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Gas-exchange response of almond genotypes to water stress

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Abstract

We studied water relations and gas exchange in six almond genotypes grafted on GF677 in response to withholding irrigation for 14 days and a subsequent 10-day rehydration period. The responses to drought stress significantly differed in the almond genotypes; the tolerant plants were distinguished and monitored. Leaf relative water content (RWC) decreased by more than 23%, leaf water potential dropped to less than –4.3 MPa, and electrolyte leakage increased to 43% in dehydration-sensitive genotypes. Photosynthesis (P_N) and stomatal conductance (g_s) of drought-sensitive genotypes were significantly reduced by 70% and 97% in response to water deficiency. Water stress significantly enhanced water-use efficiency up to 10 folds in drought-tolerant almonds. The difference between leaf temperature and its surrounding air temperature (Δ_T) increased significantly to more than 187% under water stress in drought-tolerant genotypes. In addition, the reduction in the g_s and further ability to preserve RWC were involved probably in drought-tolerance mechanism in almond. Negative significant correlations were found between Δ_T, P_N, and g_s. Based on the correlations, we suggested that Δ_T could be used as a simple measurement for monitoring water stress development in the irrigation management of almond orchards. In conclusion, 'Supernova' and the Iranian genotypes '6-8' and 'B-124', were found to be more drought-tolerant compared with other genotypes in this experiment.

Additional key words: leaf temperature; leaf water potential; photosynthetic rate; *Prunus dulcis* Mill.; relative water content; stomatal conductance.

Introduction

Almond (*Prunus dulcis* Mill.) is an important nut crop that is grown mainly under Mediterranean climate. Plants are often subjected to some drought periods during the growing season. Almond can be successfully grown in semiarid regions when the regulated deficit irrigation regime is used, nevertheless its productivity decreases (Romero *et al.* 2004). It has been reported that almond productivity may be reduced to 42–55% under dry soil conditions (Gomes-Laranjo *et al.* 2006) and different responses to drought have been reported in various almond genotypes (Matos *et al*. 1998, de Herralde *et al*. 2003, Rouhi *et al.* 2007, Yadollahi *et al.* 2011).

Gomes-Laranjo *et al.* (2006) reported a reduction in the growth beside massive leaf abscission and also a reduction in the kernel mass of almond trees under drought stress. Romero *et al.* (2004) suggested that reduced growth and productivity in almonds grown under water stress can be related to the reduction in P_N. Reductions in g_s, P_N, and transpiration (E) of almonds under water stress have been shown in previous studies (de Heralde *et al.* 2003, Romero *et al.* 2003, Isaakidis *et al.* 2004, Rouhi *et al.* 2007). Genotypic differences played a substantial role in the aforesaid reductions with regard to photosynthesis in almonds under water stress. The aim of the present research was to evaluate the effects of water stress and subsequent rehydration on water relations and photosynthesis in six almond genotypes. Moreover, our secondary objective was to improve our knowledge about the plant defensive mechanisms under drought. Finally, we tried to indicate and introduce suitable almond genotypes that are not prone to drought.

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Abbreviations: C – control; EL – electrolyte leakage; g_s – stomatal conductance; P_N – photosynthetic rate; RWC – leaf relative water content; R10 – rehydration period; WS – water-stressed plants; WUE – water-use efficiency; Δ_T – leaf-air temperature; Ψ_{Leaf} – leaf water potential.

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Materials and methods

This study was conducted in the Department of Horticultural Science, Tarbiat Modares University, during the growing season in 2012. The plant materials, which were used in this experiment, included six almond (*P. dulcis* Mill.) genotypes: 'Supernova' and 'Ferragnès' cultivars, two Iranian cultivars, namely 'Sepid' and 'Mamaei', and two newly introduced high yield, late bloom, and freeze resistant genotypes of 'B-124' and '6-8'. The plants were obtained from the almond collection orchard of Horticultural Research Division, Seed and Plant Improvement Institute, Karaj, Iran. The genotypes were grafted on uniform, GF677 rootstocks in summer 2011 and were grown in a greenhouse. Grafted plants were transplanted into new pots containing 10 kg of fine loamy soil in late winter of 2012. The soil consisted of perlite, leaf mould, and soil (1:1:1, v/v/v). The soil was comprised of silt (31.9%), clay (19.5%), and sand (48.6%), organic carbon of 3.9%, N of 0.40%, P of 346.4 mg kg^{-1}, and K of 4,280 mg kg^{-1}.

