Physiological and Antioxidant Enzymes Responses of Two Fig Cultivars under Drought Stress

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ABSTRACT

In order to evaluate the influence of drought stress on two fig cultivars ('Siah' and 'Sabz'), uniform rooted cuttings of both cultivars were potted in 7 L pots filled with soil mixture. The treatments consisted of 4 drought intervals of 4, 8, 12 and 16 days were applied to attain osmotic potentials of -0.6, -1.15, -1.5 and -1.75 bars, respectively. The results showed, in both cultivars, relative water content (RWC), leaf chlorophyll, protein and starch concentrations decreased with increasing the drought stress. In contrast, total soluble solid (TSS) and proline contents, and also the antioxidant enzyme activities increased. However, 'Siah' showed better leaf recovery and higher activity of superoxide dismutase (SOD) and catalase (CAT) enzymes and proline content than 'Sabz', indicating 'Siah' was a more drought tolerant in comparison with 'Sabz'.

Keywords: Free radical scavenging enzyme, Growth, Proline, Water stress.

INTRODUCTION

Plants regularly face adverse growth conditions, such as drought. This stress occurs when water supply to roots is limited or when the transpiration rate is very high. These two conditions often coincide under arid and semiarid climates (Reddy *et al*. 2004). The outcome of drought can lead to growth delay, reduction of productivity and in extreme cases plant demise. Plant tolerance against water deficit conditions is seen in almost all species; however its extent varies a lot (Chaitanya *et al.* 2003). Diversity is the key for selecting promising genotypes for a specific region. Plant responses to water stress varies too, from species to species and a vast range of mechanisms has been developed to deal with deleterious impact of drought such as reduction in growth rate, stem elongation, leaf expansion and orientation and stomata movement (Jung 2004). Accumulation of osmo-protectants such as proline and glycine betaine, synthesis of antioxidants such ascorbate and tocopherol and increased activity of radical scavenging enzymes such as peroxidase (POD), superoxide dismutase (SOD), ascorbic peroxidase (APX) and catalase (CAT) are other means of plants against water stress (Muller *et al.* 2006; Sircelj *et al.* 2005).

Fig (*Ficus carica* L.) is one of the most important horticultural crops grown under Mediterranean climate conditions (Rostami and Rahemi, 2013). This plant is tolerant to seasonal drought and can be cultivated under non-irrigated conditions (Kuden and Tanriver,1998). Most of world's fig production comes from rainfed orchards which are drought prone and have been affected by recent global warming phenomenon and lack

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of sufficient annual rainfall. According to FAO (2009) statistical data, Iran is one of the top producers of this horticultural crop with a net production of nearly 55000 ton per year. It has been reported that 'Sabz' and 'Siah' are two promising cultivars with high fruit quality are suitable for rainfed culture in semi arid climatic condition. Thus, the aim of this research was to evaluate the physiological and biochemical responses of two fig cultivars namely, 'Siah' and 'Sabz' and their recovery following re-watering.

MATERIALS AND METHODS

One year old, certificated uniform rooted cuttings of two fig cultivars ('Sabz' and ''Siah' '), were bought from a local commercial nursery. They were potted in 7 L plastic pots filled with a soil mixture of soil, sand and leaf mold (1:1:1, V:V;V). The pots were placed in a greenhouse with day/night temperatures of 27/22 ºC respectively, relative humidity of 35% and natural sun light. Field capacity of the pots (FC) was determined according to the protocol described by Richards (1949). Based on FC. and permanent wilting point (PWP), 4 drought intervals of 4, 8, 12 and 16 days which created the osmotic potentials of -0.6, -1.15, -1.5 and -1.75 bar in the pots, respectively, were applied. After 2 months of treatments, the following characters were measured.

Leaf relative water content (RWC) was measured by using ten leaf discs of 7 mm diameter. The fresh weight (FW) of the leaf discs of each treatment was weighed . The discs were then hydrated until saturation (constant weight) for 48 h at 5°C in darkness and they were weight (TW). Leaf discs were dried in an oven at 75 °C for 48 h to obtain dry weight (DW). Relative water content was calculated according to the following equation:

RWC % = (FW-DW)/(TW-DW) × 100

Protein concentration was determined spectrophotometrically at 595 nm using the Bio-Rad Protein Assay Dye Reagent Concentrate (Bio-Rad Laboratories, Hercules, Calif.; catalogue no. 500-0006) using Bradford (1976) method.

