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Original Research Article

Responses of Caprifig Genotypes to Water Stress and Recovery

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ABSTRACT

Caprifig (*Ficus carica* L.) as pollen sources play a major role in fig breeding programs. The aim of this study was to evaluate responses of four caprifig genotypes ('Dane Sephid', 'Pouz Donbali', 'Shah Anjiri', and 'Khormaei') to water stress and rewatering cycles. Water stress was applied to one-year-old caprifig cuttings by withholding irrigation for 14 days and was followed by a 10-day rewatering period. Growth parameters of the genotypes were significantly reduced under water stress period. Results indicated that water stress significantly reduced relative water content (RWC) and leaf water potential (Ψ_{Leaf}), and the lowest values were found in 'Dane Sephid'. Electrolyte leakage increased in parallel to decrease of leaf RWC and Ψ_{Leaf}, and EL was significantly higher in the leaves of 'Dane Sephid'. On the contrary to inorganic osmolytes, water stress enhanced proline accumulated in the leaves of caprifig genotypes with the exception to 'Dane Sephid'. After the rewatering period growth indices of 'Khormaei' and 'Shah Anjiri' were recovered to the control level. The data suggested 'Khormaei' and 'Shah Anjiri' have higher drought tolerance. The mechanism underlying the drought tolerance in caprifigs may result from their capacity of osmoregulation and maintaining cell health status.

Key words: Electrolyte leakage, leaf water potential, osmoregulation, proline, relative water content.

Abbreviations: Dry weight (DW); Electrolyte leakage (EL); Field capacity (FC); Fresh weight (FW); leaf area (LA); Reactive oxygen species (ROS); Re-watering (RW); Relative water content (RWC); Specific leaf area (SLA); Turgidity weight (TW); Water stress (WS); Leaf water potential (Ψ_{Leaf}).

INTRODUCTION

Most of world's fig (*Ficus carica* L.) production comes from Mediterranean countries. Plants usually subjected to frequent water deficit periods during growing season under such growing condition which may affect their growth and production. During drought periods, soil water is strongly retained, interfering water and mineral nutrients absorption by plants. The effects of drought stress on plant depend on the genotype, as well as the magnitude of the water deficit, and how fast the plant experiences the water deficit condition. Rapid cell turgor loss under drought affects growth in the meristems. Other physiological processes such as stomatal closure and decreased photosynthesis rate, as well as a change in water transport through the plant will be affected under prolonged drought stress condition (Figueiredo *et al.,* 1999). Moreover, reactive oxygen species formation may be increased under water stress which can damage proteins, membrane lipids and photosynthetic pigments. Reduced relative water content (RWC) and leaf water potential (Ψ_{Leaf}) under drought stress triggers accumulation of different types of compatible solutes (Hameed and Ashraf, 2008).

Although fig plants are mostly grown under rainfed conditions, studies have shown severe injuries to the plant under prolonged drought stress (Hallac Turk and Aksoy, 2011; Gholami *et al*., 2012; Karimi *et al*., 2012). Drought stress incidence results in massive leaf abscission and reduce fruit yield and its quality (Hallac Turk and Aksoy, 2011). Fig production under rainfed condition is highly dependent to precipitation level; however, global climate change and warming have caused elevated summer temperatures and reduced annual precipitation levels in many of world's fig production areas during recent years. Extensive drought incidence in Iran has greatly damaged rainfed fig orchards of central parts of the country, which has resulted in loss of more than 10% of fig trees and more than 80% reduction in the yield in 2010 (Jafari *et al*., 2012).

Improving drought tolerance in fig is an economical way to improve its productivity under drought conditions. Fortunately, there is a great genetic diversity in fig, which some of them show drought tolerance and may be used in drought tolerance breeding programs. Gholami *et al*. (2012) after screening some of fig cultivars introduced drought tolerant plants for hot and dry lands of Iran. However, to our knowledge there is very limited

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number of studies on evaluating responses of male fig genotypes (caprifigs) to drought stress. Caprifig genotypes which are locally used as pollen source for caprification, show great compatibility to dry climate. Obtaining drought tolerant caprifig genotypes via screening is essential to introduce drought tolerant male parents in fig breeding programs as pollen source. Hence, this study was aimed to evaluate drought tolerance of four Iranian caprifig genotypes by evaluating their responses to water deficit stress and rewatering cycles. The caprifig genotypes used in this study are generally used in caprification in the area and produce high quality fruits.

