

Leaf water potential, photosynthetic pigments and compatible solutes alterations in four grape cultivars under salinity

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Summary

A hydroponic culture experiment was conducted to investigate the effects of different concentrations (0, 25, 50 and 100 mM) NaCl on own-rooted table grape (*Vitis vinifera* L.) cultivars (red 'Rishbaba', red 'Sahebi', 'Dastarchin' and red 'Sultana') under greenhouse conditions. Cultivars were evaluated for growth analysis leaf area, leaf water potential and the chlorophyll a, b and carotenoid contents in relation to proline and soluble sugars accumulation. Salinity treatments caused a growth reduction ($P \leq 0.05$) in all the cultivars. Also leaf water potential and chlorophyll a, b contents decreased whereas carotenoid, proline and soluble sugars increased with increasing NaCl concentration. 'Dastarchin' and red 'Sultana' showed the salt-sensitivity, the highest loss of growth, leaf water potential and chlorophyll content and the lowest accumulation of carotenoids, proline and soluble sugars. Also salt stress significantly ($P < 0.001$) increased the rate of lipid peroxidation in the all cultivars particularly in 'Dastarchin' and red 'Sultana'. The increase in malondialdehyde content indicated that salinity induced oxidative stress. There was a significant negative correlation between leaf water potential and NaCl concentrations ($r^2: -0.781, p < 0.001$). A positive correlation was also found between lamina proline contents and NaCl concentrations ($r^2: +0.964, p < 0.001$) for all salinity treatments. Considering overall results red 'Rishbaba' and red 'Sahebi' showed higher capacity to tolerate salinity when compared to 'Dastarchin' and red 'Sultana'.

Key words: grapevine, chlorophyll a and b, lipid peroxidation, leaf area, salt stress.

Abbreviations: r-Rish: red 'Rishbaba', r-Sah: red 'Sahebi', Das: 'Dastarchin', r-Sul: red 'Sultana', MDA: Malondialdehyde.

Introduction

Salinity is a major impediment in irrigated agriculture especially in the arid and semiarid environment. Today, 20 % of the world's cultivated land and nearly half of the irrigated lands is affected by salinity (ZHU 2001). Increasing salt stress is a threat to grape growers in many regions

around the world (FISARAKIS *et al.* 2001, WALKER *et al.* 2002). Salinity is known to influence grapevine growth in many ways, including reduced grape yield, reduced shoot and root vigor, reduced leaf area and appearance of leaf burns (SHANI *et al.* 1993, FISARAKIS *et al.* 2001, MUNNS 2002). Exposure of plants to salinity, drought or extreme temperatures commonly results in a water deficit. Salt stress changes the water relations of most higher plants, and salt tolerance often depends on drought tolerance (GREENWAY and MUNNS 1980, FLOWERS and YEO 1986). Salinity may decrease biomass production because it lowers plant water potential and causes specific ion toxicities or ionic imbalances in plants (MUNNS 2002). Plants achieve osmotic adjustment under saline conditions via ion uptake or synthesis of osmotica or both (PARIDA and DAS 2005). One of the most common stress responses in plants is overproduction of different types of compatible organic solutes (SERRAJ and SINCLAIR 2002). Compatible solutes are low molecular weight, highly soluble compounds that are usually non-toxic at relatively high concentrations. These organic osmolytes are most commonly carbohydrates (such as sugars), amino acids, protein and proline (YOUSSEF *et al.* 2003). Generally, they protect plants from stress through different processes, including *via* contributing to cellular water economy, detoxification of reactive oxygen species, protection of membrane integrity, and stabilisation of enzymes/proteins (ASHRAF and FOOLAD 2006). Amino acid proline is known to occur widely in higher plants and normally accumulates in large quantities in response to environmental stresses (KAVI KISORE *et al.* 2005). In addition to its role as an osmolyte for water economy, proline helps stabilising sub-cellular structures (e.g., membranes and proteins), scavenging free radicals, and buffering cellular redox potential under stress conditions (ASHRAF and OROOJ 2006). One of the effects of free oxygen radicals accumulation in plant cells under stress is lipid peroxidation *via* oxidation of unsaturated fatty acids leading to membrane damage and electrolyte leakage (LIU *et al.* 1987, MARSCHNER 1995). Malondialdehyde (MDA), a decomposition product of polyunsaturated fatty acids, has been utilized as a biomarker for lipid peroxidation (MITTLER 2002). In the present study, four grape cultivars, growing in hydroponic culture, were subjected to salinity. The objective was to evaluate salinity effect on the leaf water potential of cultivars. We also investigated the induction of proline (a compatible solute) accumulation in plant parts by high

salinity, which could be responsible for protection against salt stress in this plant.

