

THE INFLUENCE OF SALINITY AND DROUGHT STRESS ON SODIUM, POTASSIUM AND PROLINE CONTENT OF *SOLANUM LYCOPERSICUM* L. cv. RIO GRANDE

SYED GHIAS ALI* AND ABDUR RAB²

¹Centre of Plant Biodiversity, University of Peshawar, Pakistan

²Department of Horticulture, The University of Agriculture, Peshawar, Pakistan

*Corresponding author e-mail: ghiasghias06@hotmail.com

Abstract

The influence of salinity and drought stress on sodium (Na⁺), potassium (K⁺) and proline content of *Solanum lycopersicum* L. (tomato) cv. Rio Grande was investigated by exposing the plants to five salinity levels i.e., 0 (control), 50, 100, 150 and 200 mM NaCl and four drought regimes i.e. 0 (Control), 2, 4 and 6 days, applied from seedling (4-5 true leaves) to the harvesting stage. The means across salinity levels showed an increase in proline content and Na⁺ concentration but a reduced K⁺ concentrations, resulting in high Na⁺/K⁺ ratios in shoot and root tissue. In contrast, drought stress decreased the Na⁺ and K⁺ content, Na⁺/K⁺ ratio but increased the proline content in both the root and shoot tissue. The interaction of salinity and drought significantly affected the sodium (Na⁺) and potassium (K⁺) contents, Na⁺/K⁺ and proline content of the shoot but K⁺ content and proline accumulation were not significant. The root and shoot tissue of control plants (0 mMNaCl + 0 Days drought stress) had the minimum Na⁺ content (2316 and 3490 μM/g D.wt.), Na⁺/K⁺ ratio (0.399 and 0.364) and proline content (0.72 and 1.91 μM/g F.wt.) but the highest K⁺ content (6399 and 9603 μM/g D.wt.). Whereas, the Na⁺ content increased with salinity, the K⁺ content declined. It resulted in the maximum Na⁺/K⁺ ratio of the root (1.26) and shoot (0.76) with 200 mMNaCl + 0 Days drought stress. The drought stress also increased the Na⁺/K⁺ ratio. Thus, the highest Na⁺/K⁺ ratio of root (0.78) and shoot (0.77) was recorded in plants grown under 200 mMNaCl + 6 Days drought stress. The proline content of the root and shoot were 0.462 and 1.904 μM/g F.wt. respectively in control plants which increased with increasing salinity and drought stress duration. Thus, the maximum proline content of root (10.61 μM/g F.wt.) and shoot (28.05 μM/g F.wt.) was recorded in plants exposed to 200 mMNaCl + 6 days drought stress combination.

Key words: Tomato, Salinity, Drought, Proline, Na⁺ and K⁺

Introduction

Tomato is a major vegetable crop in Pakistan, but the yield is lower than international average (Imran *et al.*, 2012). Soil salinity and limited irrigation are among the serious limitations in increasing tomato crop productivity (Araus *et al.*, 2002). Soil salinity adversely affects crop production throughout the world (Pervez *et al.*, 2009). Salinity problem may emerge when precipitation is not enough to leach the excess soluble salts from the root zone (Huq & Shoaib, 2013) or where salt rich water is used for irrigation (Marcum, 2006). Water deficit and subsequent drought stress is most common in countries of the arid and semi arid regions (Oliveira *et al.*, 2013). The global climate changes may further increase the severity of droughts, especially during the summer months of the year (Hamdy *et al.*, 2003; Munns, 2005). Due to limited water availability, the farmers are forced to use poor quality water and suboptimum irrigation (Dayal & Chauhan, 2010). The salinity and drought stress are present at the same time in the arid and semiarid regions (Gonzalez *et al.*, 2012) and constitute the major abiotic stresses causing decreased plant growth and crop productivity. High soluble salts in the soil solution increase the osmotic pressure resulting ion toxicity (Teakle & Tyerman, 2010) and low water potential and nutrient uptake by the plants (Tavakkoli *et al.*, 2011). Soil salinity and water deficit also decline the rate of photosynthesis, transpiration and other biochemical processes associated with plant growth and productivity (Tiwari *et al.*, 2010). While different crops may vary in their sensitivity to salinity (Farooq *et al.*, 2008) and drought, they require normal functioning despite high salts

concentration in the tissues (Rajendran *et al.*, 2009). The toxic effect of salts can be reduced by compartmentalization of ions at cellular and whole-plant level, synthesis of compatible solutes, change in photosynthetic pathway, alteration in membrane structure, induction of antioxidative enzymes (Ashraf & Harris, 2004; Parida & Das, 2005; Turkan & Demiral, 2009; Flowers *et al.*, 2010). Ions uptake at the optimum levels is crucial for growth (Tavakkoli *et al.*, 2011) and the excess salts is compartmentalized in the vacuole (Zhu, 2003). In saline conditions, excessive Na⁺ in the rhizosphere and subsequent uptake adversely affect metabolism and causes physiological droughts (Giannakoula & Ilias, 2013). Excess sodium inhibits uptake of K⁺, Ca⁺², Mg⁺² and NO₃⁻, the mineral elements essential for growth (Ahmad & Jabeen, 2005). The decline in uptake of K⁺, Ca⁺², Mg⁺² and NO₃⁻ results in lower Na⁺/K⁺, Na⁺/Ca⁺² and Na/Mg⁺² ratios (Hakim *et al.*, 2014). Since excess sodium ions are sequestered in vacuoles (Brini & Masmoudi, 2012), it is balanced osmotically by the synthesis of compatible solutes, such as proline (Shahid *et al.*, 2013).

Drought stress is another serious problem that may, sometime, accompany the salinity stress (Giannakoula & Ilias, 2013). Tomato is drought sensitive plant and a short period of drought can cause significant decrease in yield. It requires 70 mm of water per week during hot and dry season (Shankara *et al.*, 2005). An optimum water supply decreases the incidence of blossom end rot in tomato fruit (Vossen *et al.*, 2004). Drought stress decreases the growth and reproduction of tomato plants (Pervez *et al.*, 2009; Vijitha & Mehendran, 2010) by adversely affecting the availability, transport and partitioning of nutrients

(Makela *et al.*, 2002). The drought stress may further aggravate the salinity induced damage (Leogrande *et al.*, 2012). The present research was therefore conducted to investigate the influence of salinity and drought stress on the sodium and potassium contents, alterations in Na^+/K^+ and proline synthesis in root and shoot of tomato plants.

Materials and Methods

The influence of salinity and drought stress on sodium, potassium and proline content of tomato cv. Rio Grande plants was investigated at Center of Plant Biodiversity and Botanical Garden, Nowshera during the crop years 2011-2012. The experimental site is located about 271 meters above the sea level with a sub-humid climate and average annual rainfall of 550 mm (Harris *et al.*, 2002). The maximum temperature during the summer may be as high as 45-49°C. The roots and shoot of tomato were examined for sodium and potassium contents, sodium/potassium ratio and proline content at different levels of salinity and drought. The experiment was conducted according to two factorial randomized complete block design (RCBD) with five salinity levels i.e. control, 50, 100, 150 and 200mM of NaCl, applied with first irrigation and drought regimes i.e., 0, 2, 4, 6 days. There were three replications of each treatment and 3 plants in each replication.

