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Physiological and Biochemical Responses of Three Iranian Grapevine Cultivars to Short-Term Water Deficit Stress

Mehdi Aran[1], Bahram Abedi[1✉], Ali Tehranifar[1], Mehdi Parsa[2]

ABSTRACT

A pot experiment was conducted to assess the effect of different levels of water deficit on physiological and biochemical characteristics of three of grapevine cultivars. The factors included three commercial Iranian cultivars ('Yaghooti', 'Askari' and 'Keshmeshi') and three levels of water deficit (100, 60, 30% F.C.). Cultivars under study showed different physiological responses to water stress. It was shown that plant height, shoot and root dry weight, root length, shoot/root ratio, relative water content (RWC), leaf membrane stability index and chlorophyll content decreased with soil water content being reduced. Levels of proline, catalase, ascorbate peroxidases and guaiacol peroxidase activity increased in all the cultivars as water deficit stress levels increased. Of all the cultivars, 'Yaghooti' had the greatest RWC, chlorophyll content, catalase and ascorbate peroxidases activity and proline. This results suggest that Yaghooti is more resistant to water stress than the two other cultivars.

Keywords: Grapevine, Antioxidant enzymes, Growth, Leaf relative water content, Proline, Water deficit stress.

INTRODUCTION

Grapevines (*Vitis vinifera* L.) are generally well-adapted to arid and semiarid climates, and they appear to primarily rely on drought avoidance mechanisms in water stress situations (Chaves et al. 2010). The possibility of an increase in water scarcity due to climate change and irrigation limitations makes the search for more drought resistant cultivar an interesting goal (Serra, 2014). In grapevines it is possible to find the two drought tolerance mechanisms (with no drought escape) in the form of drought responses such as stomatal closure, decrease of cell growth and photosynthesis, activation of respiration, and accumulation of osmolytes and proteins (Chaves, 2003; Doupis et al. 2011; Serra, 2013).

In grapevine, it has been reported for several varieties and different experimental conditions (greenhouse and field; short- and long-term) that photosynthesis is resistant to water stress (Flexaset al. 2002; Souza et al. 2005). Under low to moderate water availabilities occurring under deficit irrigation, maintenance of the activity of calvin cycle enzymes and of the maximum rates of carboxylation and electron transport has generally been observed (Souzaet al. 2005). However, when stress is intensified a decline in those parameters occurs, more markedly in electron transport (Souzaet al. 2005), possibly a result of decreased ATP production.

Most plants have developed morphological and physiological mechanisms which allow them to cope with drought stress. These mechanisms mainly comprise a reduction of the leaf size, leaf rolling, dense leaf

[1] PhD student, Assistant professor and professor of Department of Horticultural Science, College of Agriculture, Ferdowsi University of Mashhad, Mashhad, Iran.
✉abedy@um.ac.ir
[2] Associated professor of Department of Agronomy, College of Agriculture, Ferdowsi University of Mashhad, Mashhad, Iran.
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pubescence, deeply developing stomata, accumulation of mucilage and other secondary metabolites in the mesophyll and increase of mesophyll compactness. Another initial reaction of plant to water deficit is the cessation of shoot growth, which is often followed by rapid resumption of growth when available water is restored in the soil (Pereira and Chaves, 1995). Water deficit also affects the development of the root system. To minimize the effects of stress, plants have evolved various adaptive responses, as for example during drought stress, plants close their stomata and accumulate compatible solutes to maintain a low water potential and avoid dehydration (Skirycz and Inze 2010).

Osmotic adjustment in terms of compatible solutes accumulation has been considered as an important physiological adaptation for plant to resist drought, which facilitates the extraction of water from dry soils and maintenance of cell turgor, gas exchange and growth in very dry environments (Chaves et al. 2003). Acting as compatible solutes as well as antioxidants, a significant rise in proline amount was observed in grapevine leaves (Doupis et al. 2011) under water stress conditions, suggesting that this amino acid has a protective role against the formation of excessive reactive oxygen species (ROS). Plants, in order to overcome oxidative stress, have developed enzymatic and non-enzymatic antioxidant defense mechanisms against scavenge ROS (Smirnoff 1993). Drought stress usually leads to oxidative stress owing to stomatal closure, which brings about the over-reduction of photosynthetic electron chain (Ben Ahmed et al. 2009) and high formation of ROS in chloroplasts and mitochondria. Understanding the physiological responses of different genotypes to moderate and severe water stress is crucial not only to determine the threshold of stress levels, but also to identify sensitive and resistant cultivars for breeding programs in grapevines.