Material and Methods

Own-rooted vines of *Vitis vinifera* cultivars: red 'Rishbaba', red 'Sahebi', 'Dastarchin' and red 'Sultana' were grown in greenhouse from September to January 2009 for growing roots. Rooted cuttings were transferred to the hydroponics culture in 2-L pots containing aerated ¼ strength Hoagland nutrient solution containing: (1M KNO₃, 1M Ca (NO₃)₂, 1M MgSO₄.7H₂O, 1M KH₂PO₄ and micronutrients 2.85 g H₃BO₃, 1.81 g MnCl₂.7H₂O, 0.22 g ZnSO₄.7H₂O, 0.08 g CuSO₄.5H₂O, 0.05 g Na₂MOO₄.2H₂O and 0.028 g Fe-EDTA). Four weeks later, uniform plants with a new shoot of 35 cm in length were selected. The plants were treated for 2 weeks with 0, 25, 50 and 100 mM NaCl. At the end of the experiment, six plants from each treatment were sampled to determine leaf area using CompuEye (leaf and symptom area) (BAKR 2005). Plants were harvested and plant parts including leaf, stem, petiole and root were weighed separately and dried at 70 °C for 48 h.

Leaf water potential (LWP): Leaf Water Potential (LWP) was determined on three to six leaves of similar age with thermocouple psychrometers (Model Wescor HR33 dew point microvoltmeter; Wescor Inc., Logan, UT, U.S.A.) and expressed in '-MPa'. It should be read within about 2 h of solar noon, normally in about 11:30 AM to 2:30 PM and select a leaf that is fully exposed to the light, Also leaf should be a healthy, fully expanded leaf with no insect holes, good color.

Chlorophyll a and b contents: Chlorophyll_a (Ch_a) and chlorophyll_b (Ch_b) concentrations were analyzed following the method of LICHTENTHALER and WELLBURN (1985). Fresh leaves (0.1 g) were used for photosynthetic pigment extraction and immersed in 5 mL of 80 % acetone. Extracts were filtered by Whatman No. 2 filter paper and absorbance was measured in a UV-visible spectrophotometer (model WPA S2100) at 646, 663 and 470 nm, Ch_a and Ch_b concentrations (mg·g⁻¹ F.W) were calculated according to the following equations:

$$\text{Chlorophyll}_a (\text{Ch}_a) = 12.25 A_{663} - 2.798 A_{646}$$

$$\text{Chlorophyll}_b (\text{Ch}_b) = 21.5 A_{646} - 5.1 A_{663}$$

$$\text{Carotenoid} = (1000 * A_{470} - 1.82 * \text{Ch}_a - 85.02 * \text{Ch}_b) / 198$$

Proline content: Proline content was calculated according to BATES *et al.* (1973). Proline concentration was determined using calibration curve and expressed as µg proline·g⁻¹ DW. Dry plant material (0.5 g) was homogenized in 10 ml of 3 % sulfosalicylic acid and the homogenate was filtered. The filtrate (2 mL) was treated with 2 mL ninhydrin reagent (1.25 mg Ninhydrin in 30 mL of Glacial acetic acid and 20 ml 6 M H₃PO₄) and incubated at 95 °C for 1 h. The reaction was terminated placing in an ice bath. The reaction mixture was vigorously mixed with 4 mL toluene. After warming at 25 °C, absorbance of the colored solutions was read at 520 nm. L-proline was used as a standard.

Soluble sugar content: Soluble sugar content in the leaf and root tissues was extracted and analyzed

according to the method of DUBOIS *et al.* (1956). Dry plant material (0.1 g) was homogenized in 10 mL of 70 % ethanol. After one week, 2 mL of supernatant was mixed with 1 mL of 5 % phenol and 5 mL of sulfuric acid. After 30 min absorbance of the cold and colored solutions was read at 485 nm.

MDA analysis: Lipid peroxidation in the leaf tissues was determined in terms of malondialdehyde (MDA) content by thiobarbituric acid (TBA) reaction as described by NOVACKY and POPHAM (1990). Briefly, 0.2 g of the leaf tissue of plants were homogenized in 5 mL of 1 % (w:v) trichloroacetic acid (TCA), then centrifuged at 8000 g for 10 min. 1 mL of supernatant was added with 4 mL of 20 % (w:v) TCA containing 0.5 % (w:v) thiobarbituric acid (TBA), and the solution was heated for 30 min at 95 °C in the warm water bathroom. The samples were cooled on ice for 5 min and recentrifuged for 5 min at 8000 g. Absorbance was measured at 532 nm. For the MDA calculation, an extinction coefficient of 155mM⁻¹cm⁻¹ was used at 532 nm. The results were expressed in µmol of malondialdehyde (MDA) equivalent per gram fresh weight.