For planting tomato seedlings, a circular structure of 54 cm diameter and 72 cm depth was made. The surface of the hole was lined with thick plastic sheet. Three tubes (54 × 36 cm, containing 9 kg media) were placed in each hole. The tubes were perforated at the bottom to allow absorption of salt solution by the rooting medium. Equal amounts of saline solution were applied to each whole to moisten the whole media. A 3.6 meter high lath house structure with G.I pipe was constructed over the experimental plot and covered with transparent plastic sheet when needed to avoid rain water to the experimental plot.

The following parameters were studied during the course of experiments:

Sodium and potassium contents: Both the roots and shoot sample were collected after harvesting the fruits. For analysis of Na^+ and K^+ content, young shoots bearing 4-5 leaves were taken. For root analysis, plants were carefully removed from the growth container. The roots system was thoroughly washed with water to remove the soil particles. Clean roots were used for estimating Na^+ and K^+ content.

Sodium content of the tissue was determined using the method of Watad *et al.* (1986). The tissue samples were oven dried at 80°C till a constant weight was achieved. The dried samples of shoots and roots were ground into a fine powder for wet digestion. For wet digestion, 5 ml of concentrated nitric acid were added to 0.2g of each ground sample. The samples were then kept at room temperature for 48 hours. On the next day the samples were placed in a hot-block set to 90°C for approximately two hours. When no further color change was seen and sample particulates were no longer visible, the sample was removed from the hot block and allowed

to cool and raised the volume of extract up to 50 ml by adding double distilled water. Samples were then analyzed for sodium content by flame photometer (JENWAY PFP7). The values obtained from flame photometer were then used to calculate the sodium content ($\mu\text{M}/\text{g D.wt.}$).

Potassium content of the tissue was determined using the method of Watad *et al.* (1986). The same solution (as for sodium content) was used for the determination of potassium content in roots and shoots by flame photometer (JENWAY PFP7).

Sodium – Potassium ratio: After determining the Na^+ and K^+ content, the Na^+/K^+ ratios in the root and shoots were calculated.

Proline content in root and shoot tips and in leaves:

Proline was determined by the method of Bates *et al.* (1973). For this purpose 0.2g of fresh and young tips from each sample of shoot and root were taken and dip into liquid nitrogen for 2-3 minutes immediately after harvest. The tissues were then crushed with a tissue miser and then homogenized with 4 ml of 3% sulfosalicylic acid ($\text{C}_7\text{H}_6\text{O}_6 \cdot \text{S} \cdot 2\text{H}_2\text{O}$). The homogenate was then centrifuged at 3000 rpm for five minutes at room temperature. The supernatant were filtered through Whatman No. 2 filter paper and again mix a 4 ml of 3% sulfosalicylic acid. The filtrates were then reacted with 2cm³ acid ninhydrin in a test tube in boiling water bath for one hour. Reaction was terminated in an ice bath. Reaction mixture was extracted with 4cm³ toluene and tubes were cool down to room temperature. Absorbance was measured at 520 nanometer against toluene blank. The values obtained were then used for calculating the proline content ($\mu\text{M}/\text{g F.wt.}$).

Results and Discussion

Shoot sodium content: Salinity and drought significantly affected the sodium concentration in shoots of tomato plants (Table 1). The sodium content of tomato shoots was the least (3870 $\mu\text{M}/\text{g D.wt.}$) in the plants treated with 0 mM NaCl solution that increased significantly to 4448, 4724 and 4880 $\mu\text{M}/\text{g D.wt.}$ with 50, 100 and 150 mM NaCl treatment respectively. The difference in 100 and 150 mM NaCl stress was, however, non-significant. The shoot sodium content increased significantly with increase in levels of NaCl stress to 200 mM. The sodium content of non stressed plants was 4293 $\mu\text{M}/\text{g D.wt.}$ and was non significant with 4346 $\mu\text{M}/\text{g D.wt.}$ after 2 days drought stress but, thereafter, increased significantly to 5241 $\mu\text{M}/\text{g D.wt.}$ with increasing drought stress duration to 4 days. The shoot sodium content, however, declined to 4421 $\mu\text{M}/\text{g D.wt.}$ with increasing drought stress to 6 days. The interaction between salinity and drought stress revealed the highest sodium content (5846 $\mu\text{M}/\text{g D.wt.}$) in the shoots of plants exposed to 200 mM NaCl stress and 4 days drought stress, that was non significantly different from 200 mM NaCl and 2 days drought stress and 100 mM NaCl and 4 days drought stress. Whereas 200 mM NaCl and 6 days drought stress resulted in the least sodium content in tomato shoots (Fig. 1).

Table 1. Effects of salinity and drought on sodium and potassium contents of tomato plant root and shoot.

Salinity levels	Sodium content ($\mu\text{M/g D.wt}$)		Potassium content ($\mu\text{M/g D.wt}$)	
	Shoot	Root	Shoot	Root
0 mM	3870 d	2337 e	8906 a	5639 a
50 mM	4448 c	2766 d	7596 b	5200 b
100 mM	4724 b	3180 c	7074 c	4661 c
150 mM	4880 ab	3376 b	5841 d	4098 d
200 mM	4955 a	3577 a	5149 e	3826 e
LSD at α 0.05	206.7	114.3	406.1	236.8
Percent change	28.04%	53.06%	42.18%	32.15%
Drought				
0 days	4293 b	3748 a	7779 a	4925 a
2 days	4346 b	3328 b	6599 b	4892 a
4 days	5241 a	2664 c	6461 b	4588 b
6 days	4421 b	2450 d	6814 b	4333 c
LSD at α 0.05	184.9	102.2	363.2	211.8
Percent change	22.1%	34.63%	16.9%	12.02%
Salinity \times Drought	Fig. 1.	Fig. 2.	Fig. 3.	-
LSD at α 0.05	412.4	228.5	812.2	Ns

Means followed by similar letters in a column are non significantly different from each other at α 0.05

The plants accumulate excessive Na^+ and Cl^- ions in the leaves under salinity stress (Roy & Mishra, 2014). Thus, the build-up of the sodium ion (Na^+) in the cytoplasm of leaf cells is a major effect of salinity stress (Jha *et al.*, 2010). The mean increase in Na^+ ions in the shoot system was 34.67% higher with 200 mM. High cytoplasmic Na^+ interferes with the binding of potassium (K^+), protein synthesis and the activation of key metabolic enzymes (Blaha *et al.*, 2000; Tester & Davenport, 2003; Munns *et al.*, 2006; Munns & Tester, 2008). Thus, the control of Na^+ transport at both the tissue and cellular level is major mechanism of salinity tolerance (Tester & Davenport, 2003; Apse & Blumwald, 2007; Munns & Tester, 2008). Drought stress decreases the nutrient uptake by the roots and its transportation to the shoots due to decrease in rate of transpiration, impaired active transport and membrane permeability (Yuncai & Schmidhalter, 2005). The decline in nutrient uptake may also be due to low soil moisture, which hinders the diffusion rate of nutrients in the soil to the absorbing root surface (Raynaud & Leadley, 2004), thus low sodium content of shoot system was observed with increasing drought stress duration.

