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The Physiological Response of Three Iranian Grape Cultivars to Progressive Drought Stress

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ABSTRACT

Investigating the role of drought stress conditions on physiological characteristics of plant may provide means to understand basic drought resistance. Differences in leaf emergence rate, leaf relative water content (RWC), membrane stability index (MSI), leaf mass area (LMA), net photosynthesis (A_{net}), stomatal conductance (g_s), transpiration rate (E), intercellular CO_2 concentration (C_i), water use efficiency (A_{net}/g_s) and recovery of gas exchange were investigated in two-year-old grapes of three *Vitis vinifera* L. cultivars ("Khoshnave", "Bidane-Sefid" and "Askari"), subjected to progressive drought stress (soil water potential: -0.2, -0.6, -1, and -1.5 MPa). The results showed temporary reduction in RWC, MSI, leaf emergence rate, LMA, A_{net}, g_s and *E*. C_i decreased with increasing drought stress. "Khoshnave" grape showed a higher photosynthesis rate than "Bidane-Sefid" and "Askari". Higher LMA of "Khoshnave" may be attributed to the potential for carbon absorbance and higher A_{net} as compared to the other two cultivars. Complete recovery of A_{net} for all cultivars occurred one day after rewatering at -0.6 MPa and four days after rewatering at -1 MPa treatments. Complete recovery of g_s was not observed in either one or four days after rewatering except for "Askari". The results showed that A_{net} of "Khoshnave" recovered quickly as compared to those in the other two cultivars. Water use efficiency was maximum in all cultivars under -1 MPa treatment. Similar patterns of A_{net}/g_s were observed for the three cultivars. "Khoshnave" had higher A_{net}/g_s as compared to "Askari" and "Bidane-Sefid" under severe drought stress conditions. "Khoshnave" cultivar, with a higher A_{net}, higher leaf emergence rate, higher LMA, rapid recovery of A_{net}, higher A_{net}/g_s was found to be promising for cultivation in rain-fed areas across the west of Iran in comparison with the other cultivars.

Keywords: Drought stress, Gas exchange, Grapevine, LMA, Water use efficiency.

INTRODUCTION

Water stress is considered to be a main environmental factor limiting crop growth and yield, including grape in Mediterranean areas (Gomez-del *et al.,* 2004). Stomatal closure in response to water stress can even occur before detectable change in leaf water potential. Water stress-induced change in photosynthetic rate can be more generally related to variation in g_s under light saturating conditions than to RWC or leaf water potential (Flexas *et al.,* 2002; Medrano *et al.,* 2002). Therefore, g_s may be a useful indicator of grapevine water stress. Predawn leaf water potential was only sensitive to severe drought stress, while stomatal conductance was responsive to mild stress (Pellegrino *et al.,* 2005), which caused decrease in A_{net}, *E* and C_i (Sircelj *et al.,* 2007). Stomatal limitations were often thought to be the short term responses to drought stress, whereas non-stomatal effects are usually considered to be more important

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during longer and more severe drought stress events (Rouhi *et al.,* 2007). In *Vitis vinifera*, photosynthetic activity decreases during typical summer days due to stomatal (closure) as well as non-stomatal (biochemical reaction) limitations (Chaves *et al.,* 1987). Photosynthesis (A_{net}) is one of the key determinants for plant productivity and survival (Chaves *et al.,* 2003).

The study of water use efficiency (A_{net}/g_s) becomes particularly conspicuous in situations where growth is affected by limiting water availability (Anyia and Herzog, 2004). Maximum water use efficiency is achieved at the limit between diffusional and metabolic limitation to photosynthesis (Flexas *et al.,* 2004).

As the water content of the plant decreases, the cells shrink and cell wall relaxes, to result in turgor maintenance. On the other hand, water stress limits the size of individual leaves, leaf number (Tiaz and Ziger, 1998; Pellegrino *et al.,* 2005) and shoot growth (Pereira and Chaves, 1995). Greater leaf mass area across the woody species set as greater allocation of support and defense functions (Castro-diez *et al.,* 2000). In Mediterranean vegetation, this is often related to leaf resistance to dry conditions (Niinemets, 2001; Wright *et al.,* 2004).