Statistic analysis: Analysis of variance was performed by the statistical program SpSS version 18 and one-way-ANOVA was used to compare the main effects and interactions between cultivars and salinity levels using GLM.

Results

The results indicated that the growth rate of shoot and root decreased under salt stress. The accumulation of dry matter decreased more in shoots than in roots, resulting in nearly 40 % increase in root/shoot ratio (data not presented). r-Rish showed higher dry matter production than all cultivars. Also r-Rish showed higher shoot/root fresh weight ratio than all cultivars (Tab. 1). In addition salinity significantly affected leaf area ($P < 0.001$). The decrease of leaf area in Das was higher than that of r-Rish and r-Sah cultivars. The reduction of leaf area at 100 mM NaCl was 22.59 and 52.24 % respectively for the r-Sah and Das when compared to their controls (Tab. 2). The chlorophyll a and b contents of leaves decreased with increasing salinity levels (Tab. 2). The decrease in r-Sul and Das cultivars were higher than r-Rish and r-Sah cultivars. The reduction in chlorophyll a content due to increased salt treatments from 0 to 100 mM NaCl was 33.97, 37.71, 52.22 and 45.55 % in leaves for the r-Rish, r-Sah, r-Sul and Das respectively (Tab. 2). Also, the chlorophyll b content was significantly decreased. The decreased values were calculated as 63.12, 51.93, 66.99 and 75.9 % in r-Rish, r-Sah, r-Sul and Das respectively at 100 mM NaCl. Salinity treatment showed a negative correlation with chlorophyll a ($r^2: -0.943, P < 0.001$) and chlorophyll b ($r^2: -0.932, P < 0.001$). Carotenoids content in four cultivars increased, but the increase in carotenoids content in r-Rish and r-Sah cultivars was higher than that of Das and r-Sul (Tab. 2).

Salinity markedly decreased leaf water potential of all the cultivars (Fig. 1). As a result, r-Rish showed a lower reduction leaf water potential than other varieties after 14 d

Table 1

Root/shoot ratio of r-Rish, r-Sah, r-Sul and Das varieties, 2 weeks after salt treatment^{ab}

Cultivar	Root/shoot dry weight ratio	Root/shoot fresh weight ratio	Dry/fresh root weight ratio	Dry/fresh shoot weight ratio
r-Rish	0.256 a	0.566 a	0.0601 a	0.134 b
r-Sah	0.22 b	0.508 b	0.0613 a	0.144 ab
r-Sul	0.19 c	0.467 c	0.0618 a	0.154 a
Das	0.225 b	0.520 b	0.0629 a	0.148 ab
Analysis of variances (F-values)				
Salinity	32.07***	16.59***	6.539***	18.85***
Cultivar	23.71***	25.0***	ns	4.131**
Salinity × cultivar	ns	ns	ns	ns

^aMeans within a column followed by the same letter are not significantly different at $p = 5\%$ level according to the tucky, ($n = 3$): ** $p < 0.01$. *** $p < 0.001$.

^bFor varieties means calculated for all salinity treatments.

Table 2

Leaf area, chlorophyll (a and b) and carotenoids contents of r-Rish, r-Sah, r-Sul and Das varieties, 2 weeks after salt treatment^{ab}

Cultivar	Leaf area (cm ²)	Chla (mgg ⁻¹ fw)	Chlb (mgg ⁻¹ fw)	carotenoids (mgg ⁻¹ fw)
r-Rish	42.50 a	10.049 b	4.71 b	0.3 a
r-Sah	43.18 a	10.91 a	5.74 a	0.284 a
r-Sul	-	9.74 c	4.7 b	0.237 b
Das	36.43 b	9.54 c	4.31 c	0.193 c
Analysis of variances (F-values)				
Salinity	22.156***	1018.095***	395.25***	876.826***
Cultivar	13.96***	65.255***	35.5***	38.252***
Salinity × Cultivar	ns	14.54***	4.20***	11.35***

^aMeans within a column followed by the same letter are not significantly different at $p = 5\%$ level according to the tucky, ($n = 3$): ns: non-significance at $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$.