MATERIALS AND METHODS

This study was conducted at the experimental greenhouse of the Department of Horticultural Science of Shiraz University, Shiraz, Iran during March to September, 2012. Plant material used in this study was involved cuttings of four Iranian male figs namely 'Daneh Sephid', 'Pouz Donbali', 'Shah Anjiri', and 'Khormaei'. These genotypes are distributed in the southern mountains of Iran. Cuttings of the genotypes were collected at the end of winter 2011 and rooted in sand medium. At the end of winter 2012 the rooted cuttings were transplanted into pots containing 12 kg of sand, leaf litter and loamy soil (1:1:1, v/v/v). Three months later, drought stress applied to the plants during their growth period.

Drought stress was applied by withholding irrigation for 14 days. The plants in the control treatment were irrigated every day to keep water content of the pots at field capacity (FC) level. After the experimental period, the drought-stressed plants irrigated to FC level and recovery rate of the genotypes was evaluated after 10 days. The experiment repeated twice. The following observations were made at three steps involving first day of the experiment, at the end of the water stress, and after the recovery period.

Shoot length and trunk diameter were measured by a ruler and a digital caliper, respectively. Number of leaves, mean leaf area (MLA), and total leaf area (TLA) were also recorded. Leaf area was measured by a leaf area meter (Area Meter AM200 – ADC Bioscientific, UK). Relative shoot length and relative leaf number were calculated using the following formula:

Relative shoot length = secondary shoot length - initial shoot length / initial shoot length
Relative leaf number = secondary leaf number - initial leaf number / initial leaf number

In the above formulae, initial shoot length and initial leaf number were recorded just before application. Water stress and secondary measurements were made after drought stress. Specific leaf area (SLA) of ten 7 mm diameter leaf discs was measured using the following formula:

SLA = Leaf disc area/Leaf discs dry weight

To evaluate the effect of the treatments on water content of the plants, RWC and Ψ_{Leaf} were determined. Relative water content was determined by using ten 7 mm diameter leaf discs. The leaf discs of each treatment were weighed (FW). They were then hydrated until saturation (constant weight) for 48 h at 5°C in darkness (TW). The leaf discs were dried in an oven at 105°C for 24 h (DW). Relative water content was calculated according to the following expression (Filella *et al.*, 1998).

$$RWC\% = (FW - DW)/(TW - DW) \times 100$$

Leaf water potential was measured with a pressure chamber at 2 o'clock PM. After excising the fully expanded leaves, they were let stop bleeding and then Ψ_{Leaf} was measured. Electrolyte leakage was used to assess membrane permeability. Electrolyte leakage was measured using an electrical conductivity meter by using the method described by Lutts *et al.* (1995). Proline content was determined in 300 mg of leaf material via the method described by Bates *et al.* (1973). The absorbance was measured at 520 nm with a UV-120-20 (Japan). L-Proline (SIGMA^{TM}) was used as standard.

One gram of dried leaf samples was burned in ash in a furnace at 550°C for 5 h. Then the ash was dissolved in 10 mL 2 N HCl and filled to 100 mL with distilled water. Potassium (K^+) and sodium (Na^+) were determined using a flame photometer (Model PFP7, Jenway, England).

The experiment was conducted as a complete randomized design with ten replications and statistical differences between measurements were analyzed following the analysis of variance (ANOVA) using SPSS 16.0 software. Means were separated using Duncan's multiple range test and differences were considered significant at a probability level of $P<0.05$.

RESULTS

The effects of drought stress and subsequent recovery periods on shoot growth indices of fig genotypes are shown in Figure 1. Comparison among the treatments and the genotypes showed that relative shoot length was significantly reduced under water stress. The lowest relative shoot length growth was found in 'Dane Sephid' and 'Khormaei'. Relative shoot length of the genotypes after rewatering was different and the highest rate of recovery was found in 'Shah Anjiri'. Drought stress reduced trunk diameter of the plants and the lowest trunk diameter was found in 'Shah Anjiri'. Trunk diameter of 'Shah Anjiri' and 'Khormaei' increased after rewatering; on the other hand, rewatering did not recovered trunk diameter of 'Dane Sephid' and 'Pouz Donbali'.