Proline was extracted and its concentration was determined by the method of Bates *et al.* (1973). Leaf segments were homogenized with 3% sulfosalicylic acid and the homogenate was centrifuged at 3,000 rpm for 20 min. The supernatant was treated with acetic acid and acid ninhydrin, boiled for one hour and then absorbance at 520 nm was determined. Contents of proline was expressed as μmol g^{-1} FW.

Leaf chlorophyll content was measured using the following procedure: chlorophyll was extracted with 80% ethanol and the extract was centrifuged at 8000 rpm for 10 min. Chlorophyll content was colorimetrically determined using the following formula:

Chlorophyll (mg·g^{-1} FW) = [20.2 (A 645) + 8.02 (A663) × V] / (1000W), where A is absorption value, V is ultimate volume of extract and W is leaf fresh weight.

Total soluble sugar and starch

To measuring soluble sugars, 150 mg of dried leaf samples was extracted two times with ethanol. Sample were centrifuged at 3500 rpm for 10 min, the volume of upper phase was reached to 25 ml. Soluble sugars was measured according to method of Dobios et al. (1956), the absorption was recorded using spectrophotometer at 490 nm (Model UV-120-20.Japan).

Starch concentration in the leaf samples was measured using anthrone reagent (McCready et al. 1950). In this method, 5 mL of cold water and 6.5mL perchloric acid (52%) were added to the residual material used for sugar analysis and mixed for 15 min. About 20 mL of water was then added and the sample was centrifuged. The supernatant was separated and the same procedure was repeated with the precipitate. The supernatants were combined and left for 30 min at 0°C. After filtration, the volumes of supernatants were adjusted to 100 mL. About 2.5 ml of cold anthrone

solution (2%) was added, and the sample was heated at 100°C for 7.5 min, then transferred immediately to an ice bath and cooled to room temperature. Absorption at 630 nm was recorded using a spectrophotometer (Model UV-120-20, Japan).

Antioxidant Enzymes

For enzyme extraction, leaves (0.5 g fresh weight) were ground to fine powder in liquid nitrogen with mortar and pestle and then homogenized in 2 ml extraction buffer of 50 mM phosphate buffer saline (PBS), pH 8, 0.1 mM EDTA, 4% polyvinyl polypyroidone (PVPP). After centrifugation (4ºC, 12000 rpm, 20 min), the supernatant was collected and used for antioxidant enzymes activities analysis.

Catalase (CAT) activity was determined by the decomposition of H_2O_2 and was measured spectrophotometrically by following the decrease in absorbance at 240 nm. The activity was calculated using CAT extinction coefficient : 0.036 mM^{-1} Cm^{-1} (Dhindsa *et al.* 1980).

Peroxidase (POD) activity was determined by Chance and Maehly (1995) method. A 100 ml of reaction mixture contained 10 ml of 1% guaiacol (V/V), 10 ml of 0.3% H_2O_2 and 80 ml of 50 mM phosphate buffer (pH 6.6). Enzyme extract was added and the increase in absorbance due to oxidation of guaiacol (extinction coefficient: 26.6 mM^{-1} cm^{-1}) was monitored at 470 nm.

Superoxide dismutase (SOD) activity was determined according to Beauchamp and Fridovich (1971). The reaction mixture contained 50 mM K-phosphate buffer (pH 7.8), 13 mM methionine, 75 µM NBT, 0.1 µM EDTA, 4 µM riboflavin and enzyme extract.The reaction was based on the measurement of inhibition in the photochemical reduction of nitroblue tetrazolium (NBT) spectrophotometrically at 560 nm. The reaction was started by adding riboflavin and placing the tubes under two 15 W fluorescent lamps for 15 min. The reaction mixture with no enzyme developed maximum color due to maximum reduction of NBT. A non-radiated reaction mixture did not develop color and served as the control. The reduction of NBT was inversely proportional to the SOD activity. One unit of SOD activity was defined as the amount of enzyme required to cause 50% inhibition of the reduction of NBT.