^bFor varieties means calculated for all salinity treatments.

of treatment, whereas Das had a higher reduction leaf water potential. Leaf water potential was lower for 100 mM salt-treated plants than for plants in the other treatments (Fig. 1). There was a significant negative correlation between leaf water potential and NaCl concentrations ($r^2: -0.781$, $p < 0.001$). Fourteen days of salinization were sufficient to increase the proline and soluble sugar contents in both lamina and roots of four cultivars, and this increase was more evident in plants at the 50 and 100 mM NaCl treatment. The proline and soluble sugar increased more in r-Rish and r-Sah than in r-Sul and Das when four cultivars were exposed to increased salt concentrations. This increase was greater in lamina than in roots (Figs 2 and 3). Salinity had a significant effect on MDA content in shoots ($P < 0.0001$). It is clear from the Fig. 4 that a sharp increase in the accumulation of MDA content was observed in all cultivars at all stress regimes, however the increase in r-Sul and Das being higher than in r-Rish and r-Sah. The levels of accumulation were 195.67, 84.5, 465.51 and 226.48 % in r-Rish, r-Sah, r-Sul and Das cultivars respectively, indicating a high rate of lipid per oxidation in r-Sul due to salt stress.

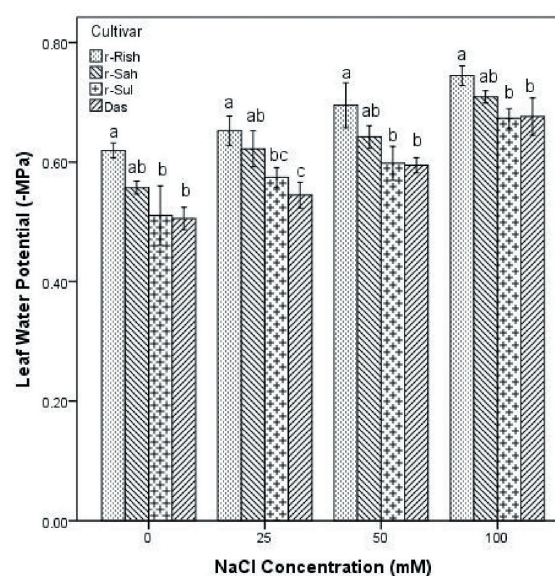


Fig. 1: Leaf water potential of r-Rish, r-Sah, r-Sul and Das treated with different concentrations of NaCl for 2 weeks. Bars are \pm SE of the means ($n = 3$) tucky $p \leq 0.05$. Different letters indicate significant differences between varieties at each salt concentration.

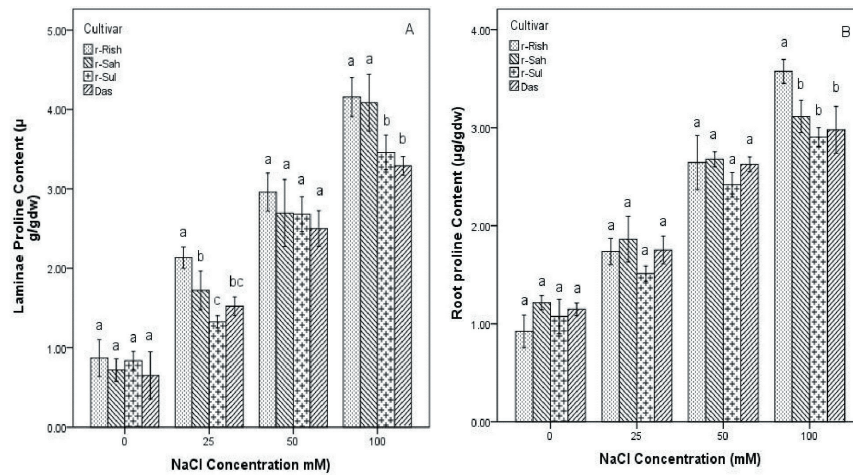


Fig. 2: Proline content in shoot (A) and root (B) of r-Rish, r-Sah, r-Sul and Das treated with different concentrations of NaCl for 2 weeks. Bars are ± SE of the means (n = 3) tucky p ≤ 0.05. Different letters indicate significant differences between varieties at each salt concentration.