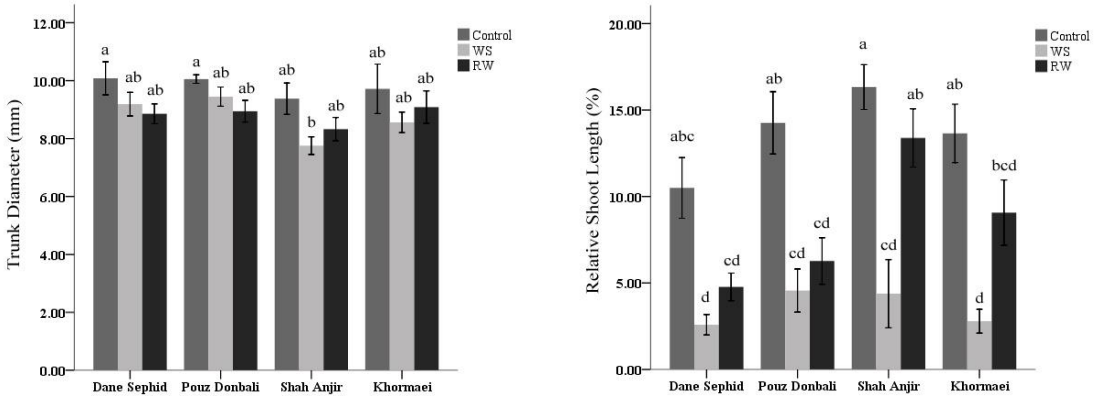

Figure 1. Shoot growth changes after water stress (WS) and rewatering (RW) periods. †. Means denoted by the same letter did not significantly differ at P <0.05 according to Duncan's multiple range test.

The effects of water stress and recovery period on leaf growth indices of fig genotypes are shown in Figure 2. Relative leaf number significantly reduced after water stress period, and the lowest value was found in 'Dane Sephid'. After the rewatering period, the lowest relative leaf number was found in 'Dane Sephid'. MLA of the genotypes was significantly different. The water stress significantly reduced LA; however, rewatering recovered LA in 'Shah Anjiri' and 'Khormaei'.

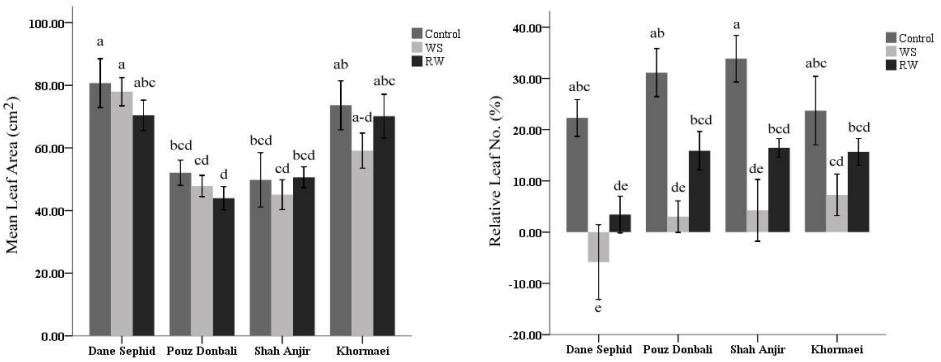

Figure 2. Leaf growth indices changes after water stress (WS) and rewatering (RW) periods. †. Means denoted by the same letter did not significantly differ at P <0.05 according to Duncan's multiple range test.

Figure 3 represents the effects of water stress and rewatering periods on SLA of the fig genotypes. Water stress significantly increased SLA, and the highest SLA was found in 'Khormaei'. SLA of the water stressed seedlings was reduced after rewatering period and the lowest SLA was found in 'Dane Sephid'.