Root sodium content: Salinity, drought and their interaction significantly affected the root sodium content. The mean root sodium content increased with increasing the levels of salinity from the least (2337 $\mu\text{M/g D.wt}$) in the control condition (0 mMNaCl stress) to 2766, 3180 and 3376 $\mu\text{M/g D.wt}$ with 50, 100 and 150 mMNaCl treatment respectively. The maximum sodium content (3577 $\mu\text{M/g D.wt}$) was observed in plants exposed to 200 mMNaCl. By contrast, the sodium content of the plant's roots decreased significantly with longer duration of drought stress. The highest Na^+ level (3748 $\mu\text{M/g D.wt}$) with 0 days drought stress (control) declined to the least (2450 $\mu\text{M/g D.wt}$) with 6 days drought stress treatment. Sodium content of the root was 3328 and 2664 $\mu\text{M/g D.wt}$ with 2 and 4 days drought stress treatments respectively (Table 1). As the sodium content increase with salinity and decrease with drought, therefore the interaction effect was also significant (Fig. 2). The plants exposed to 0 mMNaCl and 6 days drought stress had the least (2042 $\mu\text{M/g D.wt}$) sodium ions in the root, while 200 mMNaCl and 0 days drought stress had the highest sodium content (4925 $\mu\text{M/g D.wt}$). Salinity stress increases the uptake and

accumulation of sodium and chloride ions that reduces the uptake of other mineral nutrients, such as potassium and calcium (Sudhir & Murthy, 2004). The Na^+ uptake at the root/soil boundary is achieved by less selective system than other cations (Tester & Davenport, 2003). The sodium can enter plant cells through several types of channels: low-affinity inward-rectifying K^+ channels (Kronzucker *et al.*, 2013), voltage independent channels (Maathuis & Sanders, 2001) and non-selective cation channels (Demidchik & Tester, 2002). Hence increase Na^+ in the growing medium increase its uptake. The drought stress increased the Na^+ concentration in roots but severe drought decreased its uptake (Raza *et al.*, 2013). Thus, it is suggested that the rate of Na^+ translocation from root to shoot was more limited than that of other cations i.e., K^+ in water stresses (Raza *et al.*, 2013). While concentration of Na^+ in roots decreased under severe water deficit, that is independent from leaf Na^+ content, due to positive correlation with root relative water content (Fayyaz *et al.*, 2013).

Shoot potassium content: The potassium content of the tomato shoots decreased significantly with increasing salinity levels. The highest potassium content (8906 $\mu\text{M/g D.wt}$) in shoots in control plants (0 mMNaCl) decreased significantly to 7596, 7074 and 5841 $\mu\text{M/g D.wt}$ with increasing salinity levels to 50, 100 and 150 mMNaCl respectively. The least potassium content (5149 $\mu\text{M/g D.wt}$) was recorded in the shoots of the plants treated with 200 mMNaCl solution. Drought stress also reduced the potassium concentration in the shoots of tomato plants. The highest mean potassium content was 7779 $\mu\text{M/g D.wt}$ in control plants (0 days drought stress) that decreased significantly to 6500 $\mu\text{M/g D.wt}$ in plants exposed to 2 days drought stress duration. Further increase in drought stress to 4 or 6 days, however, did not have any significant effects (Table 1). The interaction between salinity and drought stress revealed the highest potassium content (9603 $\mu\text{M/g D.wt}$) in shoots of tomato plants grown in control conditions (0 mM salinity and 0 days drought stress), that gradually decreased with increasing levels of salinity or drought stress duration. The potassium content of the shoot was the least (4393 $\mu\text{M/g D.wt}$) in plants grown under 200 mMNaCl stress and 4 days drought stressed (Fig. 3).

Potassium nutrition is known to be disturbed under salt stress (Akram *et al.*, 2007). Beside a macronutrient required for plant growth and development (Amjad *et al.*, 2014), potassium ion (K^+) is a prominent inorganic plant solute that contribute to lower the osmotic potential in the stele of roots resulting in turgor pressure development and solute transport in xylem (Shabala *et al.*, 2010). Thus, an optimum level of potassium content may help in osmotic adjustment, maintenance of turgor at low leaf water potentials and, thus, minimize the adverse effects of drought and salinity stress (Wang *et al.*, 2013). The maximum potassium content in the shoots of the non-stressed (control) plants and the minimum with plant stressed with 200mM reveals a clear inhibition of potassium ions uptake by the roots (Tester & Davenport, 2003) and/or its transportation from the roots to the plant shoot (Garcia & Medina, 2013). It has been observed that transcript level of several K^+ transporter genes decline under salinity stress (Su *et al.*, 2002) and the decline in K^+ contents of the xylem and shoot (Moshaei *et al.*, 2014) and the expanding leaf tissue (Su *et al.*, 2001) indicate a decrease in the transport of K^+ (Wang *et al.*, 2013). Yet another reason for low K^+ uptakes may be due its competition with Na^+ uptakes through Na^+ - K^+ co-transporters, which may also block K^+ specific transporters of root cell under salinity (Zhu, 2002). In the present study, the K^+ uptake was reduced in all treatments under salinity stress that could be due to excessive Na^+ that is known to antagonize K^+ uptake (Sarwar & Ashraf, 2003). While, K^+ through its osmotic adjustment effect may decrease the adverse effects of salinity on the plants (Jabeen & Ahmad, 2012) because high K^+ content are commonly observed in salt tolerant species (Ashraf & Sarwar, 2002; Ashraf *et al.*, 2005). Similarly, plant species expressing low reduction in potassium despite saline conditions, are generally more tolerant to salinity (Wang *et al.*, 2013).

Root potassium content: Significant differences of potassium content were observed in roots of tomato plants treated with different salinity levels and irrigation regimes while the interaction effect was non significant (Table 1). Plants exposed to 0 mMNaCl had the highest mean root potassium content (5639 $\mu M/g$ D.wt.) followed by 5200 $\mu M/g$ D.wt. in plants exposed to 50 mMNaCl stress. The root potassium content decreased to 4661 and 4098 $\mu M/g$ D.wt. with 100 and 150 mMNaCl treatments respectively and finally to the least (3826 $\mu M/g$ D.wt.) in the plants exposed to 200 mMNaCl. Drought stress duration of 4 and 6 days also decreased the potassium content of tomato roots from 4925 $\mu M/g$ D.wt. in control plants to 4588 and 4333 $\mu M/g$ D.wt. with 4 and 6 days drought stress respectively (Table 1). The interaction of salinity and drought stress was, however, non significant.

Generally there is an increased uptake of sodium and chloride ions with a decline in the uptake of other mineral nutrients, such as potassium in plant grown under salinity stress (Sudhir & Murthy, 2004). It is observed that high concentration of external Na^+ ions decrease the intracellular potassium (K^+) influx by affecting the transport of ions across plasmalemma of root cells through rupturing of the cellular membranes (Alleva *et al.*, 2006). Thus, it increases the accumulation of Na^+ and Cl^- ions while decreases K^+ accumulation (Al-Karaki, 2000). Limited water availability also adversely affects the nutrient uptake capability of root (Ge *et al.*, 2013), due to declined rate of transpiration, impaired active

transport and membrane permeability (Akinci & Losel, 2012). Thus, K^+ uptake by roots is diminished (Nahar & Gretzmacher, 2002).

Shoot sodium potassium ratio: The Na^+/K^+ ratio in shoots increased significantly with increasing salinity levels, drought stress duration and the interaction of both the stresses (Table 2). The means across salinity revealed the least (0.439) Na^+/K^+ ratio, which increased to the maximum (0.992) in the shoots of plants exposed 200 mMNaCl.