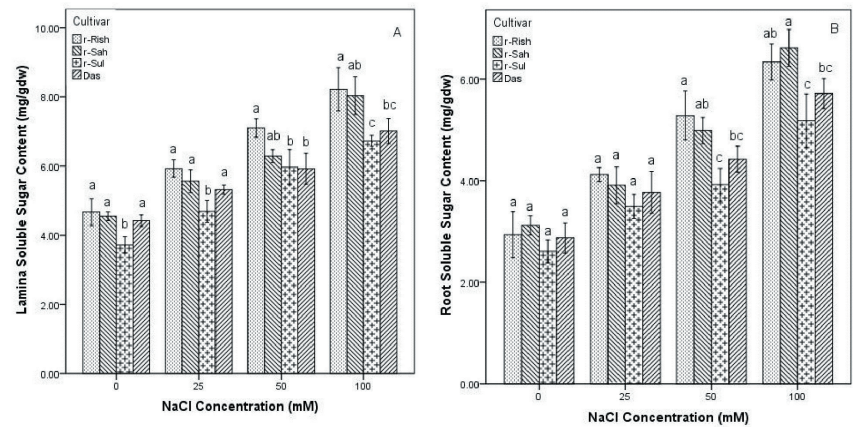


Fig. 3: Soluble Sugar content in shoot (A) and root (B) of r-Rish, r-Sah, r-Sul and Das treated with different concentrations of NaCl for 2 weeks. Bars are ± SE of the means (n = 3) tucky p ≤ 0.05. Different letters indicate significant differences between varieties at each salt concentration.

Discussion

Growth reduction is an early phenomenon and a common response in woody plants to salt stress both *in vitro* and *in vivo* (VIJAYAN *et al.* 2003). Growth response to salinity is often regarded as a basis of evaluation for tolerance (KUIPER *et al.* 1988). High salinity due to indirect effect on uptake of other nutrients probably resulted in reduction in growth and disturbance of several other physiological processes (PRIOR *et al.* 1992). In the few seconds or minutes periods of time for plants exposed to salinity, cells lose water and shrink. Over hours, cells regain their original volume but cell elongation rates are reduced, leading to lower rates of leaf and root growth. Over days, changes in cell elongation and cell division lead to slower leaf appearance and smaller final size, and leaf growth is usually more affected than root growth (HASEGAWA *et al.* 2000, HSIAO and XU 2000). According to SOTIROPOULOS *et al.* (2006 b) explants are stressed in two ways under *in vitro* salinity: by the increase in osmotic potential of culture media as a result of high solute content, and by the toxic effects of high concentrations of ions. The negative effect of salinity on plant growth and water content may be due to the occur-

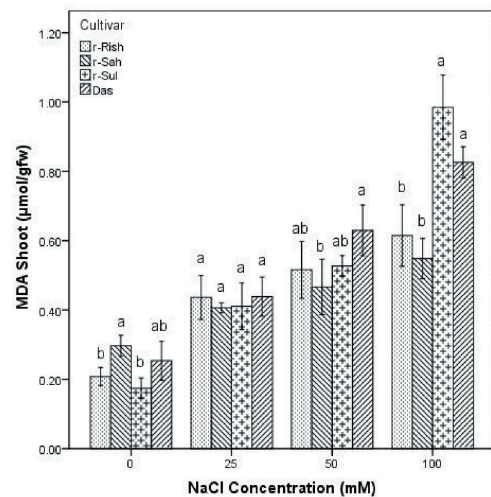


Fig. 4: MDA content of r-Rish, r-Sah, r-Sul and Das treated with different concentrations of NaCl for 2 weeks. Bars are ± SE of the means (n = 3) tucky p ≤ 0.05. Different letters indicate significant differences between varieties at each salt concentration.

ring of defect metabolism in plant cells. Since high osmotic pressure resulted from high salinity restricted plant cells to uptake water and some mineral nutrients dissolved in the