Ascorbite peroxidase (APX) was determined using a method described by Nakano and Asada (1987), by recording the decrease in absorbance at 290 nm, as ascorbate was oxidized. The assay mixture contained 90 mM potassium phosphate buffer (pH 7.0), 0.1 mM EDTA, 0.65 mM ascorbate and 1.0 mM H2O2. The reaction was initiated with the addition of approximately 40 g enzyme extract. The reaction was started with the addition of H_2O_2 and absorbance was recorded (extinction coefficient: 2.8 mM^{-1} cm^{-1}).

Design and Statistical analysis

A facterial experiment of 4(drought intervals) × 2 (cultivars) was carried out in a completely randomized design with 6 replications and each replication included 2 plants. Data were analyzed using SAS software, and Tukey's test was used for comparison of means at 5% of probability.

RESULTS AND DISCUSSION

After 19 days of initiation of the drought stress treatments, especially in 12 and 16 days, the symptoms of water stress appeared at shoot tip and marginal necrosis which extended all over the leaf surface which ended in leaf abscission. In 'Siah' 75 % of the plants showed leaf abscission while in 'Sabz' cultivar it was 50%. However, after 41 days of the stress, in all the plants in 'Siah' cultivars, that lost their leaves started to develop new shoot. Two weeks later the plants

completed their growth. In 'Sabz' only half of the plants showed recovery, but at a very slower rate than 'Siah'. Figure 1 shows leaf abscission and plant recovery. In the control and 8 days drought, the plants did not showed leaf yellowing or necrosis. Leaf abscission, was observed in both cultivars following 12 and 16 day of drought intervals. This is a tolerance strategy in plants against water stress which helps them to avoid excess transpiration and maintain their limited and precious water resources (Hare and Cress, 2004).

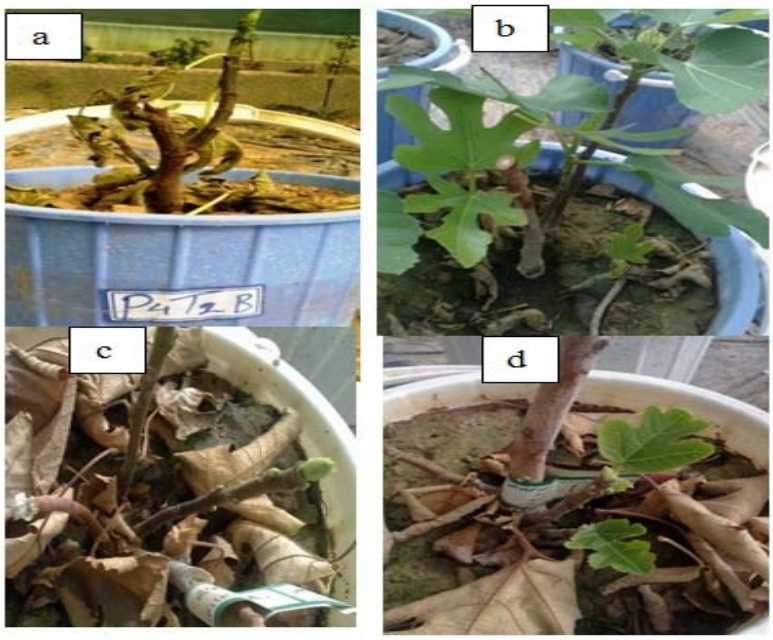

Figure 1. The effect of water deficit (16 days drought interval) on leaf abscission of two cultivars 'Siah' (a) and 'Sabz' (c) and their recovery after 41 days , 'Siah' (b) and 'Sabz' (d).

In both cultivars, leaf protein and RWC % decreased with increasing water deficit; however there was no significant difference between the two cultivars (Table 1). Regardless of cultivar, RWC % and subsequently protein content also declined along with increasing drought intervals (Figure 2). There was a direct positive correlation (r=0.78**) between RWC and protein content. Karimi *et al.* (2012) and Rostami and Rahemi (2013) also reported a positive correlation between RWC and protein. Rodriguez *et al.* (2005) also reported similar reduction of leaf RWC in *Asteriscus maritimus* grown under water deficit conditions. Osmotic adjustment is one the first steps towards drought tolerance in plants and this requires reduction of leaf RWC (Bota *et al.* 2004) which occurred in the current study. Basra and Basra (1997) showed that there was a positive correlation between leaf RWC and soil moisture, this led to stomata closure and reduced photosynthesis, and lower photosynthesis activity resulted in degradation of plant reserves such as lipids, carbohydrates and proteins.