Drought stress also increased the Na^+/K^+ ratio from the minimum of 0.572 in control plants to 0.708 with 2 days drought stress and finally to the maximum of 0.879, when tomato plants were exposed to 4 days drought stress. However, increasing drought stress to 6 days decreased sodium/potassium ratio of tomato shoots to 0.676 (Table 2). This might be due to less absorption of saline water in drought stress condition.

The interaction between salinity and drought had an additive effect of the Na^+/K^+ ratio of the shoot. It was the least (0.346) in control plants that increased with increasing salinity or drought stress duration. While the increase in Na^+/K^+ ratio of tomato shoots was relative less pronounced as a function of drought stress, it increased drastically to 0.760 with 200 mMNaCl and 0 days drought. At the same salinity levels and 4 days drought stress Na^+/K^+ ratio was the maximum (1.351) and declined with further increase in drought stress to 6 days (Fig. 4).

Increasing salinity stress levels resulted in a significant increase in Na^+ content and a considerable decrease in K^+ content, resulting in a significant increase in the sodium potassium ratio (Table 2). Increasing Na^+ concentration leads to toxic effects on plant growth due to increased sodium/ potassium ratio and K^+ displacement by Na^+ in the plant cell that may affect the plasma membrane associated H^+ -ATPase (Wakeel *et al.*, 2011). According to Blumwald *et al.* (2000), the decrease in K^+ concentration in salinity stress is caused by high external Na^+ concentration. It is well evident from the observations that high Na^+ and low K^+ accumulation occur in tomato leaves with increase salt concentration (Al-Karaki, 2000) whereas adding K^+ to NaCl and water deficit stressed plants ultimately decreased Na^+ , increased K^+ content and thus, decreased the Na^+/K^+ ratio (Wakeel *et al.*, 2011). Since, the Na^+ content increased in tomato shoot with increasing NaCl doses and decreased with water deficit condition, and the K^+ content decreased with increasing NaCl doses and drought stress.

Root sodium potassium ratio: The Na^+/K^+ ratio of tomato root increased with increasing salinity levels but decreased with increase in drought stress duration (Table 2). The Na^+/K^+ ratio of the root was the lowest (0.416) with 0 mMNaCl (control) that increased significantly to 0.530, 0.683 and 0.820 with increasing salinity stress to 50, 100 and 150 mMNaCl respectively and finally to the maximum of 0.930 when the tomato plants were exposed to 200 mMNaCl (Table 2). The drought stress treatments had the opposite effect on the Na^+/K^+ ratio of tomato root. The highest root Na^+/K^+ ratio (0.804) in control plants decreased significantly to 0.703 with 2 days drought stress. Further, the Na^+/K^+ ratio of tomato root decreased significantly to 0.599 and 0.597 in plants exposed to 4 and 6 days drought stress respectively.

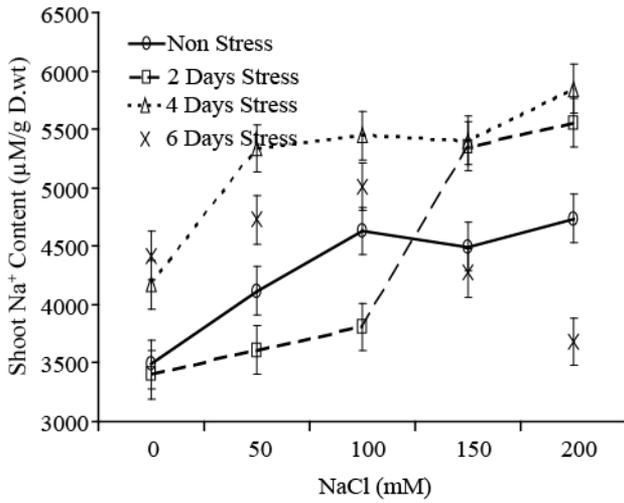


Fig. 1. Effect of salinity and drought on sodium content of tomato shoots. The vertical error bars represents LSD (412.4) at $\alpha = 0.05$.

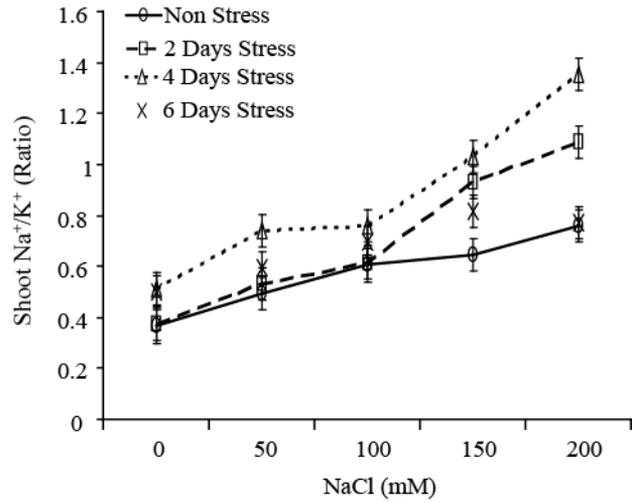


Fig. 4. Effect of salinity and drought on sodium potassium ratio of tomato shoots. The vertical error bars represents LSD (0.1280) at $\alpha = 0.05$.

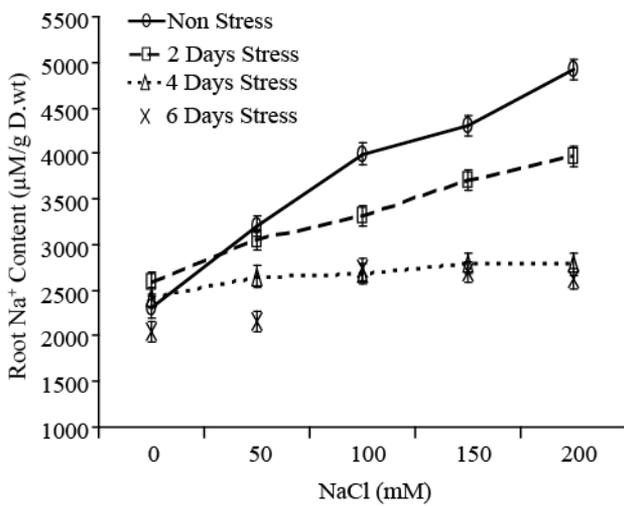


Fig. 2. Effect of salinity and drought on sodium content of tomato roots. The vertical error bars represents LSD (228.5) at $\alpha = 0.05$.

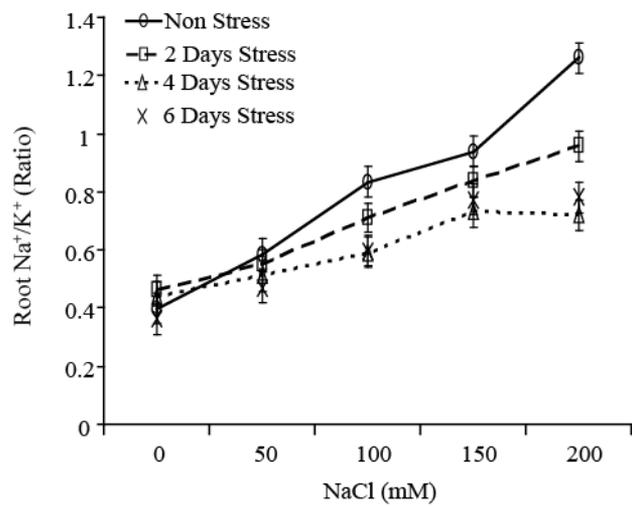


Fig. 5. Effect of salinity and drought on sodium potassium ratio of tomato roots. The vertical error bars represents LSD (0.0739) at $\alpha = 0.05$.