culture medium (CICEK and ÇAKIRLAR 2002). The chemical potential of the saline media initially establishes a water potential imbalance between the apoplast and symplast that leads to decrease in pressure potential, which might cause growth reduction (BOHNERT *et al.* 1995). On the other hand, the cellular response to water potential reduction is osmotic adjustment. It involves the transport, accumulation and compartmentation of organic solutes and inorganic ions (BOHNERT *et al.* 1995). Under high salt environment, higher plants maintain their water content by accumulation of compatible organic solute in their cytoplasm. Plant cells decrease their osmotic potential by the accumulation of inorganic and organic solutes or by loss of water. The accumulation of organic solutes might be of importance for the adjustment of the cellular water potential under conditions of reduced water availability (YOUSSEF and AL-FREDAN 2008). In organisms ranging from bacteria to higher plants there is a strong correlation between increased cellular proline levels and the capacity to survive both water deficit and the effects of high environmental salinity (AHMAD and JHON 2005). Proline plays an adaptive role in mediating osmotic adjustment and protecting the sub-cellular structures in stressed plants. Apart from protection of macromolecules from denaturation and carbon and nitrogen reserve for stress relief, proline has several other functions during stress: e.g. osmotic adjustment (VOETBERG and SHARP 1991), osmoprotection (KISHOR *et al.* 2005), free radical scavenger and antioxidant activity (SHARMA and DITZ 2006). In many studies a positive correlation between the accumulation of proline and stress tolerance in plants has been found (LUTTS *et al.* 1996, KUMAR *et al.* 2003). Also proline content have been reported to increase under NaCl stress in *Phaseolus aureus* (MISRA and GUPTA 2005), *Morus alba* (AHMAD *et al.* 2007), *Sesamum indicum* (KOCA *et al.* 2007). Plant cells growing in saline media must adjust osmotically, since a positive turgor is required for cell expansion and most biochemical, physiological, and developmental processes (GREENWAY and MUNNS 1980). Increase in sugar content only in tolerant cvs. (DOWNTON 1985) help them in osmotic adjustment (REUVENI *et al.* 1991). Proline content increased significantly in the leaves of all the cultivars as the salt concentration increased (Fig. 2 A). This increase in salt-tolerant cultivars was higher than that of the salt-sensitive cultivars. The increase of proline in lamina at 100 mM NaCl was 468.941 and 313.26 % respectively for the r-Sah and r-Sul when compared to their controls. However, increasing in proline content in r-Rish and r-Sah cultivars was higher than that of Das and r-Sul, also there were no significant differences between r-Sul and Das cultivars. Our results revealed that the leaf water potential is affected by an increase in leaf proline content. That is, an increase in proline content caused lower reduction in leaf water potential. There was a positive correlation between proline and leaf water potential. R-Rish showed a lower reduction in leaf water potential than other cultivars, whereas Das had a higher reduction in leaf water potential. The decreased values were calculated as 20.19, 27.29, 31.96 and 33.86 % in r-Rish, r-Sah, r-Sul and Das respectively at 100 mM NaCl (Fig. 1). There were no significant differences between r-Sul and Das cultivars. Chlorophyll

content reduction was observed with increasing salinity in all the cultivars (Tab. 2). PARIDA and DAS (2005) suggested that such a decrease in chlorophyll content in response to salt stress is a general phenomenon. The reduction of chlorophyll contents in abiotic stress plants might possibly be due to changes in the lipid protein ratio of pigment-protein complexes or increased chlorophyllase activity (PARIDA *et al.* 2004). Our results are consistent with several reports in a number of plant species (AGASTIAN *et al.* 2000, HAMADA and EL-ENANY 1994). In addition to chlorophyll degradation, salt-induced necroses on leaf and shoot tissues were observed in grape explants (SIVRTEPE and ERIS 1999). Moreover, reduction in chlorophyll concentrations is probably due to the inhibitory effect of the accumulated ions of various salts on the biosynthesis of the different chlorophyll fractions. Salinity affects the strength of the forces bringing the complex pigment protein-liquid, in the chloroplast structure. As the chloroplast is surrounded by a membrane its stability is dependent on the membrane stability (YEO *et al.* 1990, ALI *et al.* 2004). Increase of carotenoids content in r-Rish cultivar was higher than Das cultivar. Therefore r-Rish has a better ability to protect chlorophyll from photo oxidation. Considering MDA content in shoots, lipid peroxidation was significantly higher under salt stress than in control plants (Fig. 4). Determining the MDA content and hence, the extent of membrane lipid peroxidation, has often been used as a more reliable tool than anti-oxidative scavenging systems to assess the degree of plant sensitivity to oxidative damage (BLOKHINA *et al.* 2003). KOCA *et al.* (2007) also showed that lipid peroxidation was higher at 100 mM NaCl treatment in a salt sensitive cultivar of *Sesamum indicum* than in a salt tolerant one. Our data showed remarkable increase in shoot MDA content for Das and r-Sul at different concentration of NaCl than other cultivars. HONG *et al.* (2000) found that, under salt stress, MDA production in tobacco cell cultures was enhanced.

Conclusion

The present study was conducted to determine alterations of leaf water potential status, proline, soluble sugar and chlorophyll contents in four own-rooted grapevine cultivars under salinity stress. Parameters such as root/shoot ratio and leaf area were significantly decreased by salinity. Das and r-Sul showed the highest growth reduction. Proline and soluble sugars contents increased while there was a reduction in leaf water potential and chlorophyll a and b contents under different levels of salinity. In comparison to the other cultivars, red 'Rishbaba' and red 'Sahebi' accumulated high amounts of proline and soluble sugars in leaf blade and root particularly at 50 and 100 mM NaCl. Compared to others, these cultivars showed a slight reduction in leaf water potential. Increasing in MDA content in Das and r-Sul were higher than that of others. The results showed that red 'Rishbaba' and 'Dastarchin' had respectively a higher and a lower capacity to tolerate salt stress when compared to the other cultivars. However, all the cultivars studied seem to be relatively sensitive when exposed to salinity.