Shoots and roots were pruned at the beginning of the experiment in order to reduce the size of the experimental plants into a uniform size. Four months later, the plants were subjected to water stress by withholding irrigation for 14 d. The soil surface was covered with a polyethylene film to prevent evaporation and slow down the water stress development. The plants in the control treatment (C) were irrigated every day to keep water content of the pots at field capacity level. The water-stressed plants (WS) were irrigated to revive field capacity after the water stress period. The recovery rate of the genotypes was then evaluated after 10 d (R10). Five plants were considered per treatment. The environmental conditions in the greenhouse averaged at 33/22°C temperatures and relative humidity was 25/30% on a day/night basis with a photoperiod of 14 to 10 h of sunlight during the experiment. Light intensity at the leaf surface generally exceeded 1,500 µE m^{-2} s^{-1} at midday.

Measurements were carried out at four steps:

Step	Time
C	The beginning of the experiment
WS7	Seven days after withholding irrigation
WS14	The end of the water stress period
R10	After the rehydration period

One observation per tree was used as a replication for each parameter.

RWC of the middle stem leaves was measured by using ten 7 mm diameter leaf discs at 14:00 h. The leaf disc masses (FM) of each treatment were recorded. They were then hydrated for 48 h at 5°C in darkness. This was followed by a state of water saturation (constant mass obtained) which was finally weighed (TM). Leaf discs were oven-dried at 75°C for 72 h and dry mass (DM) was then recorded. RWC was calculated according to the following expression (Filella *et al.* 1998):

$$\text{RWC [\%]} = (\text{FM} - \text{DM})/(\text{TM} - \text{DM}) \times 100$$

Leaf water potential (Ψ_{Leaf}) was measured using a portable pressure chamber (*SKPM 1400*, *Skye Instruments*, UK) at 14:00 h. Ψ_{Leaf} was measured immediately after excising the fully expanded leaves from the middle of the stem. Electrolyte leakage (EL) in ten 7 mm diameter leaf discs was determined by using the method described by Blum and Ebercon (1981).

Leaf gas-exchange parameters were evaluated on fully expanded leaves in the middle of the stem. The measurements were taken between 14:00 h and 15:30 h. Photosynthetic parameters (P_N, g_s, and E) were measured using an open gas-exchange system with a 6 cm^2 leaf chamber (*LI-6400*, *LICOR*, Lincoln, NE, USA). Leaf relative temperature (Δ_T) was calculated as the difference between the leaf temperature and its surrounding air temperature. Leaf temperature and its surrounding air temperature were measured directly by *LI-6400*. The environmental conditions in the greenhouse during gas-exchange parameter measurements averaged: temperature of 32.9 ± 1.1°C, relative humidity of 26.0 ± 1.9%, and CO_2 concentration of 305.2 ± 1.9 ppm. Water-use efficiency (WUE) was calculated by the ratio WUE = P_N/E.

The experiment was based on a completely randomized design (CRD) consisting of five replications (one tree per replication). The data were analyzed using *SPSS* software (*Version 16.0, SPSS Inc.*). The results were subjected to analysis of variance (*ANOVA*) and the differences among the average of treatments were compared using *Duncan*'s multiple range test at $P \leq 0.05$.