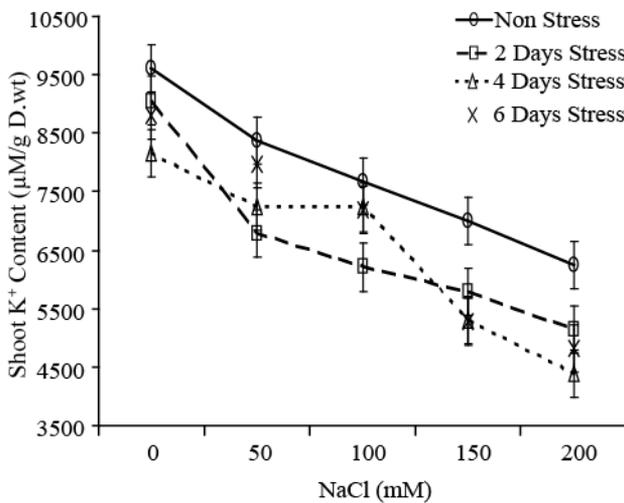


Fig. 3. Effect of salinity and drought on potassium content of tomato shoots. The vertical error bars represents LSD (812.2) at $\alpha = 0.05$.

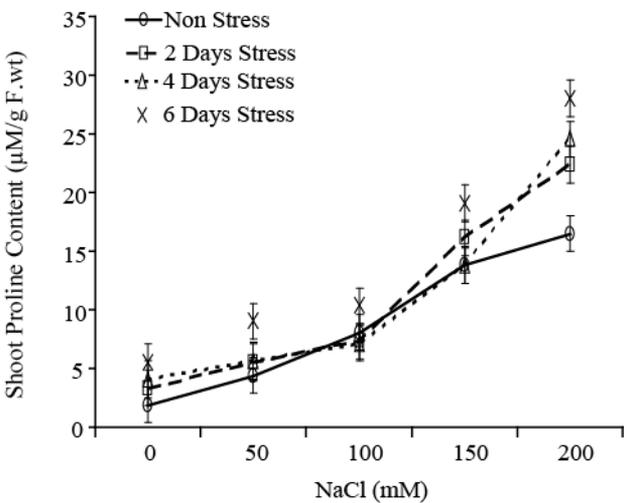


Fig. 6. Effect of salinity and drought on proline content of tomato shoots. The vertical error bars represents LSD (3.095) at $\alpha = 0.05$.

Table 2. Effects of salinity and drought on sodium/potassium ratio and proline contents of tomato plant root and shoot.

Salinity levels	Sodium potassium ratio		Proline content ($\mu\text{M/g}$ F.wt)	
	Shoot	Root	Shoot	Root
0 mM	0.439 e	0.416 e	3.713 e	2.010 e
50 mM	0.589 d	0.530 d	6.150 d	2.917 d
100 mM	0.669 c	0.683 c	8.227 c	4.202 c
150 mM	0.856 b	0.820 b	15.698 b	6.218 b
200 mM	0.992 a	0.930 a	22.867 a	9.530 a
LSD at α 0.05	0.06402	0.3696	1.547	0.8432
Percent change	125.97%	123.56%	516%	374.13%
Drought				
0 days	0.572 c	0.804 a	8.933 c	3.526 c
2 days	0.708 b	0.703 b	10.936 b	4.737 b
4 days	0.879 a	0.599 c	11.039 b	5.935 a
6 days	0.676 b	0.597 c	14.415 a	5.704 a
LSD at α 0.05	0.05726	0.03306	1.384	0.7542
Percent change	53.67%	25.75%	61.37%	68.32%
Salinity \times Drought	Fig. 4.	Fig. 5.	Fig. 6.	-
LSD at α 0.05	0.1280	0.07392	3.095	Ns

Means followed by similar letters in a column are non-significantly different from each other at α 0.05

The interaction between salinity and drought stress also significantly affected the Na^+/K^+ ratio in tomato plants and was in conformity of the influence of both the stresses applied independently. The maximum (1.262) Na^+/K^+ ratio in the root of tomato plants was recorded with the combinations of 200 mMNaCl and 0 days drought stress treatment. While increasing drought stress to 2 days at the same saline stress levels (200 mMNaCl) decreased Na^+/K^+ ratio to 0.958 but decreasing salinity stress to 150 mMNaCl and drought stress to 0 days resulted in Na^+/K^+ ratio of 0.939. The minimum Na^+/K^+ ratio 0.399 was recorded in root of control plants (0 mMNaCl + 0 days drought stress), that was statistically at par with 2, 4 and 6 days drought stress treatments and a sodium potassium ratio of 0.461, 0.440 and 0.362 respectively (Fig. 5).

Since the plants grown in saline condition, accumulates more sodium than potassium ions (Sudhir & Murthy, 2004). Generally the increased accumulation of sodium causes potassium deficiency in salt stressed plants, indicating the existence of competition effects between sodium and potassium ions (Maggio *et al.*, 2007). Because of the similarity between Na^+ and K^+ in their hydrated ionic radii (Munns, 2005), Na^+ competes with K^+ at the sites of entry and ultimately decrease the K^+ uptake (Shabala *et al.*, 2003).

During drought stress, root growth and the rates of K^+ diffusion in the soil towards the roots are restricted, that limit K acquisition and absorption (Wang *et al.*, 2013). Mineral elements uptake by crop plants is generally decreased under water stress conditions (Ashraf *et al.*, 2013), but it is also evident from the present study that in severe drought stress (6 days drought) the Na^+ uptake was

more affected than K^+ , that resulted in decreased Na^+/K^+ ratio with 6 days drought stress.

Shoot proline content: Salinity, drought and their interaction significantly affected the shoot proline content of tomato plants (Table 2). At 0 mMNaCl level, the proline content in shoot was 3.713 $\mu\text{M/g}$ F.wt. which increased to 6.150, 8.227, 15.698 $\mu\text{M/g}$ F.wt. with increasing salinity stress to 50, 100 and 150 mMNaCl respectively. The highest proline content (22.867 $\mu\text{M/g}$ F.wt.) was in plants exposed to 200 mMNaCl stress.

The proline content of tomato shoots increased slowly with increasing drought stress. The lowest proline content (8.933 $\mu\text{M/g}$ F.wt.) in control plants increased significantly to 10.936 and 11.039 $\mu\text{M/g}$ F.wt. with 2 and 4 days drought stress respectively. The difference in proline content of 2 and 4 days drought stressed plants was, however, non significant. Increasing drought stress to 6 days resulted in further increase in proline content to 14.415 $\mu\text{M/g}$ F.wt. of tomato shoot (Table 2).

The interaction of salinity levels and drought stress duration also significantly affected the proline accumulation in shoots of tomato plants. The minimum proline content (1.904 $\mu\text{M/g}$ F.wt.) was recorded in control condition, which increased significantly to 5.551 $\mu\text{M/g}$ F.wt. after 6 days drought stress. In contrast, the minimum proline content (1.904 $\mu\text{M/g}$ F.wt.) observed with 0 mMNaCl and 0 days drought stress increased to 16.494 $\mu\text{M/g}$ F.wt. when salinity stress was increased to 200 mMNaCl despite 0 days drought stress. On the same level of salinity (200 mMNaCl), the proline content increased to 28.051 $\mu\text{M/g}$ F.wt. with increasing drought stress condition to 6 days (Fig. 6).