Table 1. Interaction of cultivar and drought interval on some physiological parameters of fig.[†]

cultivar	Drought interval day (Bar)	RWC (%)	Proline (µM g^{-1}FW)	Chlorophyll (mg g^{-1} FW)	Protein (mg g^{-1}FW)	TSS (mg g^{-1} DW)	Starch (mg g^{-1} DW)
'Sabz'	4 (-0.6)	75.01 a[†]	57 c	3.46 a	86 a	124.6 c	235.9 b
	8 (-1.15)	63.91 ab	91 c	2.78 b	64 c	126.3 c	206.3 c
	12 (-1.5)	53.89 b	310 b	2.35cd	8 d	333.8 b	112.3 de
	16 (-1.75)	36.65 c	571 a	1.19 e	16 d	514.00 a	77.2 f
'Siah'	4 (-0.6)	78.09 a	58 c	3.25 a	84 ab	135.1 c	278.5 a
	8 (-1.15)	74.18 a	74 c	2.55 bc	67 bc	136.8 c	219.8 bc
	12 (-1.5)	53.70 b	380 b	2.83 b	9 d	366.1 b	127.4 d
	16 (-1.75)	36.93 c	664 a	2.06 de	7 d	554.9 a	92.9 ef
Significance							
Cultivar (C)		ns	*	ns	ns	**	*
Drought (D)		**	**	**	**	**	**
(C)×(D)		**	**	**	**	**	**

[†] In each column the means with the same letters are not significantly different at 5% probability using Tukey's test.

The highest amount of leaf proline concentration was observed in drought interval of 16 days which was significantly higher than the control. The data of table 1 shows that 'Siah' cultivar significantly had higher level of proline than 'Sabz' cultivar . In relation to leaf total chlorophyll, there was a high interaction between drought and cultivar on leaf chlorophyll content; the amount of chlorophyll decreased along with increasing drought, but in water deficit of 12 days, 'Siah' cultivar showed higher amount of chlorophyll content than 'Sabz' cultivar (Table 1).

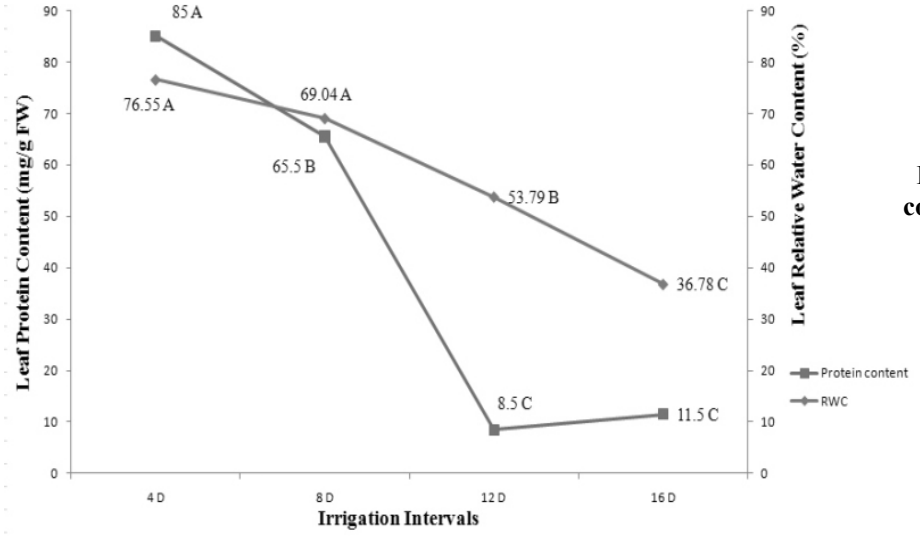

Figure 2. Changes in relative water content (RWC) and protein in two fig cultivars.