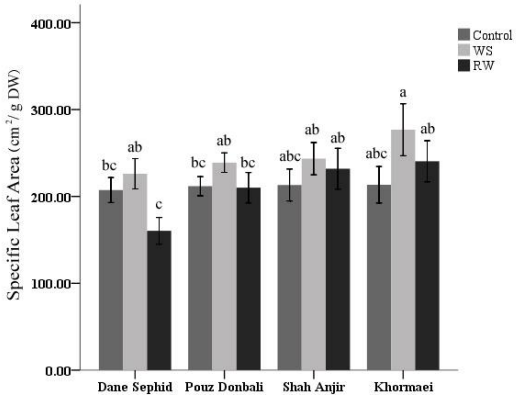

Figure 3. Specific leaf area changes after water stress (WS) and rewatering (RW) periods. †. Means denoted by the same letter did not significantly differ at P <0.05 according to Duncan's multiple range test.

Leaf water content is shown in Figure 4. Leaf relative water content was significantly reduced after water stress, and the lowest value was found in 'Dane Sephid'. Relative water content was significantly higher in the leaves of 'Khormaei' after water stress. Rewatering increased RWC of the stressed plants. Relative water content was significantly higher in the leaves of 'Khormaei' and 'Shah Anjiri' after rewatering. With the exception of 'Khormaei', Ψ_{Leaf} was significantly reduced after water stress. At the end of the water stress period, Ψ_{Leaf} was significantly higher in the leaves of 'Dane Sephid', and there was no significant difference in the other genotypes. Ψ_{Leaf} was significantly increased in the stressed plants after rewatering. After the rewatering, leaf water potential was significantly higher in the leaves of 'Dane Sephid', and the lowest Ψ_{Leaf} was found in 'Pouz Donbali' and 'Shah Anjiri'.

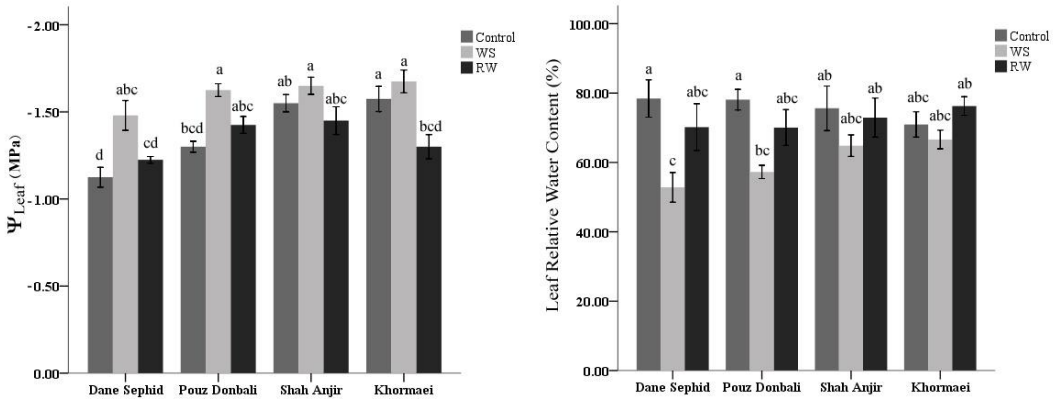

Figure 4. Leaf relative water content (RWC) and leaf water potential (Ψ_{Leaf}) changes after water stress (WS) and rewatering (RW) periods.
†. Means denoted by the same letter did not significantly differ at P <0.05 according to Duncan's multiple range test.

Drought stress increased EL in the leaves of the male fig genotypes. EL was significantly higher in 'Dane Sephid' (Figure 5). Rewatering reduced EL in the leaves of the stressed plants, however, 'Dane Sephid' was an exception. EL remained significantly higher in the stressed leaves of 'Dane Sephid'. Leaf proline concentration was significantly increased in 'Pouz Donbali', 'Shah Anjiri', and 'Khormaei' (Figure 5). At the end of water stress, the highest leaf proline concentration was found in 'Shah Anjiri', and 'Dane Sephid' had the lowest proline concentration. Proline concentration was reduced after rewatering. The highest proline concentration was found in 'Khormaei' and 'Pouz Donbali' after rewatering, and the lowest proline concentration was found in 'Dane Sephid'.