Proline is a well known amino acid that generally accumulates when plants are exposed to environmental stresses (Kavi-Kishor *et al.*, 2005). The accumulation of proline in plants grown under salinity stress is a common stress indicator and is associated with salt stress tolerance of different plant species (Demiral & Turkan, 2005). Enhanced proline synthesis is a common response of tomato plants to salinity and may determine the stress tolerance (Ali *et al.*, 2011). Proline is believed to acts as a signaling molecule that initiates adaptation to the stress (Maggio *et al.*, 2002), acts as osmolyte for osmotic adjustment (Hayat *et al.*, 2012), helps in stabilizing membranes/proteins and scavenges free radicals (Ashraf & Foolad, 2007). Thus, it decreases the adverse effects of cytoplasmic acidosis and maintains proper NADP⁺/NADPH ratios (Liang *et al.*, 2013). In plants grown under saline conditions, proline induces the expression of salt stress responsive genes and, thus, decreases the damage due to excessive Na⁺ ions accumulation (Chinnusamy *et al.*, 2005). Proline act as a compatible solute in the plants (Mansour, 2000) and, generally, increases with increase in both the salinity stress and drought stress duration (Kishor & Sreenivasulu, 2014). Thus, it is likely to observe enhanced proline synthesis with increasing salinity levels or with drought stress duration.

Root proline content: The proline content in roots varied significantly with different levels of salinity and drought stress but the interaction of salinity and drought stress was not significant (Table 2). The root proline content at 0 mMNaCl stress was 2.010 $\mu\text{M/g}$ F.wt. that increased to 2.917, 4.202 and 6.218 $\mu\text{M/g}$ F.wt. with increasing salinity stress to 50, 100 and 150 mMNaCl respectively. The highest proline accumulation in the roots (9.530 $\mu\text{M/g}$ F.wt.) was observed, when tomato plants were exposed to 200 mMNaCl treatment.

Drought also increased the proline content in roots of tomato plants. The concentration of proline in roots was 3.526 $\mu\text{M/g}$ F.wt. in control plants that increased to 4.737 $\mu\text{M/g}$ F.wt. with 2 days drought stress. The proline content of the roots increased further to 5.935 $\mu\text{M/g}$ F.wt. with 4 days drought stress treatment but declined non-significantly to 5.704 $\mu\text{M/g}$ F.wt. when the drought stress was extended to 6 days.

The accumulation of proline under stressful conditions especially salinity stress has been correlated with salt stress tolerance (Ali *et al.*, 2011). The proline content in roots of alfalfa is found to increase eight fold when the plants are exposed to salt stress conditions (Trinchant *et al.*, 2004). Similarly, salt-tolerant plants are known to accumulate high levels of proline in response to salinity (Demiral & Turkan, 2005). Increased proline synthesis is not associated with salinity stress alone but its accumulation is also commonly observed in plants subjected to drought stress. For example, in rice plants subjected to water deficit have higher proline concentration in the leaves (Hsu *et al.*, 2003) and the rate of proline accumulation and utilization is significantly higher in the drought-tolerant cultivars (Nayyar & Walia, 2003). The protective role of enhanced proline synthesis is also evident from the fact that exogenous application of

proline enhances the stress tolerance of the plant, probably due to its role as osmoprotectants (Noreen *et al.*, 2013). For example, the adverse effects of salinity can be decreased (Bakht *et al.*, 2012) and plant growth can be enhanced by exogenous application of proline in plants grown under saline conditions (Patade *et al.*, 2014).

It can be concluded that salinity increase the Na⁺ of the root and shoot with concomitant decrease in K⁺ of the root and shoot, leading to increased Na⁺/K⁺ ratio. In contrast, extended drought stress (6 days) decreased the accumulation of Na⁺. As a result the Na⁺/K⁺ ratio increased in roots but showed a mixed trend in the shoot system with increasing drought stress duration. Salinity and drought stress also increased the synthesis and accumulation of proline in both the root and shoots system. However, the proline accumulation was greater in the shoot than the root system.

References

- Ahmad, R. and R. Jabeen. 2005. Foliar spray of mineral elements antagonistic to sodium a technique to induce salt tolerance in plants growing under saline conditions. *Pak. J. Bot.*, 37(4): 913-920.
- Akinci, S. and D.M. Losel. 2012. "Plant Water-Stress Response Mechanisms, Water Stress," I. Md. and M. Rahman (Ed). *Water Stress, Intech Europe*, pp. 15-42.
- Akram, M., M.A. Malik, M.Y. Ashraf, M.F. Saleem and M. Hussain. 2007. Competitive seedling growth and K⁺/Na⁺ ratio in different maize (*Zea mays* L.) Hybrids under salinity stress. *Pak. J. Bot.*, 39(7): 2553-2563.
- Ali, S.G., A. Rab, N.U. Khan and K. Nawab. 2011. Enhanced proline synthesis may determine resistance to salt stress in tomato cultivars. *Pak. J. Bot.*, 43(6): 2707-2710.
- Al-Karaki, G.N. 2000. Growth of mycorrhizal tomato and mineral acquisition under salt stress. *Mycorrhiza*, 10(1): 51-54.
- Alleva, K., C.M Niemietz, C. Maurel, M. Parisi, S.D. Tyerman and G. Amodeo. 2006. Plasma membrane of *Beta vulgaris* storage root shows high water channel activity regulated by cytoplasmic pH and a dual range of calcium concentrations. *J. Exp. Bot.*, 57(3): 609-621.
- Amjad, M., J. Akhtar, M. Anwar-ul-Haq, S. Imran and S.E. Jacobsen. 2014. Soil and foliar application of potassium enhances fruit yield and quality of tomato under salinity. *Turk J. Biol.*, 38: 208-218.
- Apse, M.P. and E. Blumwald. 2007. Na⁺ transport in plants. *FEBS Letters*, 581: 2247-2254.
- Araus, J.L., G.A. Slafer, M.P. Reynolds and C. Royo. 2002. Plant breeding and drought in C-3 cereals: what should we breed for? *Ann. Bot.*, 89(7): 925-940.
- Ashraf, M. and M.R. Foolad. 2007. Roles of glycinebetaine and proline in improving plant abiotic stress tolerance. *Environ. Expt. Bot.*, 59: 206-216.
- Ashraf, M. and P.J.C. Harris. 2004. Potential biochemical indicators of salinity tolerance in plants. *Plant Sci.*, 166: 3-16.
- Ashraf, M., M. Shahbaz and Q. Ali. 2013. Drought-induced modulation in growth and mineral nutrients in canola (*Brassica napus* L.) *Pak. J. Bot.*, 45(1): 93-98.
- Ashraf, M.Y. and G. Sarwar. 2002. Salt tolerance potential in members of Brassicaceae. Physiological studies on water relations and mineral contents. In: Prospects for saline Agriculture. (Eds.): R. Ahmad and K.A. Malik. Kluwer Academic Publishers, Netherlands, pp. 237-245.
- Ashraf, M.Y., K. Akhtar, G. Sarwar and M. Ashraf. 2005. Role of rooting system in salt tolerance potential of different guar accessions. *Agron. Sust. Dev.*, 25: 243-249.