The result indicate without respect to different cultivars, there was a negative correlation between leaf proline content and chlorophyll, as increasing drought intervals, a sharp increased in leaf proline content, and a sharp decreased in total chlorophyll was observed (Figure 3). Leaf chlorophyll degradation in plants exposed to water stress might be due to change of conversion of gluthamate to proline instead of chlorophyll (Madhavarao *et al.* 2006). It has been reported that drought inhibits the photosynthesis of plants, damages the photosynthetic apparatus, and causes changes in chlorophyll content and components (Taiz and Zeiger, 2010). In the current study, 'Siah' had higher levels of proline in comparison to 'Sabz'. Osmolytes such as proline, are one of the most important means of plants against stress conditions such as drought, they are soluble in the solution within cell or in the surrounding fluids, and maintain the osmotic balance of the cells (Wang *et al.* 2004). Proline accumulates in all plant organs under drought stress but the fastest accumulation rate belongs to the leaves (Hare and Cress, 2004).

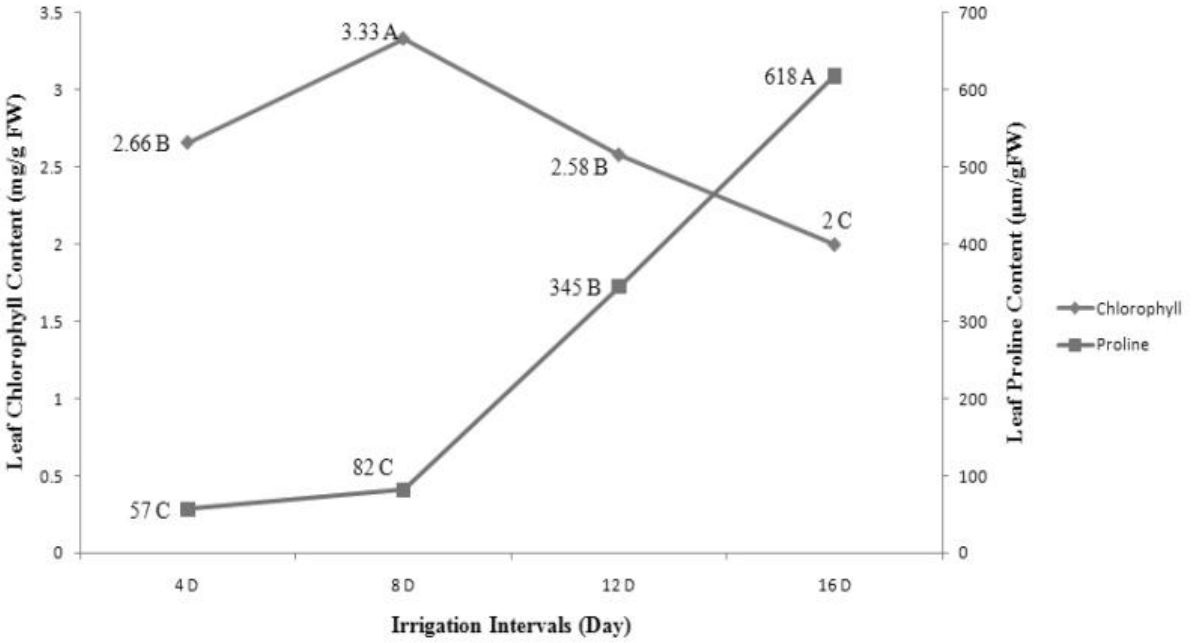

Figure 3. Changes in leaf chlorophyll and proline contents in average of two fig cultivars.

It can be expected that plants with higher proline content within their organs and leaves might be more tolerant to water deficit conditions, because the amino acid proline have the capacity to mitigate the adverse impact of drought on water potential of plant cells and maintain turgor for longer period of time.

Although with increasing drought period, leaf TSS content increased in both cultivars, however 'Siah' showed significantly higher TSS content than 'Sabz'. In contrast, the amount of starch decreased with increasing drought interval. The highest level of leaf starch content (278.5 mg g^{-1} DW) was observed in 'Siah' in drought period of 4 days and the lowest one (77.2 278.5 mg g^{-1} DW) in 'Sabz' in drought period of 16 days (Table 1).