In order to better understand the responses of grapevines to different levels of water deprivation, a set of selected physiological and biochemical parameters (plant height, shoot and root dry weight (DW), relative water content (RWC), leaf membrane stability index (MSI), chlorophyll content, proline, catalase (CAT), ascorbate peroxidases (APX) and guaiacol peroxidase (GPX) activity) were analyzed in three grapevine cultivars.

The aim of the present study was to investigate the sequence of physiological and biochemical changes induced by drought stress levels in grapevines grown under natural weather conditions, with controlled water regimes, and to evaluate the changes of selected parameters known as protective substances at different intensities of drought stress.

MATERIALS AND METHODS

Cuttings of three grapevine (*Vitis vinifera* L.) cultivars namely, 'Yaghooti', 'Askari', and 'Keshmeshi' were rooted and left to grow in 20 L PVC pots filled with a mixture of leaf mould, sand, and soil (1:1:1, v/v/v) and a gravel layer at the bottom. Volumetric water content at field capacity was ~25%. The plants were grown under natural weather conditions (mean temperature, 28.5°C and mean humidity 20.7% at during the course of the experiment) in Ferdowsi University of Mashhad, Iran (lat. 36° 18' 27.31" N, long. 59° 31' 43.44" E, altitude 1050 m). The potted grapevines were irrigated daily for 3 months to field capacity level, until the plants were established.

The experiment started in June 21, 2014 and 2015. The grapevines of each cultivar were divided in three groups: control plants, moderate drought-stressed plants and severe drought-stressed plants. Control plants were maintained in optimal soil water conditions (100% F.C.) during the whole experimental period, whereas the moderate and severe drought-stressed plants were irrigated with 60% and 30% F.C. for 60 days, respectively.

Vine height (H), shoot and root dry weight (DW), root length and shoot/root ratio were determined at the end of the experiment. Shoots and roots were dried at 80 °C for 48 h to obtain the dry weight.

Chlorophyll content was determined using the method of Dere et al. (1998). To measure relative water content (RWC), fresh weight (FW) of two excised leaves per plant was weighed and placed in plastic bags in the dark with their petioles plunged in distilled water overnight to allow them to reach full turgor and, hence, to determine their turgid weight (TW). These leaves were then dried at 75 ºC for 48 h and their dry weight (DW) was recorded. Relative water content was calculated using the following equation (Guha et al. 2010):

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

Leaf membrane stability index (MSI) was determined according to the method of Premchandra et al. (1990) modified by Sairam (1994). Proline content was estimated by the method of Bates et al. (1973). Plant material was homogenized in 3% aqueous sulfosalicylic acid and the homogenate was centrifuged at 10,000 rpm. The supernatant was used for the estimation of the proline content. The reaction mixture, consisted of 2 ml of acid ninhydrin and 2 ml of glacial acetic acid, was boiled at 100 °C for 1 h. After finishing of the reaction in ice bath, the reaction mixture was extracted with 6 ml of toluene, and absorbance was read at 520 nm.

The methods used for determining catalase (CAT) and ascorbate peroxidases (APX) activities were reported by Jiang and Zhang (2002). APX activity was measured by monitoring the reduction in absorbance at 290 nm as ascorbate was oxidized, as described by Nakano and Asada (1981). Guaiacol peroxidase (GPX) was recorded at 470 nm as described by Castillo et al. 1984.

Statistical design and analysis

The experimental units were arranged in a factorial based on a complete randomized block design with four replications. Data were statistically evaluated by analysis of variance (ANOVA) to assess the significance of the main factors and the significance of interactions. Combined analysis of variance was carried out assuming environment (years and blocks) as random and treatments (cultivars and drought stress) as fixed factors. JMP8 software was used to test the significant differences among the treatments and the interactions. When there were significant differences, means were separated by Tukey HSD test at the probability level $p<0.05$.