References

- AGASTIAN, P.; KINGSLEY, S. J.; VIVEKANADAN, M.; 2000: Effect of salinity on photosynthesis and biochemical characteristics in mulberry genotypes. *Photosynthetica* **38**, 287-290.
- AHMAD, P.; JHON, R.; 2005: Effect of salt stress on growth and biochemical parameters of *Pisum sativum* L. *Arch. Agron. Soil Sci.* **51**, 665-672.
- AHMAD, P.; SHARMA, S.; SRIVASTAVA, P. S.; 2007: *In vitro* selection of NaHCO₃ tolerant cultivars of *Morus alba* (Local and Sujanpuri) in response to morphological and biochemical parameters. *Hort. Sci* **34**, 115-123.
- ALI, Y.; ASLAM, Z.; ASHRAF, M. Y.; THAIR, G. R.; 2004: Effect of salinity on chlorophyll concentration, leaf area, yield and yield components of rice genotypes grown under saline environment. *Inter. J. Environ. Sci. Tech* **1**, 221-22.
- ASHRAF, M.; FOOLAD, M. R.; 2007: Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environ. Exp. Bot.* **59**, 206-216.
- ASHRAF, M.; OROOJ, A.; 2006: Salt stress effects on growth, ion accumulation and seed oil concentration in an arid zone traditional medicinal plant ajwain (*Trachyspermum ammi* [L.] Sprague). *J. Arid Environ.* **64**, 209-220.
- BAKR, E. M.; 2005: A new software for measuring leaf area, and area damaged by *Tetranychus urticae* Koch. *J. Appl. Entomol.* **129**, 173-175.
- BOHNERT, H. J.; NELSON, D. E.; JENSEN, R. G.; 1995: Adaptations to environmental stresses. *Plant Cell* **7**, 1099-1111.
- CICEK, N.; CAKIRLAR, H.; 2002: The effect of salinity on some physiological parameters in two maize cultivars. *Bulg. J. Plant Physiol.* **28**, 66-74.
- DOWNTON, W. J. S.; 1985: Growth and mineral composition of the Sultana grapevine as influenced by salinity and rootstock. *Aust. J. Agr. Res.* **36**, 425-434.
- FISIRAKIS, I.; CHARTZOULAKIS, K.; STAVRAKAS, D.; 2001: Response of sultana vines (*V. vinifera* L.) on six rootstocks to NaCl salinity exposure and recovery. *Agric. Water Manag.* **51**, 13-27.
- FLOWERS, T. J.; YEO, A. R.; 1986: Ion relations of plants under drought and salinity. *Aust. J. Plant Physiol.* **13**, 75-91.
- GREENWAY, H.; MUNNS, R.; 1980: Mechanisms of salt tolerance in non-halophytes. *Ann. Rev. Plant Physiol* **31**, 149-190.
- HAMADA, A. M.; EL-ENANY, A. E.; 1994: Effect of NaCl salinity on growth, pigment and mineral element contents, and gas exchange of broad bean and pea plants. *Biol. Plant* **36**, 75-81.
- HASEGAWA, P. M.; BRESSAN, R. A.; ZHU, J. K.; BOHNERT, H. J.; 2000: Plant cellular and molecular responses to high salinity. *Ann. Rev. Plant Physiol. Plant Mol. Bio.* **51**, 463-499.
- HONG, Z.; LAKKINENI, K.; ZHANG, Z.; VERMA, D. P.; 2000: Removal of feedback inhibition of delta(1)-pyrroline-5-carboxylate synthetase results in increased proline accumulation and protection of plants from osmotic stress. *Plant Physiol.* **122**, 1129-1136.
- HSIAO, T. C.; XU, L. K.; 2000: Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. *J. Exp. Bot* **51**, 1595-1616.
- KOCA, M.; BOR, M.; OZDEMIR, F.; TURKAN, I.; 2007: The effect of salt stress on lipid peroxidation, antioxidative enzymes and proline content of sesame cultivars. *Environ. Exp. Bot* **60**, 344-351.
- KISHOR, P. B. K.; SANGAM, S.; AMRUTHA, R. N.; LAXMI, P. S.; NAIDU, K. R.; RAO, K. S.; 2005: Regulation of proline biosynthesis, degradation, uptake and transport in higher plants: its implications in plant growth and abiotic stress tolerance. *Curr. Sci* **88**, 424-38.
- KUIPER, P. J. C.; KUIPER, D.; SCHUIT, J.; 1988: Root functioning under stress conditions: An introduction. *Plant Soil.* **111**, 249-253.
- LIU, Y. L.; MAO C. L.; WANG, L. J.; 1987: Advances in salt tolerance in plants. *Commun. Plant Physiol.* **23**, 1-7. (in Chinese).