Results

'Ferragnès' was the only genotype which showed a significant reduction (6.6%) in RWC at WS7. RWC significantly decreased at WS14. However, RWC decreased more in 'Mamaei' (23.4%), 'Sepid' (20.3%), and 'Ferragnès' (20.0%) than in 'Supernova' (15.1%), 'B-124' (12.2%), and '6-8' (16.3%). RWC of the WS plants recovered to the control level after rehydration (Table 1). Ψ_{Leaf} ranged between 1.53 to 2.06 MPa for the genotypes in the C treatment. Water stress significantly decreased Ψ_{Leaf} and the lowest value (−4.36 MPa) was recorded in the leaves of 'Ferragnès' at WS14. The highest Ψ_{Leaf} was found after WS14 in the leaves of 'Supernova' (−3.76 MPa) and

Table 1. Effects of water stress on leaf relative water content (RWC), leaf water potential (Ψ_{Leaf}), and electrolyte leakage (EL) in the leaves of almond genotypes at control level (C), 7 days after withholding irrigation (WS7), at the end of water stress period (WS14), and after the rehydration period (R10). Values within the same genotypes followed by *the same letter* do not differ significantly according to the *Duncan*'s multiple range test ($P \leq 0.05$).

Genotype/Stage	RWC [%]	Ψ_{Leaf} [MPa]	EL [%]
Supernova/C	83.5 ± 1.44^{a}	-1.74 ± 0.05^{a}	5.60 ± 1.09^{b}
Supernova/WS7	85.5 ± 0.60^{b}	-2.18 ± 0.06^{b}	8.00 ± 0.39^{b}
Supernova/WS14	68.4 ± 1.42^{a}	-3.76 ± 0.12^{c}	21.91 ± 0.21^{a}
Supernova/R10	82.7 ± 1.79^{a}	-2.35 ± 0.05^{b}	7.73 ± 1.35^{b}
6-8/C	86.7 ± 1.28^{a}	-1.83 ± 0.02^{a}	4.58 ± 0.02^{b}
6-8/WS7	84.4 ± 1.00^{a}	-2.54 ± 0.17^{b}	7.49 ± 0.67^{b}
6-8/WS14	70.4 ± 1.51^{b}	-4.01 ± 0.04^{c}	17.80 ± 0.50^{a}
6-8/R10	84.0 ± 0.44^{a}	-2.83 ± 0.07^{b}	6.04 ± 0.32^{b}
B-124/C	85.8 ± 0.58^{a}	-2.06 ± 0.14^{a}	6.93 ± 0.51^{b}
B-124/WS7	85.7 ± 0.36^{b}	$-2.35^{a} \pm 0.08^{b}$	8.41 ± 0.86^{b}
B-124/WS14	73.6 ± 0.59^{a}	-3.56 ± 0.14^{c}	13.98 ± 0.67^{a}
B-124/R10	87.4 ± 0.46^{a}	-2.60 ± 0.13^{b}	4.07 ± 0.30^{c}
Sepid/C	84.1 ± 0.55^{a}	-1.98 ± 0.07^{a}	6.68 ± 0.40^{c}
Sepid/WS7	84.3 ± 0.92^{a}	-2.71 ± 0.02^{b}	8.14 ± 0.28^{b}
Sepid/WS14	63.8 ± 1.86^{b}	-4.11 ± 0.01^{c}	40.19 ± 6.32^{a}
Sepid/R10	83.7 ± 1.25^{a}	-1.82 ± 0.12^{a}	8.40 ± 0.30^{b}
Mamaei/C	83.1 ± 1.12^{a}	-1.53 ± 0.06^{a}	9.05 ± 0.35^{b}
Mamaei/WS7	86.9 ± 0.44^{a}	-2.01 ± 0.03^{b}	10.01 ± 1.38^{b}
Mamaei/WS14	59.7 ± 4.53^{b}	-4.16 ± 0.15^{c}	52.62 ± 4.25^{a}
Mamaei/R10	85.6 ± 0.80^{a}	-1.85 ± 0.11^{b}	11.53 ± 1.06^{b}
Ferragnès/C	85.8 ± 0.58^{a}	-2.06 ± 0.14^{a}	4.77 ± 0.40^{c}
Ferragnès/WS7	79.2 ± 2.02^{ab}	-3.08 ± 0.02^{c}	10.20 ± 3.41^{b}
Ferragnès/WS14	65.8 ± 5.61^{b}	-4.36 ± 0.06^{d}	26.40 ± 4.52^{a}
Ferragnès/R10	83.2 ± 0.65^{a}	-2.14 ± 0.07^{b}	6.27 ± 0.34^{c}

'B-124' (−3.56 MPa). Ψ_{Leaf} significantly increased in the leaves of WS plants after the rehydration period (Table 1). However, with the exception of 'Sepid', it did not recover enough to match the C treatment in the leaves of the other genotypes.