Grapevine cultivars have been deemed to be adapted to arid conditions and produce high yield and product quality under non-optimal conditions (Gomez del *et al.,* 2004). Grapevine avoiding water stress deployed a range of physiological mechanisms in response to stress (Schultz, 1996). The selection of the best cultivar, based on ecophysiological drought stress characterization, is of ultimate importance for poetizing the production in dry environments. "Khoshnave" vineyards in west of Iran are typically non-irrigated but "Bidane-Sefid" and "Askari" vineyards are. To the best of authors' knowledge, net photosynthesis response, and thus indirect productivity, to drought stress in the three grape cultivars ("Khoshnave", "Bidane-Sefid" and "Askar") has not yet been studied. Therefore the aim of the present study was to compare photosynthetic gas exchange patterns of the three grape cultivars ("Khoshnave", "Bidane-Sefid" and "Askar")) to the progressive water deficit regimes and subsequent recovery period across the west parts of Iran.

MATERIALS AND METHODS

Two-year-old, own-rooted plants of three grape (*Vitis vinifera* L.) cultivars ("Khoshnave", "Bidane-Sefid" and "Askar") were grown outdoor in the experimental site of the Department of Horticulture, University of Kurdistan, Sanandaj, Iran. The plants were grown in 18 L plastic pots (one plant per pot) filled with loamy soil. Pots were randomly and periodically rotated to minimize the effect of environmental heterogeneity. The trees were watered equally until June 2008 and then were subjected to a progressive drought stress. The experiment was comprised of factorial combinations of three cultivars by four watering regimes in a randomized complete block design. Water stress was imposed by withholding water from the plants until soil water potential reached -0.2 (CT), -0.6 (S1), -1 (S2) and -1.5 (S3) MPa during June-July 2008. Soil water content was determined through gypsum block and TDR (Time Domain Reflectometry). The physiological measurements were made in the four drought stress treatments, one as well as four days after rewatering. All measurements were made on sunny days using the fully irradiated youngest mature leaf (5^{th} to 7^{th} leaf from apex).

Leaf relative water content (RWC) was estimated gravimetrically according to the method of Galmes *et al.* (2007). Leaf membrane stability index (MSI) was determined according to the method of Premchandra *et al.* (1990) modified by Sairam (1994). To measure leaf emergence rate, number of leaves produced during the experiment was counted (Pellegrino *et al.,* 2005).

Leaf mass area (LMA) was calculated in four fully expanded young leaves from different plants of each species under different drought stress treatments. Leaf area was determined with an AM-100 leaf area meter (Light box model, Delta t) and then, the dry masses of these leaves were determined after oven drying for 24 hours at 70°C. LMA was calculated as the ratio of dry mass/leaf area (Muraoka *et al.,* 2002; Galmes *et al.,* 2007).

Leaf gas exchange measurements were made in the middle of the day at 11 am in the summer (with clear sky). For each treatment, six plants were transferred outdoors under natural irradiance. Net photosynthesis (A_{net}), stomatal conductance (g_s), transpiration rate (E) and intercellular CO_2 concentration (C_i) were also measured. Water use efficiency was calculated as the ratio of A_{net}/g_s. Measurements were performed on two well exposed and fully expanded mature but topmost leaves of each plant using a portable IRGA (LCA-4, Analytical Development Co., Hoddesdon, England). From the data collected, charts and curve fittings were performed using Microsoft Excel software and comparisons among the means were statistically analyzed using a factorial based on complete block design through SAS. Treatment means were compared using least significant difference test at 5% significance level.

REAULTS AND DISCUSSION

The three investigated grape cultivars here showed a clear difference in their response to different applied drought stress levels. RWC did not show significant differences among the cultivars and different drought stress treatments, however, "Askari" had a lower RWC than those in "Khoshnave" and "Bidane-Sefid" (Table 1). The results demonstrated 4.3%, 5.7% and 4.0% reductions in RWC levels for "Khoshnave", "Askari" and "Bidane-Sefid", respectively, at S3 treatment as compared to control. On

Table 1. Means of relative water content (RWC), membrane cell stability index (MSI), leaf emergence rate and leaf mass area (LMA) for each of the three grape cultivars under different drought stress treatments.