3. RESULTS AND DISCUSSION

Results showed that drought stress had significant effects on most traits in the three cultivars at statistical levels ($P\leq0.05$ and $P\leq0.01$). The effect of year, year×cultivar, year×drought and year×cultivar×drought stress on measured traits were not significant. The results indicated that the three grapevine cultivars showed a difference in their response to water stress. Plant height, shoot and root dry weight (DW), and root length tended to be higher in the well-watered plants than in water deficit-treated plants for all the three cultivars. With respect to plant height, 'Yaghooti' and 'Keshmeshi', were significantly the tallest compared to control treatment; however, in the moderate stress, 'Askari' was the tallest. Regarding severe stress, 'Yaghooti' was the tallest which was in the same level of significance with 'Keshmeshi' (Fig. 1A). Similar results were reported by Ramteke et al (2005); Satisha et al (2006) and Rayees et al (2013). Cramer et al. (2007) has also observed that the growth of grapevine shoots was reduced under the conditions of a relatively moderate water deficit.

Shoot dry weight (DW) and root length were generally reduced by water stress treatments in the three cultivars (Table 1). The production of dry matter was significantly reduced by water stress in the three cultivars. In the control, moderate and severe stress, 'Yaghooti' had higher shoot DW. 'Yaghooti' had higher root length in control, whereas in severe stress, 'Keshmeshi' had significantly the greatest root length when compard to 'Askari'. Root DW experienced a significant reduction under both treatments of drought stress. In the control treatment, 'Askari' proved to have the greatest root DW, whereas in severe stress treatment, 'Yaghooti' had higher root DW when compared to 'Askari' (Table 1). Shoot/root ratio of 'Yaghooti' was significantly higher than those of 'Askari' and 'Keshmeshi' at control and severe stress treatments (Table 1).

As suggested by Shao et al. (2008), the decrease in dry matter may be due to the considerable reduction of photosynthesis and plant growth. Changing resource pools (e.g., water or nutrient availability) may affect the distribution of biomass (Morse and Bazzax, 1994). Decreasing root DW in olive under drought conditions may be caused by a decrease in the accumulation of root carbohydrates (Arji and Arzani 2000). Therefore, plants with high amounts of dry mass under drought stress can be considered as drought tolerant genotypes. The lowest reduction in DW of the whole plant (47.9%) was observed in 'Yaghooti', which might be a reason for the lower sensitivity of this cultivar to drought stress. The greatest reduction in whole plant DW, 63.7% and 52%, was found in 'Keshmeshi' and 'Askari', respectively. These findings are consistent with the results reported by Zokaee-Khosroshahi et al (2014). The morphological adaptability of plants may be one of the mechanisms of their adaptation to arid conditions and drought tolerance (Pire et al. 2007).

