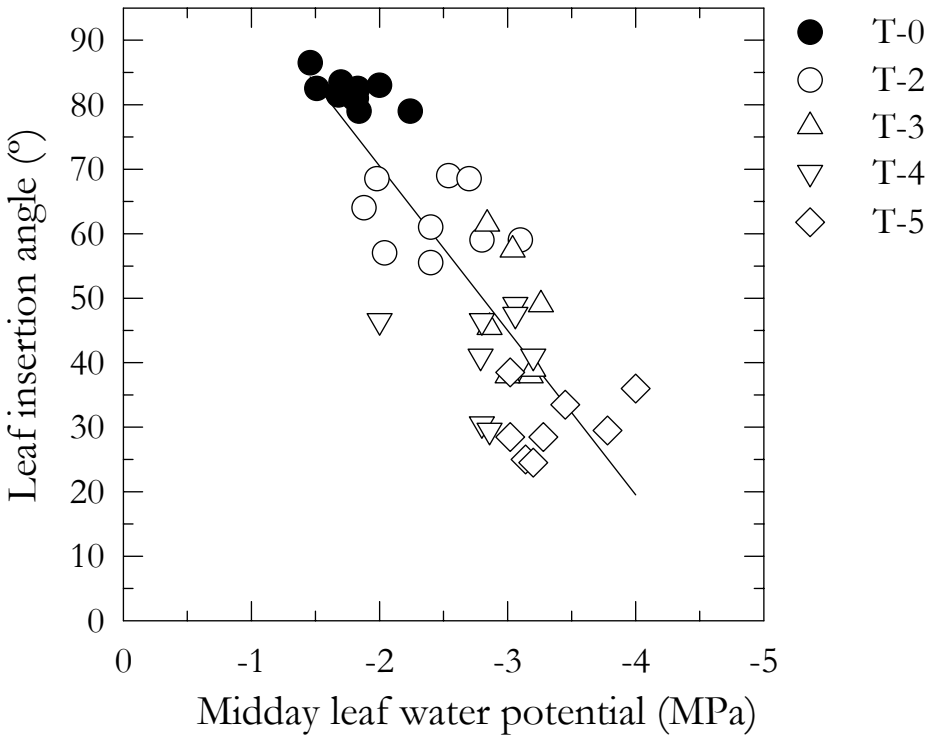


Fig. 1. Ruiz-Sánchez et al., 2000



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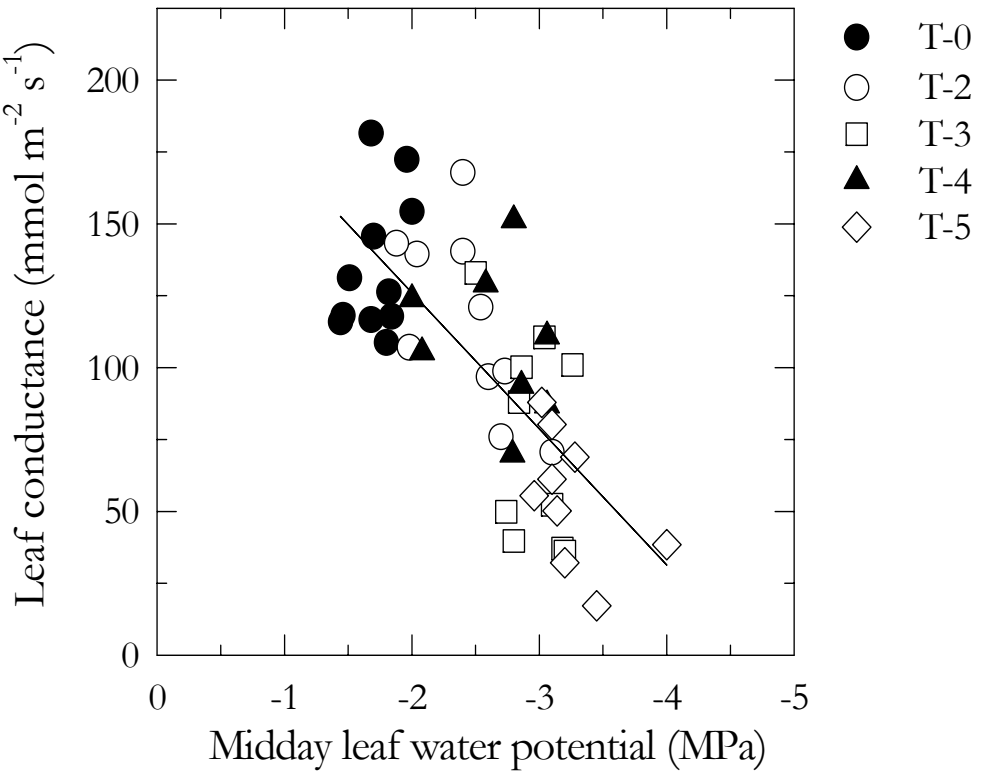