	RWC (%)	MSI (%)	Leaf number	Leaf mass area (mg cm^{-2})
'Khoshnave'				
CT	89.95±0.67a	77.38±0.69bc	10.17±0.726a	7.491±0.35a
S1	89.32±0.07ab	78.99±0.51ab	8.00±0.00b	7.17±0.34ab
S2	88.16±0.17abc	78.35±0.64ab	8.33±0.17b	6.62±0.07bc
S3	86.20±0.67cd	74.04±0.64e	5.83±0.17c	6.09±0.04cd
'Askari'				
CT	87.86±1.79abc	78.06±0.37ab	7.83±0.17b	5.79±0.24de
S1	88.58±0.09abc	80.00±0.513a	8.00±0.50b	5.26±0.41ef
S2	87.45±0.36abcd	77.31±1.25bcd	5.33±0.44c	4.71±0.34fgh
S3	82.87±0.53e	75.65±1.15cde	4.00±0.29d	4.88f±0.24fgh
'Bidane-Sefid'				
CT	88.59±2.16abc	77.85±0.12abc	7.67±0.17b	5.16±0.07efg
S1	88.97±0.22ab	79.80±0.71a	6.00±0.29c	4.93±0.52fgh
S2	86.82±0.86bcd	75.16±0.16de	5.67±0.17c	4.38±0.12gh
S3	85.14±0.55de	71.74±0.90f	3.00±0.00e	4.32±0.24h

Each value is a mean of 9 measurements. CT, S1, S2 and S3 indicate the different application of drought stress levels, with a water potential of soil of -0.2, -0.6, -1 and -1.5 MPa, respectively; values are measured only during stress treatment (CT, S1, S2 and S3) and before the subsequent recovery period. Within a column, values followed by different letters are significantly different (P≤ 0.05).

the other hand, the reductions in A_{net} at S3 treatment and as compared with control were 97.6%, 97.2% and 99.3% for "Khoshnave", "Askari" and "Bidane-sefid", respectively. The smallest change in leaf RWC in reaction to drought stress was observed for these three grape cultivars, indicating a hydro stable nature, typical for drought avoiding species. In some species like grapevine, A_{net} progressively declines during water stress, which is also accompanied by very low reduction in RWC (Flexas *et al.,* 2004). Among such C3 plants as grapevine, water-stress-induced changes in photosynthetic rate can be more generally related to variation in g_s under light saturation conditions than to RWC or leaf water potential (Flexas *et al.,* 2004). Ghaderi *et al*. (2005) observed no significant differences in RWC under different drought stress regimes in grapevine when the amount of A_{net} was reduced sharply. On the other hand, the isohydric behavior would be expected to limit the range of leaf water potential response to the differences in soil water content induced by irrigation treatment in grape (Sousa *et al.,* 2006). Significant differences in MSI (Table 1) was not observed among the three cultivars except in S2 and S3 treatments in which "Khoshnave" had a higher MSI than "Bidane-sefid". In the current study, a reduction in MSI at S3 treatment coincided with RWC decline. The reduction in cell membrane stability, with increasing drought stress, was also reported by Hura *et al.* (2007), and Pereira and Chaves (1995).

A progressive reduction in the rate of A_{net} and g_s was observed in the studied cultivars. Mean values of A_{net} for plants not exposed to drought stress were 14.2, 12.5 and 11.6 µmol CO_2 m^{-2} s^{-1}, respectively, for "Khoshnave", "Askari" and "Bidane-Sefid" (Table 2). The values of A_{net} in the three cultivars were similar at the highest drought stress applied in this experiment. From Table 2, it can be seen that "Askari" and "Bidane-Sefid" had the largest reductions in A_{net} as a consequence of drought stress imposed under S2 conditions. Maximal reductions in A_{net} for all cultivars were observed at S3. A comparison of S2 values

Table 2. Mean values of net photosynthetic rate (A_{net}), stomatal conductance (g_s) and water use efficiency (A_{net}/g_s) for each of the three grape cultivars under different drought stress treatments.