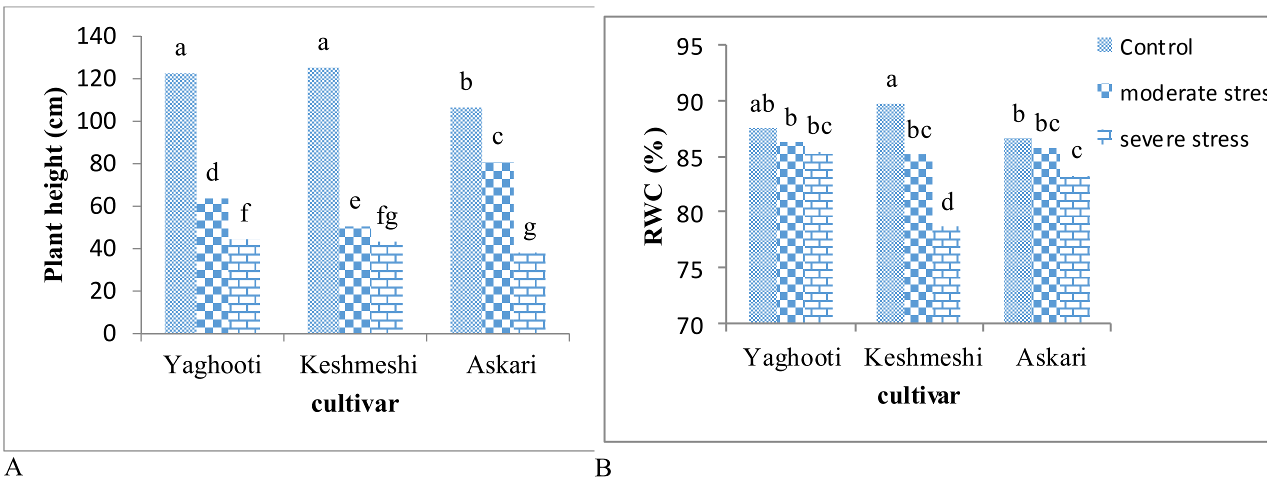

Figure 1. Effect of water deficit stress on height (A) and RWC (B) of grapevine cultivars. Data shown are means of the two years.

Table 1. Effect of water deficit stress on shoot and root dry weight, root length, shoot/ root ratio, MSI and chlorophyll content of three grapevine cultivars. Data shown are means of the two years.

Cultivar	Water treatment	Shoot DW (g)	Root length (cm)	Root DW (g)	Shoot/ root	MSI (%)	Chl a (mg g^{-1} FW)	Chl b (mg g^{-1} FW)	Chl t (mgg^{-1} FW)
	100% F.C.	34.9a†	88.81a	16.41b	2.13a	81.89a	10.37a	3.44a	13.81a
Yaghooti	60% F.C.	17.36d	71.53c	15.5bc	1.125cd	77.98b	8.96ab	3.36ab	12.21b
	30% F.C.	13.33e	52.25de	13.38cde	1.006cd	74.26cd	8.17bc	2.85abc	11.03bcde
	100% F.C.	26.97b	81.12b	16.72ab	1.61b	80.31ab	8.32bc	2.84bc	11.16bcd
Keshmeshi	60% F.C.	13.67e	68.5c	15.22bcd	0.91de	73.5cd	7.53c	2.59c	10.12de
	30% F.C.	5.07f	55.5d	10.76f	0.47f	71.97d	6.96c	2.43c	9.76e
	100% F.C.	22.64c	79.75b	18.99a	1.19c	81.78a	9.01ab	2.91abc	11.9bc
Askari	60% F.C.	12.76e	69.12c	12.79def	0.99cd	79.03ab	7.62ab	2.71c	10.71cde
	30% F.C.	8.05f	49e	11.92ef	0.68ef	75c	7.05c	2.5c	10.09de

When water deficit develops, a sequence of physiological and biochemical events will occur. The first and most sensitive response to water deficit in plants is the reduction in growth processes due to loss of cell turgor (Larcher, 2006). In this research, all grapevine cultivars presented similar growth in plant height, shoot and root DW, and root length during the experimental period. The reduction observed in plants grown water deficit must be explained due to the lower turgor pressure caused by the low-soil water availability, which involves processes such as cell division and elongation (Shao et al., 2008).

Drought stress induced a significant decrease in leaf relative water content (RWC) of all three cultivars during the drought period (Fig. 1B). The RWC of 'Yaghooti' was significantly more than those of 'Askari' and 'Keshmeshi' at severe stress. 'Keshmeshi' had the highest RWC in the control treatment, however, this cultivar showed a lower RWC in severe stress. In this experiment 'Keshmeshi' demonstrate a higher decrease of RWC (12.3%) compared to 'Yaghooti' (2.3%) and 'Askari' (3.7%) suggesting that 'Yaghooti' is more tolerant to water stress than the other cultivars. Resistance of a plant to drought is related to its ability to maintain high RWC in leaves under stress (Faraloni et al. 2011). Significant changes in leaf RWC during the period of osmotic stress suggest that the dehydration may be the most important contributory factor in osmotic potential decrease. Under harsh drought stress, a reduction in RWC was a common response (Pérez-Pérez et al. 2007). In drought tolerant cultivars, the maximum RWC may be due to maintenance of the cell turgidity while in drought susceptible cultivars, cell turgidity was lost readily. These results are in agreement with the findings reported by Koundouras et al. (2008), Ghaderi et al. (2011), Rayees et al. (2013) and Zokaee-Khosroshahi et al. (2014). The current results showed that the RWC of leaves increased as available water increased, so that the maximum and minimum amounts of RWC were observed in control and severe stress treatments, respectively. Similar results were obtained by Rayees et al. (2013) who showed that imposition of water stress caused the RWC of leaves to decrease substantially in all genotypes by the end of stress cycles.