As it has been indicated in figure 4 there was a negative correlation (R=-0.95**) between leaf starch and soluble sugars content and with reduction of starch content, leaf soluble sugars rose significantly. Starch serves as the main carbohydrate store in most plants and can rapidly be mobilized to provide soluble sugars. Metabolism by which this happens is very sensitive to changes in the environment. In addition to diurnal fluctuations in starch levels, salt and drought stress generally leads to a depletion of starch content and to the accumulation of soluble sugars in leaves (Kaplan and Guy, 2004; Basu *et al.* 2007; Kempa *et al.* 2008). Sugars that accumulate in response to stress can function as osmolytes to maintain cell turgor and have the ability to protect membranes and proteins from stress damage (Kaplan and Guy, 2004).

The result showed that there was a high interaction between cultivar and drought on SOD and CAT activity. The highest SOD (304.7 U g FW^{-1}) and CAT (97.5 U g FW^{-1}) activities were achieved in 'Siah' in drought period of 12 days (Table 2). There was no significant difference between the two cultivars in relation to POD and APX activities. In both cultivars, along with increasing drought, POD activity increased. The highest activity was achieved in drought interval of 12 days, however, a significant decline in POD activity was observed in drought of 16 days. In relation to APX, it was 16 days of drought that showed highest activity of APX (Table 2).

Table 2. Interaction of cultivar and drought interval on activity of free radical scavenging enzyme

Cultivar	Drought interval day (Bar)	SOD (U g FW^{-1})	CAT (U g FW^{-1})	POD (U g FW^{-1})	APX (U g FW^{-1})
'Sabz'	4 (-0.6)	31.0 d†	12.1 d	39.1 c	136.5 cd
	8 (-1.15)	48.2 d	42.6 c	52.0 bc	185.8 cd
	12 (-1.5)	247.0 b	79.0 b	258.8 a	470.5 b
	16 (-1.75)	96.2 c	32.5 c	93.17 b	581.0 a
'Siah'	4 (-0.6)	33.3 d	11.1 d	62.6 bc	97.1 d
	8 (-1.15)	48.0 d	47.5 c	62.1 bc	207.8 c
	12 (-1.5)	304.7 a	97.5 a	306.5 a	479.3 b
	16 (-1.75)	99.4 c	35.3 c	103.1 b	672 .0 a
Significance					
Cultivar (C)		*	**	ns	ns
Drought (D)		**	**	*	**
(C)×(D)		**	**	**	**

† In each column the means with the same letters are not significantly different at 5% probability using Tukey's test.

Oxidative stress has been cited as another factor responsible for reduction of chlorophyll content in plants under stresses such as drought. Upon moderate drought conditions, photosynthesis decreases mainly due to stomata closure, as stress progresses excess energy may result in increased production of reactive oxygen species (ROS) in chloroplasts, mitochondria and peroxysomes (Taiz and Zeiger, 2010). Excessive ROS production can

cause oxidative stress which damages plants by oxidizing photosynthetic pigments, membranes, lipids, proteins and nucleic acids (Mittler *et al.,* 2004). To keep ROS levels under control the plants have non-enzymatic and enzymatic antioxidant system, such as SOD, POD, APX and CAT to protect cells from oxidative damages, (Mittler, 2002). As it has been indicated in table 2, drought caused augmentation of activity of these radical scavenging enzymes which were in accordance with previous investigations (Alguacil *et al.,* 2006; Csiszar *et al*., 2005; Bakalova *et al.,* 2004; Badawi *et al.,* 2003). It has been reported that constitutive activity and induced activity of antioxidant enzymes are higher in more stress tolerant plants, and this can be considered as a marker for selecting them (Turkan *et al.,* 2005). In the current study, 'Siah' fig had higher activity of these enzymes and can be expected that this cultivar must be more tolerant than 'Sabz', which was true in most of the measured parameters

CONCLUSION

In both fig cultivars, drought affected the physiological and the antioxidant enzymes, however 'Siah' accumulated more proline, soluble sugars and starch, and also had higher activity of SOD and CAT enzymes. Parallel to the above changes, 'Siah' showed better and faster recovery after a long drought duration which is a desirable character for rainfed regions. It may be concluded from the current study that 'Siah'is more drought tolerant than 'Sabz'.