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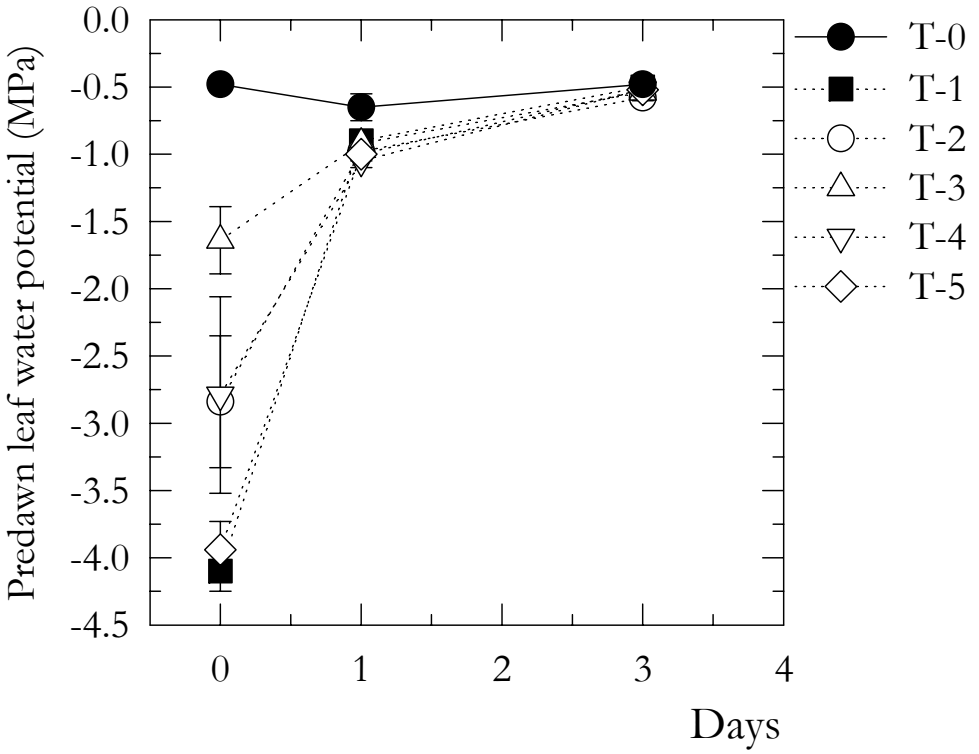

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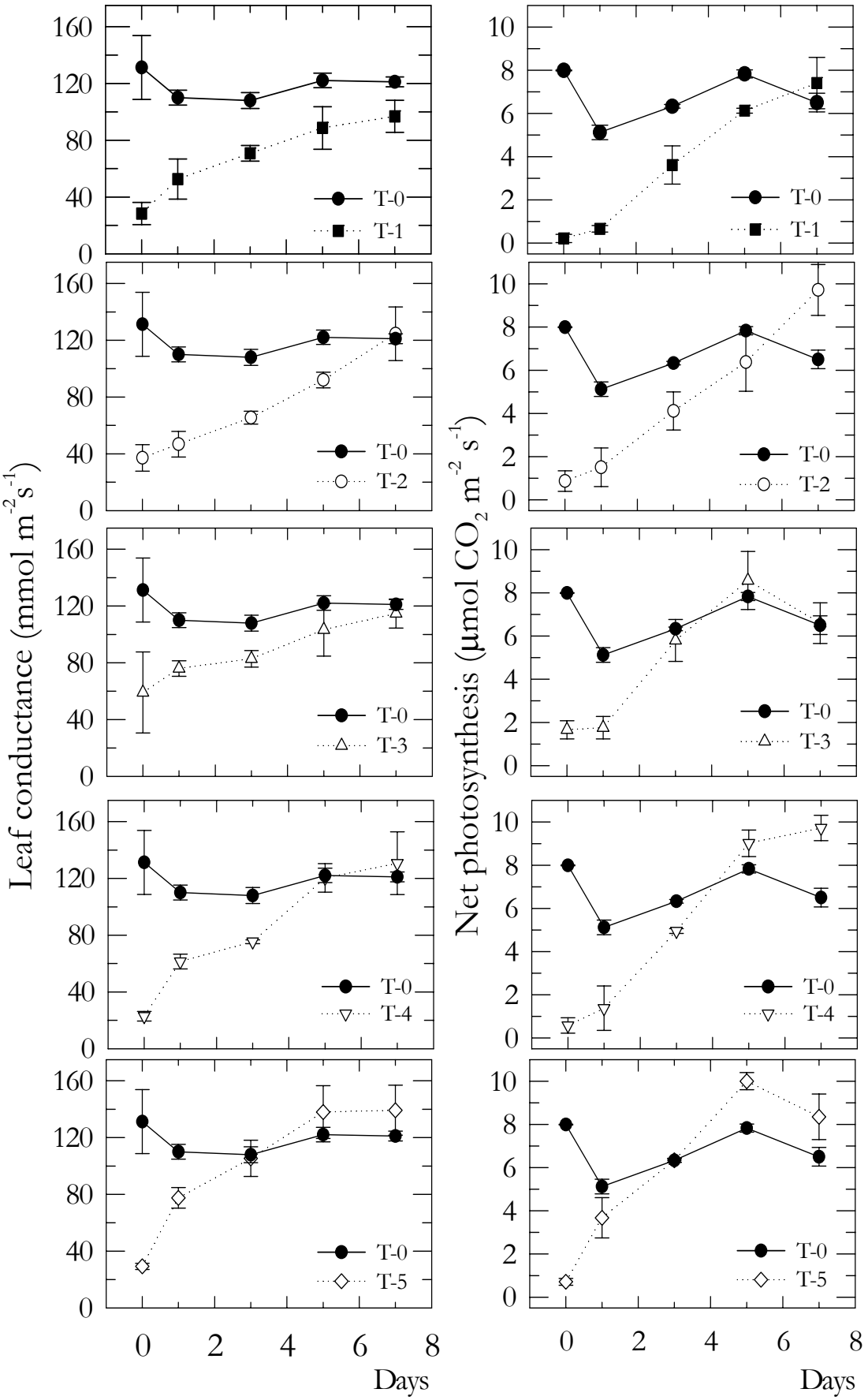

Fig. 5. Ruiz-Sánchez et al., 2000