- MARSCHNER, H.; 1995: Part I. Nutritional physiology. In: H. MARSCHNER (Ed.): *Mineral Nutrition of Higher Plants*, 2nd ed., 18-30, 313-363. Acad. Press, London.
- MISRA, N.; GUPTA, A. K.; 2005: Effect of salt stress on proline metabolism in two high yielding genotypes of green gram. *Plant Sci.* **169**, 331-339.
- MISRA, A. N.; SAHU, S. M.; MISRA, M.; SINGH, P.; MEERA, I.; DAS, N.; KAR, M.; SAHU, P.; 1997: Sodium chloride induced changes in leaf growth, and pigment and protein contents in two rice cultivars. *Biol. Plant* **39**, 257-262.
- MITTLER, R.; 2002: Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci.* **7**, 405-410.
- MUNNS, R.; 2002: Comparative physiology of salt and water stress. *Plant Cell Environ.* **25**, 239-250.
- PARIDA, A. K.; DAS, A. B.; 2005: Salt tolerance and salinity effects on plants: a review. *Ecotox. Environ. Safety* **60**, 324-349.
- PARIDA, A. K.; DAS, A. B.; MITTRA, B.; 2004: Effects of salt on growth, ion accumulation, photosynthesis and leaf anatomy of the mangrove *Bruguiera parviflora*. *Trees Struct. Funct.* **18**, 167-174.
- PRIOR, L. D.; GRIEVE, A. M.; CULLIS, B. R.; 1992: Sodium chloride and soil texture interactions in irrigated field grown Sultana grapevines. II. Plant mineral content, growth and physiology. *Aust. J. Agric. Res.* **43**, 1067-1083.
- REUVENI, M.; LERNER, H. R.; POLJAKOFF-MAYBER, A.; 1991: Salinity induced changes in hexokinase activity of carrot cells insuspension culture life. *Sci. Adv. Plant Physiol.* **10**, 13-19.
- SHANI, U.; WAISEL, Y.; ESHEL, A.; XUE, S.; ZIV, G.; 1993: Responses to salinity of grapevine plants with split root system. *New Phytol.* **124**, 695-701.
- SHARMA, S. S.; DIETZ, K. J.; 2006: The significance of amino acids and amino acid-derived molecules in plant responses and adaptation to heavy metal stress. *J. Exp. Bot.* **57**, 711-26.
- SERRAJ, R.; SINCLAIR, T. R.; 2002: Osmolyte accumulation: can it really help increase crop yield under drought conditions? *Plant Cell Environ* **25**, 333-341.
- SOTIROPOULOS, T. E.; FOTOPoulos, S. DIMASSI, K. N.; TSIRAKOGLou, V.; 2006 b: Response of the pear rootstock to boron and salinity *in vitro*. *Biol. Plant* **50**, 779-781.
- VIJAYAN, K.; CHAKRABORTI, S. P.; GHOSH, P. D.; 2003: *In vitro* screening of mulberry (*Morus* spp.) for salinity tolerance. *Plant Cell Rep.* **22**, 350-357.
- VOETBERG, G. S.; SHARP, R. E.; 1991: Growth of the maize primary root in low water potentials. III. Roles of increased praline depositions in osmotic adjustment. *Plant Physiol.* **96**, 125-130.
- YOUSSEF, A. M.; HASSANEIN, R. A.; HASSANEIN, A. A.; MORSY, A. A.; 2003: Changes in quaternary ammonium compounds, proline and protein profiles of certain halophytic plants under different habitat conditions. *Pak. J. Biol. Sci.* **6**, 867-882.
- YOUSSEF, A. M.; AL-FREDAN, M. A.; 2008: Community composition of major vegetations in the coastal area of Al-Uqair, Saudi Arabia in response to ecological variations. *J. Biol. Sci* **8**, 713-721.
- YEO, A. R.; YEO, M. E.; FLOWERS, S. A.; FLOWERS, T. J.; 1990: Screening of rice (*Oryza sativa* L.) genotypes for physiological characters contributing to salinity resistance and their relationship to overall performance. *Theo. Appl. Genet.* **79**, 377-384.
- ZHU, J. K.; 2001: Plant salt tolerance. *Trends Plant Sci.* **6**, 66-71.
- WALKER, R. R.; BLACKMORE, D. H.; CLINGELEFFER, P. R.; CORRELL, R. L.; 2002: Rootstock effects on salt tolerance of irrigated field-grown grapevines (*Vitis vinifera* L. cv. Sultana). I. Yield and vigor inter-relationships. *Aust. J. Grape Wine Res.* **8**, 3-14.

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