	A_{net} (µmol CO_2 m^{-2} S^{-1})	g_s (mmol H_2O m^{-2} S^{-1})	(A_{net}/g_s) [µmol (CO_2) mol^{-1} (H_2O)]
"Khoshnave"			
CT	14.17±0.35a	537.30±14.90b	26.38±1.04de
S1	10.46±0.71c	201.70±21.07d	52.32±2.67c
S2	4.053±0.28e	42.33±6.36f	98.55±10.95a
S3	0.34±0.02g	10.00±0.00fg	34.33±1.67d
"Askari"			
CT	12.46±0.71b	346.00±24.00c	36.07±0.50d
S1	8.64±0.08d	157.30±11.57e	55.41±3.40c
S2	2.94±0.09f	31.67±4.18fg	95.10±8.58a
S3	0.36±0.02g	16.67±2.03fg	21.99±1.71de
"Bidane-Sefid"			
CT	11.60±0.08b	593.30±31.79a	19.69±1.26e
S1	10.44±0.44c	205.70±6.33d	50.80±1.75c
S2	2.19±0.14f	28.33±1.67fg	77.87±6.84b
S3	0.02±0.00g	4.00±0.00g	5.00±0.00f

Each value is the mean obtained from 18 measurements. CT, S1, S2 and S3 indicate the different application of drought stress levels, with a water potential of soil at -0.2, -0.6, -1 and -1.5 MPa, respectively; they were measured at PAR intensities above 1000 µmol $m^{-2}s^{-1}$. Within a column, values followed by different letters are significantly different (P≤ 0.05).

with *CT* ones obtained indicated that 71.4%, 76.4% and 81.1% reductions in A_{net} were obtained for "Khoshnave", "Askari" and "Bidane-sefid", respectively. During the experimental period, g_s values were the highest for *CT* when compared to the other treatments. In S2-plants, g_s decreased dramatically to below the threshold of 0.05 mol of H_2O m^{-2} s^{-1} that generally identifies the stage at which metabolic limitation of photosynthesis occurs (Flexas *et al.,* 2004). The gradual decrease in A_{net} and g_s values with increasing drought stress, even at low drought stress levels, is a characteristic response of drought-adapted plants, as it has often been documented in almond (Rouhi *et al.,* 2007; Romero *et al.,* 2004). A close relationship between A_{net} and g_s, as observed in this study (Figure 1) was also documented for grapevine (Escalona *et al.,* 1999). Therefore, based on these results it seems that "Khoshnave" had a higher stability in A_{net} reduction and a more stable assimilation behavior as compared to other cultivars. Higher relationship between A_{net} and g_s for "Khoshnave" (Figure 1) may be related to higher resistance of this cultivar to drought stress. According to Chaves (1991), this close relationship between A_{net} and g_s is also a common feature of drought-adapted species. Use of g_s as an indicator of the intensity of water stress has revealed a more general pattern of photosynthetic response to progressive water stress that is somewhat independent of the water stress imposition, the environmental conditions and the genotype. In fact, *it is* g_s response to many internal and external factors involved in hormonal signaling, which makes g_s an integrative parameter of all the signals associated with the plant responding to water stress (Flexas *et al.,* 2004). Bacelar *et al.* (2007) documented that water stress caused a marked decline on the photosynthetic and stomatal conductance in olive.

Reduction of A_{net} and g_s was accompanied by an initial reduction of C_i and then an increase in C_i in the three cultivars (Table 3). This indicated that for these cultivars stomatal conductance is the dominant factor that limits assimilation, irrespective of any