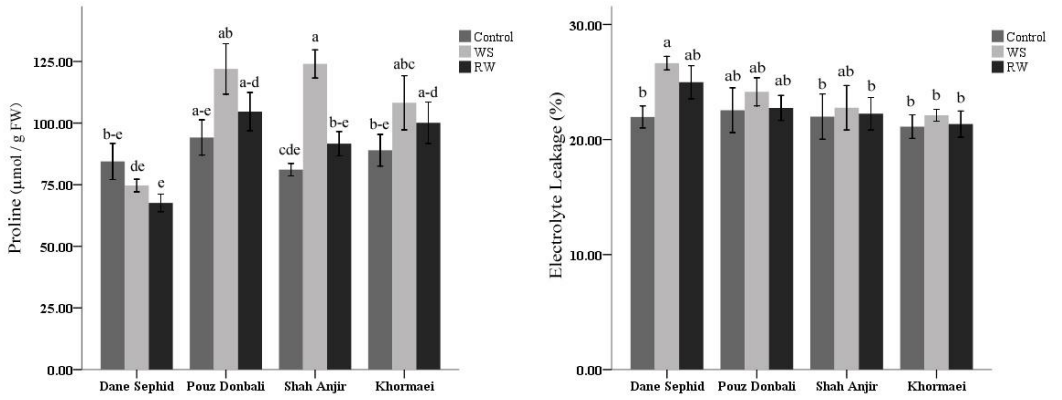

Figure 5. Electrolyte leakage (EL) and leaf proline concentration changes after water stress (WS) and rewatering (RW) periods.
†. Means denoted by the same letter did not significantly differ at P <0.05 according to Duncan's multiple range test.

K^+ concentration was significantly reduced under drought stress, and the lowest K^+ concentration was found in 'Shah Anjiri' and 'Dane Sephid' (Figure 6). K^+ concentration was significantly higher in the leaves of 'Dane Sephid', after water stress. With the exception of 'Shah Anjiri', K^+ concentration increased after rewatering. After rewatering, the highest K^+ concentration was found in the leaves of 'Dane Sephid'; however, 'Shah Anjiri' had the lowest K^+ concentration. Leaf Na^+ concentration was not affected by water stress and rewatering periods (Figure 6).

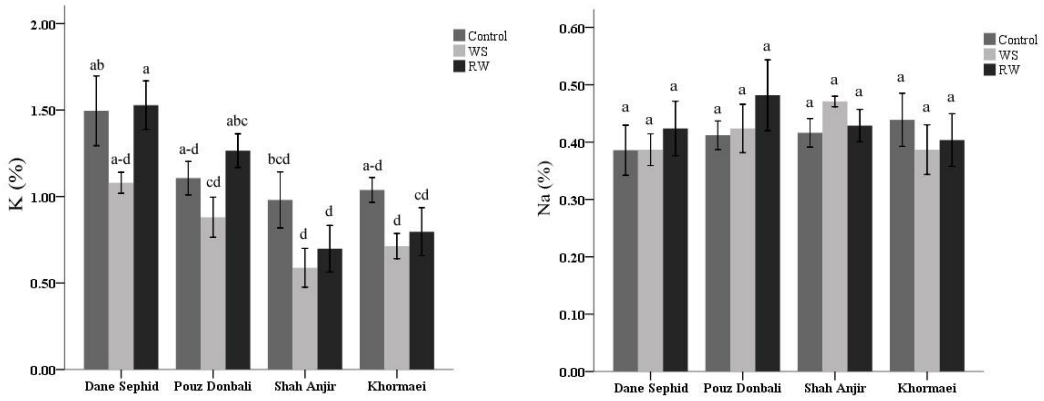

Figure 6. Changes of potassium (K%) and sodium (Na%) concentrations in the leaves after water stress (WS) and rewatering (RW) periods. †. Means denoted by the same letter did not significantly differ at P <0.05 according to Duncan's multiple range test.

Na^+: K^+ ratio was significantly increased in the leaves of the stressed plants (Figure 7). At the end of water stress period, the highest Na^+: K^+ ratio was found in 'Shah Anjiri', and 'Dane Sephid' had the lowest value. Na^+: K^+ ratio of the stressed plants was significantly reduced after rewatering; however 'Khormaei' was an exception. The highest Na^+: K^+ ratio was found in the leaves of 'Shah Anjiri', and the lowest value was found in 'Dane Sephid' after rewatering period.