Significant differences were observed among the cultivars in terms of leaf membrane stability index (MSI). Water stress treatments caused a decline in MSI. At the level of moderate and severe stress, 'Askari' had the greatest percent among MSI of cultivars.

According to Ghaderi et al (2011), significant differences were observed in MSI among the three grapevine cultivars in drought treatments, in which 'Khoshnave' had higher MSI than the other cultivars. The reduction in cell membrane stability, as a result of increasing drought stress, was also reported by Hura et al. (2007). Under water deficit, cell membranes undergo some changes such as an increase in permeability and a decrease in selectivity, which can be viewed through the increase in electrolyte leakage (Blokhina et al. 2003).

Water stress treatments resulted in lower Chlorophyll (a + b) contents in all three grapevine cultivars (Table 1), so that a significant reduction in this variable was observed in the stressed grapevine compared to the control. In all the three treatments of irrigation, the highest value of Chl content was observed in 'Yaghooti'. The decrease in the level of chlorophyll pigments in plants grown under drought stress has been reported by many investigators. Reduction in chlorophyll under low leaf water potentials can be attributed to the sensitivity of this pigment to increasing environmental stresses, especially to salinity and drought, a finding which has been reported by several researchers (Guerfel et al. 2009; Gholami et al. 2012). According to Smirnoff (1993), chlorophyll content reduction in plants under stress conditions has been regarded as typical symptom of oxidative stress and might be the result of pigment photo-oxidation, chlorophyll degradation and/or chlorophyll synthesis deficiency.

Significant differences in proline content were found among cultivars and watering regimes (Fig. 2A). Under the severe stress conditions, the highest proline accumulation was registered in the 'Yaghooti' cultivar, and no significant differences existed among the other cultivars. Under moderate stress, the highest proline content was found in 'Yaghooti' and 'Askari' cultivars, which showed significant differences with 'Keshmeshi'. Plants accumulate compatible solutes, such as proline, in response to stress to facilitate water uptake. Proline accumulation was correlated with a variety of stress conditions and is now regarded as a major non-enzymatic antioxidant (Szabados and Savouré 2010) Being associated to water stress tolerance, the accumulation of compatible solutes may help to maintain the relatively high water content necessary for plant growth and cellular function (Toumi et al. 2007). It is accepted that proline has an important and complex role in drought tolerance of plants and the assistance of osmotic adjustment (Kavi Kishor et al., 2005). According to Ashraf and Foolad (2007), aside from its role as an osmoregulator, proline also contributes to membrane stabilization and radical oxygen scavenger, preventing plants from being damaged by environmental stresses.

In the present study, the increase in stress severity brought about an increase in proline content which can be explained by the activation of biosynthetic enzyme such as P5CS (Vaseva et al. 2012) or probable involvement and activation of other enzymes involved in proline biosynthesis, such as P5CR (Szabados and Savouré, 2010), or the possible down-regulation of enzymes involved in proline catabolism. This increase of proline content resulting from increase in severity of stress helped the plants to maintain tissues water status and avoid the drought-induced damage (Jiang and Huang, 2002).

Water stress treatment resulted in a significant increase in activity of ascorbate peroxidases (APX) and guaiacol peroxidase (GPX) in all cultivars. APX activity was greater in 'Yaghooti' than 'Askari' and 'Keshmeshi' in severe drought stress (Fig. 2B).

Moreover, 'Keshmeshi' had a significant lower APX activity than other cultivars in all water stress treatments. Ascorbate peroxidase, able to scavenge the H_2O_2 produced by SOD using ascorbate as the electron donor (Noctor and Foyer, 1998). Unlike other cultivars, 'Askari' showed a higher GPX activity in severe drought stress (Fig. 2C).