EL increased by developing water stress, however, 'Sepid' and 'Ferragnès' were the only genotypes with significantly higher EL at WS7 (8.1% and 10.2%, respectively). The highest EL was found at WS14 in the leaves of 'Mamaei' (52.6%). 'B-124' had the lowest EL (14%) after WS14. EL recovered to the values of C plants after R10; however, it did not fully recover to the respective control level in WS 'Sepid' plants (Table 1).

Water stress significantly reduced P_N in all genotypes, however, P_N in 'Supernova' and '6-8' remained unchanged until the WS7. The lowest P_N at WS7 was found in 'Mamaei' [4.0 $\mu mol(CO_2)\ m^{-2}\ s^{-1}$], a 57% reduction compared with C. At WS14, 'Mamaei' showed the highest reduction in P_N (70%), but '6-8' with 37% reduction in P_N was able to maintain photosynthesis at the higher level. With the exception of 'Sepid', P_N of the other genotypes recovered to the C level after R10 period. P_N of rehydrated '6-8' plants was significantly higher than the C (Table 2). WS significantly reduced g_s (Table 2). g_s in 'Supernova' did not significantly reduce until WS7 (only 13.1%), however, it significantly decreased in the leaves of the other cultivars, although 'Sepid' showed the greatest reduction (87.0%) at this stage. The lowest g_s values were found after WS14. However, with the exception of 'Supernova', there were no significant differences between g_s at WS7 and WS14 period in the leaves of other almond genotypes. At WS14 period, 'Ferragnès' showed the highest reduction (97.4%) in g_s and the lowest reduction (about 90%) was found in the leaves of 'Supernova' and '6-8'. After R10 period, g_s significantly increased to reach the C values in the leaves of the almond genotypes with the exception of 'Sepid'.

WUE significantly increased by WS development, however, it remained unchanged in the leaves of 'Mamaei' during the experiment. WUE in the leaves of 'Supernova', '6-8', and 'B-124' did not change significantly when measured at WS7 period, compared to well-watered C plants (Table 2). WUE increased significantly in the leaves of 'Sepid' and 'Ferragnès' by 281.1% and 226.0%, respectively, when measured at WS7 period. The WUE of cultivar '6-8' increased by more than 10 fold – the highest – whereas it increased by just 217.2% in 'Mamaei', which was the lowest WUE increase.

Table 2 shows Δ_T changes during the experiment. Δ_T significantly increased at WS7 measurements, however, Δ_T changes in 'Supernova' leaves (with 0.7°C increase) were not statistically different from the C level at that time.

Table 2. Effects of water stress on net photosynthetic rate (P_{N}), stomatal conductance (g_{s}), water-use efficiency (WUE), and leaf relative temperature (Δ_{T}) in the leaves of almond genotypes at control level (C), 7 days after withholding irrigation (WS7), at the end of water stress period (WS14), and after the rehydration period (R10). Values within the same genotypes followed by *the same letter* do not differ significantly according to the *Duncan*'s multiple range test ($P \leq 0.05$).