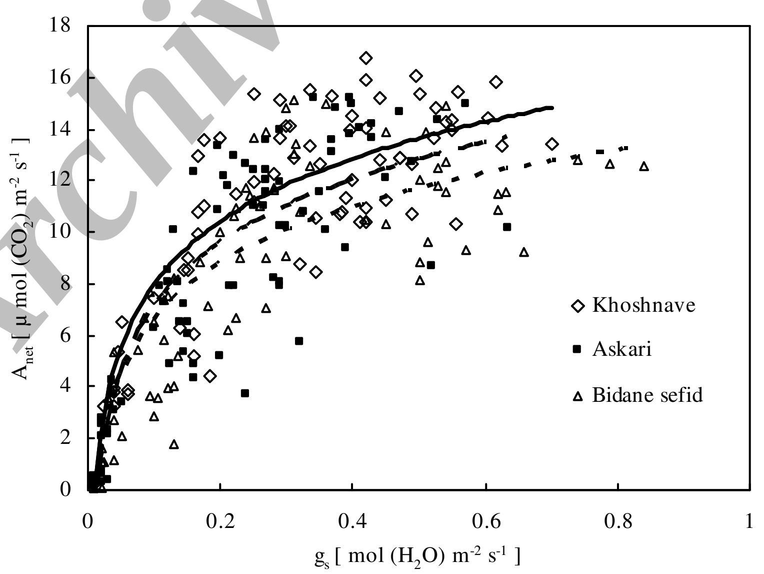

Figure 1. Relationship between net photosynthesis (A_{net}) and stomatal conductance (g_s) in three grape cultivars; "Khoshnave" (upper line), "Askari" (middle line) and "Bidane-Sefid" (lower line). Each symbol is a tow measurement for par intensities above 1000 µmolm^{-2}s^{-1}. Regression equations were: *y= 3.5231Ln(x)+16.088,* R^2*= 0.8339* ("Khoshnave"); *y= 3.5443Ln(x)+15.305,*R^2*= 0.7622* ("Askari"); *y= 3.1666Ln(x)+13.906,* R^2*= 0.7919* ("Bidane-Sefid")

Table 3. Mean values of transpiration (E) and intercellular CO_2 concentration (C_i) for each of the three grape cultivars under the different drought stress treatments.

	E (mmol H_2O $m^{-2}S^{-1}$)	C_i (µmol mol^{-1})
"Khoshnave"		
CT	10.77±0.61a	263.30±8.34cd
S1	6.53±0.47c	214.90±8.03efg
S2	3.20±0.49d	202.50±15.40fg
S3	0.58±0.06e	340.00±7.11b
"Askari"		
CT	8.21±0.95b	231.30±7.38ef
S1	5.73±0.34c	219.20±4.80efg
S2	2.05±0.10d	196.10±3.23g
S3	0.68±0.05e	357.00±12.92b
"Bidane-Sefid"		
CT	10.90±0.66a	281.60±19.96c
S1	6.78±0.09c	237.50±1.97de
S2	2.23±0.04d	240.10±4.06de
S3	0.46±0.02e	454.00±12.84a

Each value is a mean determined from 18 measurements. CT, S1, S2 and S3 indicate the different application of drought stress levels, with a water potential of soil at -0.2, -0.6, -1 and -1.5 MPa, respectively; they were measured at PAR intensities above 1000 µmol $m^{-2}s^{-1}$. In each column, values followed by different letters are significantly different ($P \leq 0.05$).

metabolic impairment until S3 conditions. The consequence of increase C_i in the three cultivars specially in "Bidane-Sefid" suggests an initial decrease of CO_2 availability at mesophyll level caused by stomatal closure, followed by a non-stomatal limitation for CO_2 assimilation which may be the principle cause for increase C_i. According to Ramanjulu *et al.* (1998) this increase C_i indicates a decrease of carboxylation efficiency. This would mean that at these drought stress levels non-stomatal limitation is dominant in these cultivars. A_{net} further decreases when g_s drops to between 0.15 and 0.05 mol H_2O m^{-2} s^{-1}. A continuous decline in sub-stomatal CO_2 concentration suggests that stomatal closure is still the dominant limitation for photosynthesis. In this stage, water use efficiency still increased in all cultivars studied in this experiment and reached its maximum values at g_s 0.05 mol of H_2O m^{-2} s^{-1} (Table 2). The above results are consistent with the results obtained by Flexas *et al.* (2004). Increasing C_i in S3 treatment obtained at g_s below 0.05 mol H_2O $m^{-2}s^{-1}$ showed that may be due to photosynthesis impairment.