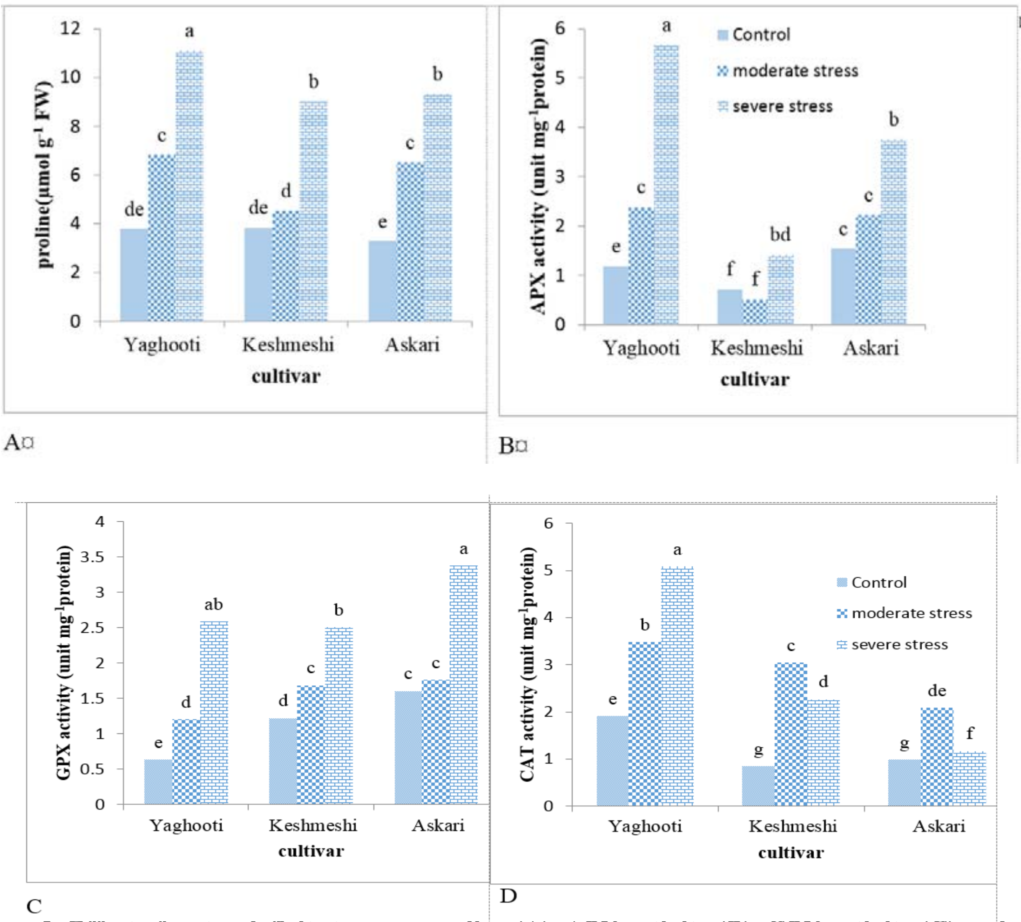

Figure 2. Effect of water deficit stress on proline (A), APX activity (B), GPX activity (C) and catalase activity (D) of three grapevine cultivars. Data shown are means of the two years. Columns with the same letters are not significantly different using Tukey HSD test (p≤0.05).