Genotype/Stage	P_{N} [μmol(CO$_2$) m^{-2} s^{-1}]	g_{s} [μmol(CO$_2$) m^{-2} s^{-1}]	WUE [P_{N}/E]	Δ_{T} [^{o}C]
Supernova/C	8.51 ± 0.32^{a}	0.061 ± 0.006^{a}	2.41 ± 0.13^{b}	-1.46 ± 0.24^{b}
Supernova/M	9.46 ± 0.94^{a}	0.053 ± 0.015^{a}	2.98 ± 0.49^{b}	-0.76 ± 0.54^{b}
Supernova/D	2.97 ± 0.21^{b}	0.006 ± 0.0007^{b}	10.47 ± 1.20^{a}	1.10 ± 0.23^{a}
Supernova/R	10.26 ± 1.35^{a}	0.089 ± 0.033^{a}	2.41 ± 0.44^{b}	-1.27 ± 0.71^{b}
6-8/C	8.10 ± 0.94^{b}	0.064 ± 0.023^{b}	2.22 ± 0.35^{b}	-1.09 ± 0.49^{bc}
6-8/WS7	7.01 ± 0.11^{b}	0.020 ± 0.0008^{b}	5.71 ± 0.35^{b}	$-0.22^{a} \pm 0.14^{b}$
6-8/WS14	5.08 ± 0.11^{c}	0.002 ± 0.0006^{c}	23.07 ± 5.13^{a}	0.66 ± 0.04^{a}
6-8/R10	12.01 ± 0.40^{a}	0.102 ± 0.015^{a}	2.09 ± 0.18^{b}	-1.61 ± 0.32^{c}
B-124/C	10.92 ± 1.26^{a}	0.104 ± 0.024^{a}	2.07 ± 0.32^{b}	-1.71 ± 0.50^{c}
B-124/WS7	7.11 ± 0.21^{bc}	0.020 ± 0.001^{b}	4.88 ± 0.16^{b}	-0.08 ± 0.07^{b}
B-124/WS14	4.96 ± 0.44^{c}	0.010 ± 0.002^{b}	6.96 ± 2.06^{a}	1.49 ± 0.16^{a}
B-124/R10	11.53 ± 0.81^{a}	0.112 ± 0.026^{a}	2.16 ± 0.11^{b}	-2.54 ± 0.45^{c}
Sepid/C	13.51 ± 0.26^{a}	0.216 ± 0.015^{a}	1.43 ± 0.10^{b}	-3.00 ± 0.10^{c}
Sepid/WS7	7.60 ± 0.68^{b}	0.028 ± 0.010^{bc}	4.02 ± 1.29^{a}	$-0.87^{a} \pm 0.21^{b}$
Sepid/WS14	$4.93^{b} \pm 0.43^{c}$	0.014 ± 0.0009^{c}	5.28 ± 0.47^{a}	0.08 ± 0.12^{a}
Sepid/R10	8.61 ± 2.10^{b}	0.099 ± 0.055^{b}	2.09 ± 0.75^{b}	-1.67 ± 0.71^{b}
Mamaei/C	9.36 ± 0.53^{b}	0.178 ± 0.040^{a}	1.33 ± 0.19^{a}	-3.40 ± 0.65^{b}
Mamaei/WS7	4.00 ± 0.55^{c}	0.020 ± 0.002^{c}	2.98 ± 0.26^{a}	-0.47 ± 0.06^{a}
Mamaei/WS14	2.80 ± 0.07^{c}	0.018 ± 0.004^{c}	2.89 ± 1.07^{a}	0.38 ± 0.07^{a}
Mamaei/R10	11.23 ± 0.34^{a}	0.157 ± 0.009^{b}	1.68 ± 0.008^{a}	-3.13 ± 0.25^{b}
Ferragnès/C	10.38 ± 0.87^{a}	0.116 ± 0.026^{a}	1.73 ± 0.23^{c}	-2.08 ± 0.43^{c}
Ferragnès/WS7	5.64 ± 1.04^{b}	0.019 ± 0.0008^{b}	3.91 ± 0.64^{b}	-0.29 ± 0.06^{b}
Ferragnès/WS14	4.45 ± 0.07^{c}	0.003 ± 0.0003^{b}	7.65 ± 0.96^{a}	0.77 ± 0.06^{a}
Ferragnès/R10	12.37 ± 0.77^{a}	0.153 ± 0.023^{a}	1.67 ± 0.13^{c}	-2.60 ± 0.25^{c}

'B-124' showed the highest increase (up to 95%) and 'Sepid' had the lowest increase (29%) in Δ_{T} at WS7 measurement. Δ_{T} increased more than 100% in the leaves of almond genotypes after WS14 period. The highest rate of Δ_{T}, which increased at this stage (187%), was found in 'B-124'; 'Sepid' had the lowest increase (102%). With the exception of 'Sepid', Δ_{T} recovered to the C level after R10 period. Significant negative correlations were found between Δ_{T} and P_{N}, and g_{s} (Fig. 1). However, no such reasonable correlations were found between the leaf temperature or air temperature and the photosynthetic parameters (data not shown).