- Bakht, J., M.J. Khan, M. Shafi, M.A. Khan and M. Sharif. 2012. Effect of salinity and ABA application on proline production and yield in wheat genotypes. *Pak. J. Bot.*, 44(3): 873-878.
- Bates, L., R.P. Waldren and I.D. Teare. 1973. Rapid determination of free proline for water-stress studies. *Plant and Soil*, 39: 205-207.
- Blaha, G., U. Stelzl, C.M.T. Spahn, R.K. Agrawal, J. Frank and K.H. Nierhaus. 2000. Preparation of functional ribosomal complexes and effect of buffer conditions on tRNA positions observed by cryoelectron microscopy. *Method Enzymol.*, 317: 292-306.
- Blumwald, E., G.S. Aharon and M.P. Apse. 2000. Sodium transport in plant cells. *Biochim. Biophys. Acta*, 1465: 140-151.
- Brini, F. and K. Masmoudi. 2012. Ion transporters and abiotic stress tolerance in plants. *ISRN Mol. Bio.*, 1-13.
- Chinnusamy, V., A. Jagendorf and J.K. Zhu. 2005. Understanding and improving salt tolerance in plants. *Crop Sci.*, 45: 437-448.
- Dayal, B. and R.S. Chauhan. 2010. Recharge of saline water aquifers with rain water and its impact on water quality and crop production. *Biological Forum*, 2(2): 36-37.
- Demidchik, V. and M. Tester. 2002. Sodium fluxes through non selective cation channels in the plasma membrane of protoplasts from Arabidopsis roots. *Plant Physiol.*, 128: 379-387.
- Demiral, T. and I. Turkan. 2005. Comparative lipid peroxidation, antioxidant defense systems and proline content in roots of two rice cultivars differing in salt tolerance. *Environ. Exp. Bot.*, 53: 247-257.
- Farooq, M.R., M.A. Haq, J. Akhtar, M.A. Randhawa and T. Maqsood. 2008. Comparative response of wheat (*Triticum aestivum* L.) genotypes to brackish water at seedling stage. *Pak. J. Agri. Sci.*, 45(4): 439-443.
- Fayyaz, P., E. Etemadi, N.J. Manesh and R. Zolfaghari. 2013. Sodium and potassium allocation under drought stress in Atlas mastic tree (*Pistacia atlantica* subsp. *mutica*). *J. Biogeosci. Forest*, 6: 90-94.
- Flowers, T.J., P.M. Gaur, C.L.L. Gowda, L. Krishnamurthy, S. Srinivasan, K.H.M. Siddique, N.C. Turner, V. Vadez, R.K. Varshney and T.D. Colmer. 2010. Salt sensitivity in chickpea. *Plant Cell Environ.*, 33: 490-509.
- Garcia, M. and E. Medina. 2013. Effect of salt stress on salt accumulation in roots and leaves of two sugarcane genotypes differing in salinity tolerance. *J. Trop. Agric.*, 51(1): 15-22.
- Ge, T.D., N.B. Sun, L.P. Bai, C.L. Tong and F.G. Sui. 2013. Effects of drought stress on phosphorus and potassium uptake dynamics in summer maize (*Zea mays*) throughout the growth cycle. *Acta Physiol. Plant.*, 34(6): 2179-2186.
- Giannakoula A.E. and I.F. Ilias. 2013. The effect of water stress and salinity on growth and physiology of tomato (*Lycopersicon esculentum* Mill.) *Arch. Biol. Sci. Belgrade*, 65(2): 611-620.
- Gonzalez, A., W. Tezara, E. Rengifo and A. Herrera. 2012. Ecophysiological responses to drought and salinity in the cosmopolitan invader *Nicotianaglauca*. *Braz. J. Plant Physiol.*, 24(3): 213-222.
- Hakim, M.A., A.S. Juraimi, M.M. Hanafi, M.R. Ismail, M.Y. Rafii, M.M. Islam and A. Selamat. 2014. The effect of salinity on growth, ion accumulation and yield of rice varieties. *J. Anim. Plant Sci.*, 24(3): 874-885.
- Hamdy, A., R. Ragab and E. Scarascia-Mugnozza. 2003. Coping with water scarcity: Water saving and increasing water productivity. *Irrig. Drain.*, 52: 3-20.
- Harris, D., A. Rashid, S. Ali and P.A. Hollington. 2002. On-Farm' seed priming with maize in Pakistan. Proceeding of the 8th Asian Regional Maize Workshop, Bangkok, Thailand. pp. 314-322.
- Hayat, S., Q. Hayat, M.N. Alyemeni, A.S. Wani, J. Pichtel and A. Ahmad. 2012. Role of proline under changing environments: A review. *Plant Signal Behav.*, 7(11): 1456-1466.
- Hsu, S.Y., Y.T. Hsu and C.H. Kao. 2003. The effect of polyethylene glycol on proline accumulation in rice leaves. *Biol. Plant.*, 46: 73-78.
- Huq, S.M.I. and J.U.M. Shoaib. 2013. The Soils of Bangladesh. Springer, Dodrecht, The Netherlands. pp. 57.
- Imran, M., M.A. Khan, M. Azeem, N. Ahmed, R. Binyamin and A. Riaz. 2012. Screening of tomato germplasm for the source of resistance and its management against ToMV. *Pak. J. Phytopathol.*, 24(1): 53-57.
- Jabeen, N. and R. Ahmad. 2012. Improvement in growth and leaf water relation parameters of sunflower and safflower plants with foliar application of nutrient solutions under salt stress. *Pak. J. Bot.*, 44(4): 1341-1345.
- Jha, D., N. Shirley, M. Tester and S.J. Roy. 2010. Variation in salinity tolerance and shoot sodium accumulation in Arabidopsis ecotypes linked to differences in the natural expression levels of transporters involved in sodium transport. *Plant Cell Environ.*, 33: 793-804.
- Kavi-Kishor, P.B., S. Sangam, R.N. Amrutha, P. Sri-Laxmi, K.R. Naidu, K.R.S.S. Rao, S. Rao, K.J. Reddy, P. Theriappan and N. Sreenivasulu. 2005. Regulation of proline biosynthesis, degradation, uptake and transport in higher plants: Its implications in plant growth and abiotic stress tolerance. *Curr. Sci.*, 88 (3): 424-438.
- Kishor, P.B.K. and N. Sreenivasulu. 2014. Is proline accumulation per se correlated with stress tolerance or is proline homeostasis a more critical issue? *Plant Cell Environ.*, 37(2): 300-311.
- Kronzucker, H.J., D. Coskun, L.M. Schulze, J.R. Wong and D.T. Britto. 2013. Sodium as nutrient and toxicant. *Plant Soil*, 369(1): 1-23.
- Leogrande, R., O. Lopedota, F. Montemurro, C. Vitti and D. Ventrella. 2012. Effects of irrigation regime and salinity on soil characteristics and yield of tomato. *Ita. J. Agro.*, 7: 50-57.
- Liang, X., L. Zhang, S.K. Natarajan and D.F. Becker. 2013. Proline mechanisms of stress survival. *Antioxid. Redox Sign.*, 19(9): 998-1011.
- Maathuis, F.J.M. and D. Sanders. 2001. Sodium uptake in Arabidopsis roots is regulated by cyclic nucleotides. *Plant Physiol.*, 127: 1617-1625.
- Maggio A, S. Miyazaki, P. Veronese, T. Fujita, J.I. Ibeas, B. Damsz, M.L. Narasimhan, P.M. Hasegawa, R.J. Joly and R.A. Bressan. 2002. Does proline accumulation play an active role in stress-induced growth reduction. *Plant J.*, 31: 699-712.
- Maggio, A., G. Raimondi, A. Martino and S. De Pascale. 2007. Salt stress response in tomato beyond the salinity tolerance threshold. *Environ. Exp. Bot.*, 59: 276-282.
- Makela, P., J. Karkkainen and S. Somersalo. 2002. Effect of Glycinebetaine on chloroplast ultrastructure, chlorophyll and protein content, and RuBPCO activities in tomato grown under drought or salinity. *Biologia Plantarum*, 43(3): 471-475.
- Mansour, M.M.F. 2000. Nitrogen containing compounds and adaptation of plants to salinity stress. *Biol. Plant*, 43(4): 491-500.
- Marcum, K.B. 2006. Use of saline and non-potable water in the turfgrass industry: Constraints and developments. *Agr. Water Manage*, 80: 132-146.
- Moshaei, M.R., G.A. Nematzadeh, H. Askari, L. Haghghi, A.S.M. Nejad and A.A. Ahmadi. 2014. Assessment of some physiological parameters and HAK1-type transporter transcriptional changes in *Aeluropuslittoralis* under NaCl stress. *J. Pure Appl. Microbio.*, 8(2): 1051-1057.