Catalase (CAT) activity was clearly induced by water deficiy treatment in all cultivars. CAT activity in 'Yaghooti' increased as drought intensified, so this cultivar had the highest values of CAT activity in comparison with other cultivars (Fig. 2D). However, CAT activity in 'Askari' and 'Keshmeshi' increased under moderate stress and decreased in severe stress. In order to keep reactive oxygen species (ROS) under control, plants have evolved a well-developed antioxidant defense system (Gill and Tuteja, 2010). In the present study, progressive drought stress generally caused an increase in activity of APX, GPX and CAT enzymes that coordinate ROS concentration. Møller et al. (2007) suggested that high levels of antioxidant enzyme activity can increase plant resistance to drought stress. Gholami et al. (2012) reported an activation of ROS scavenging enzymes and plant antioxidants, including GPX and APX, in fig in response to drought stress treatments. During the drought stress period, 'Yaghooti' showed high level of APX and CAT activities, suggesting that antioxidant protection in this cultivar could be attributed mainly to APX and CAT. But the highest value of CAT in 'Askari' and 'Keshmeshi' cultivars obtained at moderate drought stress. APX activity observed in leaves can protect chloroplast, which under the existed stress conditions maintained electron flows. Simova-Stoilova et al. (2010) reported an increase in CAT activity in wheat under drought stress, but it was higher especially in sensitive varieties. In another study, Sun et al. (2013) reported an increase in CAT activity in chrysanthemum during and after water stress. The finding that the APX, GPX and CAT activities change significantly with drought in 'Yaghooti', 'Askari' and 'Keshmeshi' suggests that these enzymes have a major antioxidative function in grapevine. Increased GPX activity, a key H_2O_2 detoxifying enzyme showed that it plays a positive role in controlling the cellular level of H_2O_2 under drought stress conditions. Similar increase in GPX activity has been reported by other researches (Ratnayaka et al. 2003; Nazarli et al. 2011).

The result of this experiment indicates that osmotic stress caused a number of physiological and biochemical changes in grapevine plant, including decrease in height, shoot and root DW, RWC, MSI and chlorophyll, and increase in proline content, APX, GPX and CAT activities. The increased synthesis of proline, APX, GPX and CAT activities might exhibited a protective mechanism against the cellular structures from oxidative damage.

In the present study, based on the responses of cultivars to different levels of drought stress, it can be concluded that 'Yaghooti' seems to be a more resistant cultivar to water stress compared to 'Askari' and 'Keshmeshi' cultivars. Based on the results, it can be said that 'Keshmeshi' cultivar has the lowest resistant cultivar to water stress compared to 'Askari' and 'Yaghooti' cultivars. Further research especially under field conditions is needed to support this statement.

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تأثير الكرب المائي على الخصائص الفسيولوجية والبيوكيميائية لثلاثة اصناف من العنب الإيراني

مهدي أران[1]، بهرم عابدي[1]، علي طهرانيفار[1]، مهدي بارسا[2]

ملخص

نفذت هذه التجربة في أصص بهدف دراسة تأثير مستويات مختلفة من الاجهاد المائي على الصفات الفسيولوجية والبيوكيميائية لثلاثة اصناف من العنب، وقد شملت التجربة عاملين، العامل الاول ثلاثة اصناف ايرانية تجارية من العنب وهي (ياقوتى، عسكرى و كشمشى)، اما العامل الثاني الاجهاد المائي وعلى ثلاث مستويات 30، 60 و 100% من السعة الحقلية. وقد بينت الدراسة انخفاض في ارتفاع النبات، عدد الافرع، الوزن الجاف للجذور، طول الجذور، نسبة الافرع الى الجذور، المحتوى المائي النسبي و كذلك محتوى الكلورفيل ونفاذية الاوراق كلما انخفض المستوى المائي في التربة، كذلك أظهرت النتائج زيادة ملحوظة في الصفات البيوكيميائيه مثل البرولين، انزيم كاتاليز، نشاط اسكوربات بيروكسيديز و جوايكول بيروكسيديز بزيادة الاجهاد المائي لكل الاصناف، بينت النتائج أن الصنف ياقوتى كان مميزاً من حيث المحتوى النسبي للماء، محتوى الكلورفيل، كاتليز، نشاط اسكوربات بيروكسيديز ومحتوى البرولين . وتشير هذه النتائج إلى أن الصنف ياقوتى هو أكثر قدرة على مقاومة الإجهاد المائي من الصنفين الأخرين.

الكلمات الدالة: العنب، انزيمات مضادات الاكسدة، النمو، المحتوى المائي النسبي للورقه، البرولين، الاجهاد المائي.

[1] قسم علم المحاصيل، كلية الزراعة، جامعة فيردوسي، مشهد، ايران.

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