Discussion

In the present research, withholding irrigation resulted in gradual reductions in RWC and Ψ_{Leaf} in the leaves of almond genotypes. Ψ_{Leaf} showed higher sensitivity to water stress. At WS7, RWC was not affected in most genotypes; however, Ψ_{Leaf} significantly decreased in all genotypes. These results suggest that the osmoregulation mechanisms were used by most of almond genotype to retain turgor and sustain photosynthesis during early stages of water stress. Campos *et al.* (2005) and Karimi *et al.* (2013) showed that accumulation of proline and soluble carbohydrates is involved in osmoregulation in almond. The lowest RWC and Ψ_{Leaf} values in 'Ferragnès', 'Mamaei', and 'Sepid' at the end of the water stress period were associated with wilted leaves and leaf abscission. Ψ_{Leaf} was lower than that in C after rehydration; however, 'Sepid' was an exception. This may be due to residues of osmolites in the leaves.

The rise of reactive oxygen species formation during cell dehydration causes oxidative damages to cell membrane and photosynthetic apparatus (Tang *et al.* 2002, Bian and Jiang 2009). Lower EL is associated with the maintenance of the integrity of cell membranes under water stress. Significant increases in EL in 'Sepid', 'Mamaei', and 'Ferragnès' in WS7 stage was probably related to higher susceptibility to water loss. It has been found that preserving cell membrane integrity occurs in the leaves of tolerant plants during dehydration (Bukhov *et al.* 1990, Bajji *et al.* 2002, Karimi *et al.* 2012). In the present study, EL recovered to the C level in the leaves of almond genotypes after the rehydration period. This indicated that cell membranes repaired; 'Sepid' was an exception. Such a rapid recovery seems to be critically essential for the plant to tolerate periodic drought stress during the growing season.

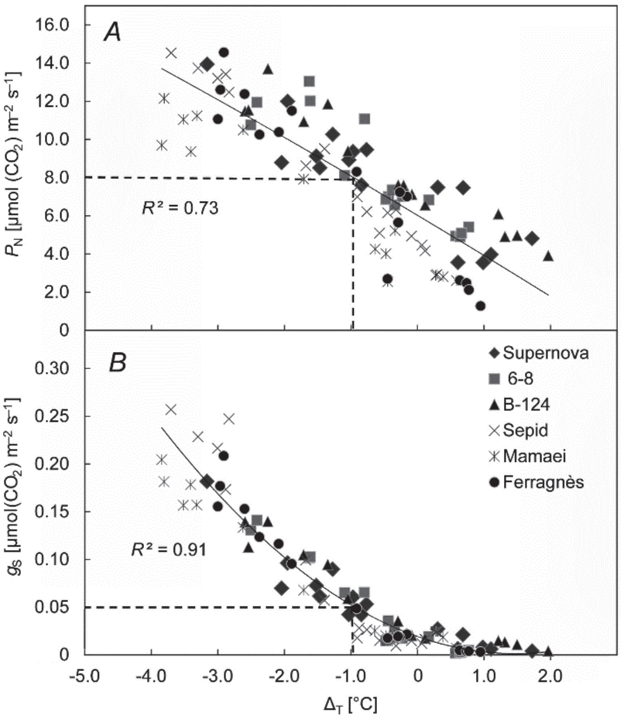

Fig. 1. Correlation between leaf-air temperature (Δ_T) and (*A*) photosynthetic rate (P_N) and (*B*) stomatal conductance (g_s) in the leaves of almond genotypes.