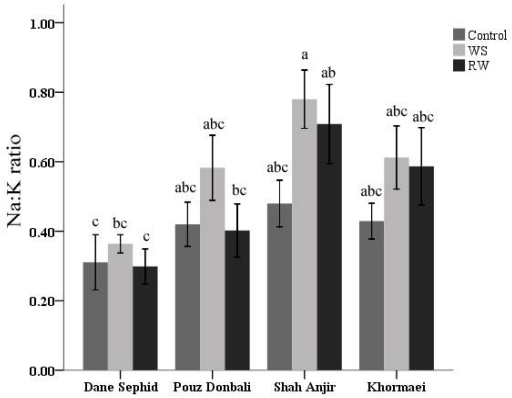

Figure 7. Na:K ratio changes after water stress (WS) and rewatering (RW) periods. †. Means denoted by the same letter did not significantly differ at P <0.05 according to Duncan's multiple range test.

DISCUSSION

Adverse effect of drought stress on plant growth is well documented. Growth reduction by water deficit stress is caused by changes in several physiological processes. Reduced stem elongation and leaf expansion of the genotypes under drought stress (Figures 1 and Figure 2) was in accordance to reduced RWC and Ψ_{Leaf} and loss of cell turgidity in apical meristem and leaf mesophyll tissues. Cell growth is considered one of the most drought-sensitive physiological processes due to loss of turgor pressure. The reduction in plant height (Figure 1) could be attributed to decline in cell enlargement and massive leaf abscission in plant under water stress (Manivannan *et al.,* 2007). Leaf area expansion depends on leaf turgor, temperature, and assimilating supply for growth. Drought-induced reduction in leaf area is ascribed to suppression of leaf expansion through reduction in photosynthesis (Rucker *et al.,* 1995). Trunk diameter also reflected the effects of water stress. Reduced water

availability causes shrinking of xylem vessels and reduced radial growth of trunk. These results are in agreement with the findings of Bradford and Hsiao (1982) and Chartzoulakis *et al.* (1993).

In addition to loss of turgidity, stem and leaf growth may be inhibited at low water potential despite complete maintenance of turgor in the growing regions as a result of osmotic adjustment. This suggests that the growth inhibition may be metabolically regulated possibly serving an adaptive role by restricting the development of transpiring area under water stress condition (Sharp, 1996). Reduced leaf area and defoliation represent an adaptation strategy by diminish water loss and increasing water deficit tolerance (Halim, 1989).

Although MLA was reduced (Figure 2), SLA was increased under the water stress period (Figure 3). The result is in contrast with Karimi *et al.* (2012) which reported reduced SLA of fig under osmotic stress *in vitro*. Rao *et al.* (2008) reported SLA increased in four species under drought stress. Increasing SLA under water stress shows that leaf expansion is less sensitive than leaf weight to drought stress. A higher SLA is a consequence of a decrease in the density or thickness of foliar tissue (Centritto, 2002). Ennajeh *et al.* (2010) found that water stress reduced leaf tissue density in olive cultivars, especially in the drought tolerant cultivar.

Water stress significantly reduced Ψ_{Leaf} and RWC of the fully expanded leaves (Figure 4). Maintaining high RWC under water stress usually has been considered as a good indicator of drought tolerance (Shaw *et al.*, 2002). Our findings showed significant reduction in RWC in the leaves of fig genotypes under drought stress, which was in accordance to Karimi *et al.* (2012) and Gholami *et al*. (2012). 'Khormaei' and 'Shah Anjiri' were able to retain RWC and Ψ_{Leaf} at higher level during the water stress period. Maintaining RWC has been reported to play an important role in the stress tolerance of fig (Karimi, *et al.,* 2012). Stomatal closure and roots ability to continue water absorption help plants to maintain RWC and Ψ_{Leaf} under lower soil water potential. Higher RWC and Ψ_{Leaf} in 'Khormaei' and 'Shah Anjiri' during water stress period suggest the possibility of a tolerance strategy by reducing water loss and evading water stress during the first stage of water stress development.

Lower EL was associated with the higher Ψ_{Leaf} and RWC. EL is an index to estimate membrane dysfunction under stress. In this study, water stress increased cellular EL, and it was significantly higher in the leaves of 'Dane Sephid'. Excessive production of reactive oxygen species (ROS) under water stress is one of the major causes of loss of cell membrane stability (Anderson *et al.,* 1990; Beltrano *et al.,* 1997; Navari-Izzo *et al.,* 1997). Findings of Rostami and Rahemi (2013) on caprifigs and reports of Gholami *et al.* (2012) on figs showed that lower EL in the leaves of drought tolerant caprifigs might be attributed to increase in antioxidant enzymes activities and inhibition of lipid peroxidation via ROS scavenging. Accumulation of osmolytes, such as proline, is another possible explanation to the maintenance of cell membrane integrity in the leaves of drought tolerant genotypes under water stress.