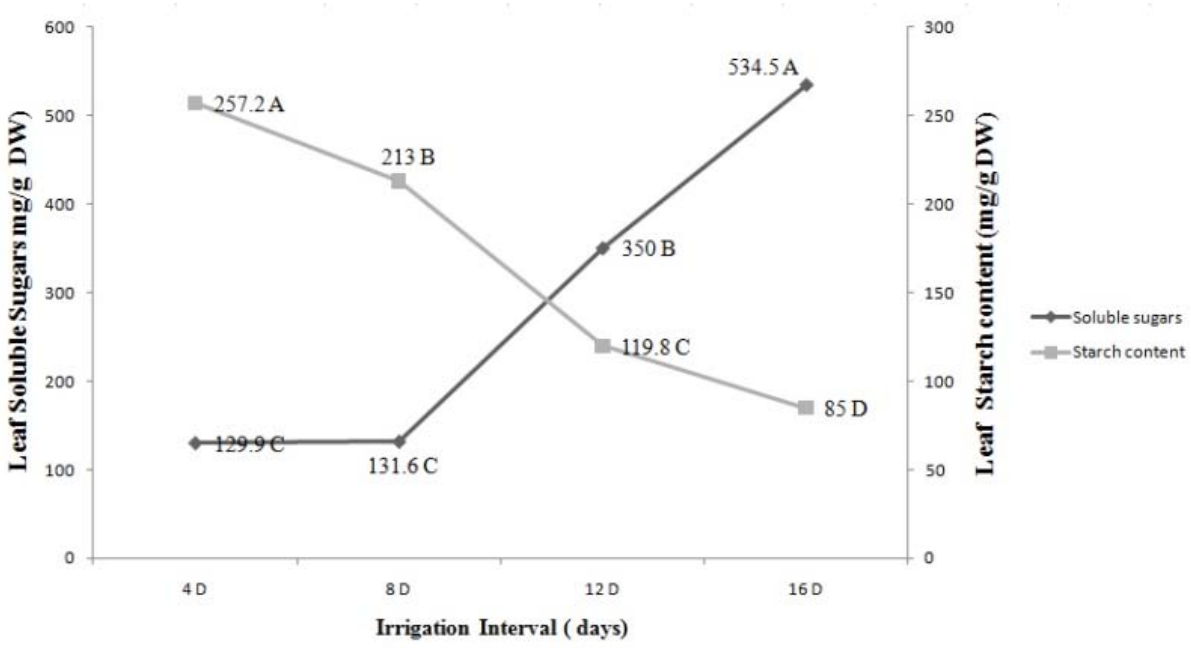

Figure 4. Changes in leaf soluble sugar and starch concentrations in average of the two fig cultivars.

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الاستجابات الفسيولوجية واستجابة انزيمات مضادات الأكسدة لأثنين من أصناف التين تحت ظروف إجهاد الجفاف

كتايون شهيدى راد[1]، اختر شكافنده[2*]، بابک جمالى[3]

ملخص

من أجل تقييم تأثير إجهاد الجفاف على صنفين من التين ('سياه "و" سابز')، تم زراعة قصاصات مجذرة متماثله من كلا الصنفين بأوعية بحجم 7 لترمليئة بخليط التربة. وتألفت المعاملات من 4 فترات من الجفاف تشمل 4 و 8 و 12 و 16 يوما تم تطبيقها لتحقيق الاجهادات الاسموزية لل0.6- ، 1.15-، 1.5,– و 1.75 – بار، على التوالي. وأظهرت النتائج، في كلا الصنفين، ان تركيزات المحتوى المائي النسبي(RWC) ، الكلوروفيل في الورقه والبروتين وتركيز النشا قد تناقصت مع زيادة إجهاد الجفاف. في المقابل، فإن مجموع المواد الصلبة الذائبة (TSS) ومحتويات البرولين، وكذلك أنشطة الانزيمات المضادة للأكسدة قد زادت. ومع ذلك، أظهر الصنف "سياه" أفضل نتائج لقدرة الورقة عالاسترجاع والنشاط العالي لانزيمات سوبر اكسيد دس ميوتيز (SOD) والكاتلاز (CAT) ومحتوى البرولين مقارنة مع صنف "سابز"، مشيرا إلى أن صنف "سياه" كان أكثر تحملا للجفاف مقارنة مع صنف"سابز."

الكلمات الدالة: الجذر الحر الكاسح للانزيم، النمو، البرولين، الإجهاد المائي.

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