Reducing g_s under water-deficit condition is an adaptation mechanism utilized by plants to reduce water loss. The results of the current study showed that even a moderate water stress could significantly reduce g_s which consequently led to a reduced P_N in some almond genotypes. Reduced P_N in the leaves of 'Sepid', 'Mamaei', and 'Ferragnès' during WS7 measurements showed higher sensitivity of these genotypes to water stress. On the other hand, preserving P_N in the leaves of 'Supernova', 'B-124', and '6-8' under severe water stress could be attributed to lesser cell membrane damage, high temperature adaptation, and higher osmoregulation ability (Herppich and Peckmann 1997).

Stomatal control of *E* leads to a reduction in *E* and prevents leaf cooling. In this study, Δ_T significantly increased in parallel to developing water stress. Increases in Δ_T ranged between 1.7 (in '6-8) to 3.7°C (in 'Mamaei') at the end of the water stress period. The negative correlation between Δ_T and g_s suggested that a reduced g_s triggerred Δ_T elevation. In 'Sepid', 'Mamaei', and 'Ferragnès', Δ_T was lower at the end of the drought period, which could be probably attributed to severe dehydration, wilting of leaves, changes in leaf orientation toward sunlight, and reduced radiation absorption. The results denoted the ability of 'Supernova', '6-8', and 'B-124' to continue in photosynthesis under elevated leaf temperatures and reduced g_s, which is probably related to higher drought tolerance. Photosynthesis is highly sensitive to elevated temperatures (Berry and Björkman 1980). The negative correlation between Δ_T and P_N suggests that the occurrence of heat stress in the leaves was concurrent with water stress in almonds. Schapendonk *et al.* (1989) showed that the increase in leaf temperature under drought stress reduces quantum efficiency. The imbalance between the photochemical activity of PSII and the electron requirement for photosynthesis leads to photoinhibition under such a condition (Epron *et al.* 1992). Increased leaf temperature and reduced P_N of the WS almonds indicated that the photoinhibitory phenomenon might have occurred. However, as g_s is directly reduced by WS, it is difficult to separat the direct effects of WS from the effects of elevated leaf temperature on reduced P_N (Gates 1968). The data suggest that the limitation in P_N during the first stages of drought stress was primarily due to stomatal closure. Furthermore, heat accumulation and cell injuries are also involved in reducing the P_N under prolonged drought stress. Even though it is hard to indicate which factor has affected the others, the results showed the applicability of using Δ_T as a cheap and simple measurement to evaluate g_s and *E* in almonds. We believe that when Δ_T reaches less than –1°C, we might expect a 50% reduction in P_N, 70% reduction in *E*, and 80% reduction in g_s. This can be beneficial for determining the critical point in timing the irrigation of almond trees.

Maintaining P_N under reduced g_s and *E* during WS led to the increase in WUE. Boyer (1982) stated that the WUE is critical to plant survival and crop yield. Higher WUE under drought stress is probably a consequence of gas-exchange regulation. The *E* parameter is more influenced by water deficit than P_N is. 'Supernova', '6-8', and 'B-124' had higher WUE during the WS period which showed their ability to save water and uphold physiological activities under water-deficit conditions. The present results are in agreement with findings of Escalona *et al.* (1999) and Bota *et al.* (2001). On the other hand, the relatively high WUE found in the drought-sensitive cultivar 'Ferragnès' might be attributed to severe dehydration and very low *E*. Despite the fact that the P_N/E ratio showed an increased photosynthetic efficiency in the leaves of almonds under WS, the data might cause confusions in some cases. To consider other physiological responses beside WUE is recommended if screening for drought tolerance.

In conclusion, 'Supernova', '6-8', and 'B-124' were grouped as drought-tolerant and 'Sepid', 'Mamaei', and 'Ferragnès' were classified as drought-sensitive. The drought-tolerant almonds were able to retain leaf water content *via* osmoregulation, lesser cell membrane damage, higher photosynthetic capacity, and WUE under reduced g_s and elevated leaf temperature. Reasonable correlations between Δ_T, g_s, and P_N over a wide range of water availability for different almond genotypes suggested that Δ_T is a fast and simple measurement for monitoring photosynthesis and orchard water management. However, measuring the Δ_T requires precise instruments. More experiments are needed to confirm the practicability of this finding.

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