In this study water stress enhanced proline accumulation in the leaves of fig genotypes, however, 'Dane Sephid' was an exception (Figure 6). Karimi *et al.* (2012) reported a marked increase in proline content in a drought tolerant fig cultivar under water stress. Water stress induces proline accumulation in many plant species by increasing its biosynthesis and/or inactivation of its degradation (Hare *et al.,* 1999). Proline as an osmoregulator, or as an osmo-protector may help plant tolerate water stress (Bellinger and Larher , 1987; Ozden *et al.,*, 2009). Turkan *et al.* (2005) and Verslues *et al.* (2006) showed that proline by scavenging ROS and acting as a cell membrane stabilizer may protect cells against oxidative stress during dehydration.

Inorganic ions also may be used as compatible solutes. Such compounds are alternatives to organic osmotica and their accumulation helps plants to save energy to grow under water stress (Patakas *et al.,* 2002). K^+ is a major ion in turgor maintenance as well as regulation and may become involve in osmotic adjustment (Zhao *et al.,* 2006). In this study K^+ concentration significantly decreased under water stress (Figure 7) and did not involve in osmoregulation. Na^+:K^+ ratio was significantly increased under drought stress due to reduced K^+ concentration in the leaves. Schier and McQuattie (2000) and Kirnak *et al.* (2001) also showed that leaf K^+ concentration was decreased by water stress. This is probably due to less availability of the ion for absorption under water stress. However, higher Na^+:K^+ ratio indicates the ability of the roots to continue absorbing Na^+ under drought stress. Na^+ is chemically similar to K^+. Na^+ can replace the nutrient K^+ in its nonspecific function as an osmolyte in the vacuole (Ward *et al.,* 2009).

Recovery of physiological functions after water stress is a consequence of plant stress tolerance. The differences in the recovery rate among giving genotypes provide a useful clues to select proper plants for periodic droughts of dry lands. In this study, the fig genotypes started to recover their physiological functions after rewatering; however, the rate of recovery was different. Growth recovery of the caprifig genotypes was not the same after rewatering period. Leaf expansion, stem elongation, and trunk diameter growth of 'Khormaei' and 'Shah Anjiri' recovered after the rewatering period. However, stem and leaf stunted growth was observed in 'Dane Sephid' and 'Pouz Donbali' after rewatering. New leaf regeneration was found after rewatering period; however, leaf formation was significantly lower in 'Dane Sephid'. Stem growth and leaf formation after rewatering period may show the extent of structural damage of water stress to apical and lateral meristems. Higher rates of leaf abscission during water stress may also contribute to stunted growth of the sensitive genotypes after rewatering. Higher growth rate observed in drought tolerant genotypes after the rewatering period can also be related to higher leaf RWC and Ψ_{Leaf} which may be due to higher osmotic potential during water stress. Proline can be used as a carbon and nitrogen source for recovery after water stress. Our data suggested that higher proline accumulation in the leaves of drought tolerant caprifigs is probably involved in their fast recovery.

In conclusion, caprifig genotypes were grouped as drought tolerant ('Khormaei' and 'Shah Anjiri') and sensitive ('Dane Sephid' and 'Pouz Donbali'). The drought tolerant genotypes were able to maintain water level in the leaves during water stress period, reduced stress injury, and their growth were recovered after the rewatering period. The results RWC and Ψ_{Leaf} are good indices to evaluate drought tolerance in caprifig. EL data showed drought tolerance in caprifig genotypes may be associated to keep cell membrane functioning and integrity under water stress, and its rapid recovery. It was concluded that proline accumulation during drought stress not only helps caprifig in osmoregulation, but also is probably involved in its fast recovery. However, K^+ may not be related with higher drought resistance because drought tolerant genotypes did not show significant accumulation of K^+. It appears that Na^+ may be involved in osmoregulation and helps caprifigs to adjust osmotic pressure under water stress.

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