Higher LMA in "Khoshnave" (Table 1) might contribute to the higher potential for carbon absorption and higher tolerance to drought as compared with the other two cultivars. High leaf mass area values in Mediterranean vegetation are often related to leaf resistance to dry conditions (Niinemets, 2001). According to the results of this study, low water availability affected leaf emergence rate (Table 1). "Khoshnave" had the highest leaf emergence rate during the stress period, this response may be related to the higher A_{net} in this cultivar. "Askari" also produced a higher leaf emergence rate than "Bidane-sefid". Drought stress reduced both leaf area and number (Tiaz and Ziger, 1998). Pellegrino *et al.* (2005) reported that leaf emergence rate of grape was the most sensitive to drought stress. Differences among MSI, A_{net} and C_i in the three cultivars under similar drought stress plans showed that "Khoshnave" has an array of tolerance mechanisms during drought stress period. Transpiration (E) clearly decreased as a response to increasing drought stress (Table 3). *E* values for S1, S2 and S3 were not significantly different among the cultivars. E reduction under drought stress is one of the plant responses for water maintenance (Bacelar et al., 2007). Similar results have been reported for apple (Sircelj *et al.,* 2007).

"Bidane-Sefid" had a lower power for recovery of A_{net} after rewatering under severe drought stress (Table 4). A higher percent of A_{net} recovery after drought for "Khoshnave" can be related to the greater tolerance of this cultivar to drought. According to Torrecillas *et al.* (1996), rapid recovery of A_{net} after stress conditions can be related to a greater physiological tolerance to drought. In the present study, when g_s was lower than 0.05 mol of H_2O $m^{-2}s^{-1}$ A_{net} didn't reover one day after rewatering. However, four days after rewatering of the plants, A_{net} recovered completely for S2 but not for S3. Therefore, it is expected that under severe drought stress, at least four days after rewatering was needed for complete recovery of A_{net} in grape. Flexas *et al*. (2004) reported complete recovery of A_{net} four days after rewatering under severe drought stress, not similar to the present results. This difference shows that A_{net} recovery is dependent on the drought severity and the type of cultivars. Similar results have been reported for almond (Romero *et al.,* 2004). Rouhi *et al.* (2007) mentions that recovery of A_{net} rate after severe drought stress did not happen three weeks after rewatering for almond. Stomatal conductance (g_s) of the plants studied in the present study showed a slow rate of recovery as compared with A_{net} recovery. "Bidane-Sefid" had significantly a lower percent of g_s recovery compared with the other two cultivars (Table 4). These results show that A_{net} recovery was quicker than g_s recovery in "Khoshnave" but A_{net} and g_s recovery were similar in "Askar" and "Bidane-Sefid". Flexas *et al.* (2004) reported that g_s recovery was similar to A_{net} recovery. Such differences in the results may be related to the experimental conditions and also to the type of cultivars. The drought induced alteration in bulk of abscisic acid may explain the slow stomatal recovery, that could be a result of the persistent effects of that hormone produced during the water stress period (Miller *et al.,* 1998). Montanaro *et al.* (2007) reported that A_{net} recovered to values up to 80% of irrigated plants by day 2 after rewatering in Kiwifruit, but g_s of these plants showed a slow rate of recovery even 13 days after irrigation was reinitiated.

Table 4. Net photosynthesis rate (A_{net}) and stomatal conductance (g_s) of water-stressed plants as % of irrigated plants during one and four days after rewatering.

	One day after rewatering		Four days after rewatering	
	A_{net} recovery (%)	g_s recovery (%)	A_{net} recovery (%)	g_s recovery (%)
"Khoshnave"				
S1recovery	94.95±2.56a	66.59±0.99b	-	-
S2recovery	82.42±2.27b	65.92±3.49b	100.00±0.00a	84.75± 4.38b
S3recovery	58.63±6.59cd	41.93±2.65c	87.63±2.49bc	71.87b±4.89bc
"Askari"				
S1recovery	97.54±1.24a	83.6±7.75a	-	-
S2recovery	68.41±1.44c	60.46±3.85b	97.43±2.57ab	98.83±1.17a
S3recovery	53.33±4.94d	58.93±2.13b	88.09±6.55abc	98.47±1.53a
"Bidane-Sefid"				
S1recovery	99.72±0.28a	60.20±2.53b	-	-
S2recovery	47.99±4.55de	25.78±1.22d	100.00±0.00a	82.99±6.48b
S3recovery	41.01±4.09e	16.55±0.91e	83.18±3.74c	61.23±4.64c

Measurements were taken at PAR intensities above 1000 μmol m^{-2} s^{-1}. Each value is a mean determined from 18 measurements. In each column, values followed by different letters are significantly different, (P≤ 0.05).

"Khoshnave" had higher A_{net}/g_s than "Bidane-Sefid" at S2 conditions (Table 2). The valus of A_{net}/g_s were significantly higher for "Khoshnave" than for "Askari" and "Bidane-Sefid" at S3. The increase of A_{net}/g_s under water stress is attributed to biomass production being less reduced by drought than water use (Anyia and Herzog, 2004). This cultivar ("Khoshnave") characterized by a high value of A_{net}/g_s appears to be the most promising for production on relatively dry sites. Increasing of A_{net}/g_s under mild drought stress is a response more typical of an isohydric strategy (Poni *et al.,* 2007).

From the behavior of cultivars in the present study, it is considered that "Khoshnave" is promising for cultivation in rain-fed areas in west Iran as compared to "Askari" and "Bidane-Sefid". "Bidane-Sefid" indicated the lowest suitibility for cultivation in these conditions. Further research especially under field conditions is needed to support this statement.

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واکنش فیزیولوژیکی سه رقم انگور ایرانی به تنش خشکی فزاینده

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چکیده

ارزیابی نقش تنش آبی بر خصوصیات فیزیولوژیکی گیاه ممکن است اساس ارزیابی مقاومت به خشکی را فراهم کند. تفاوت در میزان برگ تولید شده، محتوای نسبی آب برگ (RWC)، شاخص پایداری غشاء سلولی (MSI)، نسبت وزن به سطح برگ [Leaf mass area (LMA)]، میزان فتوسنتز (A_{net})، هدایت روزنه ای (g_s)، تعرق (E)، CO_2 زیر روزنه ای (C_i)، کارایی مصرف آب ($A_{net/}\ g_s$) و بازیابی فتوسنتز و هدایت روزنه‌ای در سه رقم انگور دوساله (خوشناو، بیدانه سفید و عسکری) تحت تنش خشکی فزاینده (۰/۲-، ۰/۶-، ۱- و ۱/۵- مگاپاسکال) مورد ارزیابی قرار گرفتند. نتایج، کاهش RWC، MSI، میزان تولید برگ، LMA، A_{net}، g_s و E را تحت تنش خشکی را نشان داد. این در حالی بود که میزان C_i ابتدا کاهش و تحت شرایط تنش شدید خشکی (۱/۵- مگاپاسکال) افزایش یافت. رقم خوشناو میزان A_{net} بیشتری در مقایسه با رقم بیدانه سفید و عسکری داشت. LMA بیشتر رقم خوشناو ممکن است به این رقم در افزایش قابلیت فراوری کربن و داشتن A_{net} بیشتر در مقایسه با دو رقم دیگر کمک کرده باشد. بازیابی کامل فتوسنتز برای هر سه رقم یک روز بعد از آبیاری مجدد در تیمار ۰/۶- مگاپاسکال و چهار روز بعد از آبیاری مجدد در تیمار۱- مگاپاسکال روی داد. بازیابی کامل g_sیک و چهار روز بعد از آبیاری مجدد در هیچکدام از ارقام مورد مطالعه روی نداد. نتایج نشان داد که در رقم خوشناو بازیابیA_{net} در مقایسه با دو رقم دیگر سریعتر صورت گرفت. $A_{net/}g_s$ تحت تیمار ۱- مگاپاسکال در هر سه رقم بالاترین میزان بود. الگوی مشابه تغییرات $A_{net/}g_s$ در هر سه رقم وجود داشت. تحت شرایط تنش شدید رقم خوشناو دارای کارایی مصرف آب بیشتری در مقایسه با دو رقم دیگر بود. بر اساس واکنشهای رقم خوشناو به مقادیر مختلف تنش خشکی (A_{net} بالاتر، میزان تولید برگ بیشتر، LMA بیشتر، بازیابی سریعتر A_{net} و کارایی مصرف آب بیشتر به نظر می رسد که این رقم برای کشت در شرایط دیم در غرب ایران در مقایسه با دو رقم دیگر مناسب تر باشد.