- Munns, R. 2005. Genes and salt tolerance. Bringing them together. *New Phytol.*, 167: 645-663.
- Munns, R. and M. Tester. 2008. Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol.*, 59: 651-681.
- Munns, R., R.A. James and A. Lauchli. 2006. Approaches to increasing the salt tolerance of wheat and other cereals. *J. Exp. Bot.*, 57: 1025-1043.
- Nahar, K. and R. Gretzmacher. 2002. Effect of water stress on nutrient uptake, yield and quality of tomato (*Lycopersicon esculentum* Mill.) under subtropical conditions. *Die Bodenkultur*, 53(1): 45-51
- Nayyar, H. and D.P. Walia. 2003. Water stress-induced Pro accumulation in contrasting wheat genotypes as affected by calcium and abscisic acid. *Biol. Plant.*, 46: 275-279.
- Noreen, S., H.U.R. Athar and M. Ashraf. 2013. Interactive effects of watering regimes and exogenously applied osmoprotectants on earliness indices and leaf area index in cotton (*Gossypium hirsutum* L.) crop. *Pak. J. Bot.*, 45(6): 1873-1881.
- Oliveira, A.B., N.L.M. Alencar and E.G. Filho. 2013. Comparison between the water and salt stress effects on plant growth and development, responses of organisms to water stress, In: (Ed.): Tech, Dr. Sener Akinci, Chapter 4. pp. 67-94.
- Parida, A.K. and A.B. Das. 2005. Salt tolerance and salinity effects on plants: a review. *Ecotox. Environ. Safe*, 60(3): 324-349.
- Patade, V.Y., V.H. Lokhande and P. Suprasanna. 2014. Exogenous application of proline alleviates salt induced oxidative stress more efficiently than glycine betaine in sugarcane cultured cells. *Sugar Tech.*, 16(1): 22-29.
- Pervez, M.A., C.M. Ayub, H.A. Khan, M.A. Shahid and I. Ashraf. 2009. Effect of drought stress on growth, yield and seed quality of tomato (*Lycopersicon esculentum* L.). *Pak. J. Agri. Sci.*, 46(3): 174-178.
- Rajendran, K., M. Tester and S.J. Roy. 2009. Quantifying the three main components of salinity tolerance in cereals. *Plant Cell Environ.*, 32(3): 237-249.
- Raynaud X. and P.W. Leadley. 2004. Soil characteristics play a key role in modelling nutrient competition in plant communities. *Ecology*, 85(4): 2200-2214.
- Raza, M.A.S., M.F. Saleem, G.M. Shah, M. Jamil and I.H. Khan. 2013. Potassium applied under drought improves physiological and nutrient uptake performances of wheat (*Triticum aestivum* L.). *J. Soil Sci. Plant Nutr.*, 13(1): 175-185.
- Roy, C. and R. Mishra. 2014. Impact of NaCl stress on the physiology of four cultivars of *S.lycopersicum*. *Res. Plant Biol.*, 4(2): 09-20.
- Sarwar, G. and M.Y. Ashraf. 2003. Genetic variability of some primitive bread wheat varieties to salt tolerance. *Pak. J. Bot.*, 35(5): 771-777.
- Shabala, S., L. Shabala and E.V. Volkenburgh. 2003. Effect of Ca²⁺ on root development and root ion fluxes in salinised barley seedlings. *Funct. Plant Biol.*, 30: 507-514.
- Shabala, S., S. Shabala, T.A. Cuin, J. Pang, W. Percey, Z. Chen, S. Conn, C. Eing and L.H. Wegner. 2010. Xylem ionic relations and salinity tolerance in barley. *Plant J.*, 61: 839-853.
- Shahid, M.A., M.Y. Ashraf, M.A. Pervez, R. Ahmad, R.M. Balal and F. Garcia-Sanchez. 2013. Impact of salt stress on concentrations of Na⁺, Cl⁻ and organic solutes concentration in pea cultivars. *Pak. J. Bot.*, 45(3): 755-761.
- Shankara, N., J.V.L. Jeude, M. Goffau, M. Hilmi and B.V. Dam. 2005. Agrodok 17, Cultivation of tomato production, processing and marketing. Agromisa Foundation and CTA, Wageningen.
- Su, H., D. Golladack, C. Zhao and H.J. Bohnert. 2002. The expression of HAK-type K⁺ transporters is regulated in response to salinity stress in common ice plant. *Plant Physiol.*, 129(4): 1482-1493.
- Su, H., D. Golladack, M. Katsuhara, C. Zhao and H.J. Bohnert. 2001. Expression and stress-dependent induction of potassium channel transcripts in the common ice plant. *Plant Physiol.*, 125(2): 604-614.
- Sudhir, P. and S.D.S. Murthy. 2004. Effects of salt stress on basic processes of photosynthesis. *Photosynthetica*, 42: 481-486.
- Tavakkoli, E., F. Fatehi, S. Coventry, P. Rengasamy and G.K. McDonald. 2011. Additive effects of Na⁺ and Cl⁻ ions on barley growth under salinity stress. 2011. *J. Exp. Bot.*, 62(6): 2189-2203.
- Teakle, N.L. and S.D. Tyerman. 2010. Mechanisms of Cl⁻ transport contributing to salt tolerance. *Plant Cell Environ.*, 33(4): 566-589.
- Tester, M. and R. Davenport. 2003. Na⁺ tolerance and Na⁺ transport in higher plants. *Ann. Bot.*, 91: 503-527.
- Tiwari, J.K., A.D. Munshi, R. Kumar, R.N. Pandey, A. Arora, J.S. Bhat and A.K. Sureja. 2010. Effect of salt stress on cucumber: Na⁺/K⁺ ratio, osmolyte concentration, phenols and chlorophyll content. *Acta Physiol. Plant.*, 32: 103-114.
- Trinchant, J.C., A. Boscari, G. Spennato, G.V. de Sype and D. Le Rudulier. 2004. Prolinebetaine accumulation and metabolism in alfalfa plants under sodium chloride stress. Exploring its compartmentalization in nodules. *Plant Physiol.*, 135(3): 1583-1594.
- Turkan, I. and T. Demiral. 2009. Recent developments in understanding salinity tolerance. *Environ. Exp. Bot.*, 67: 2-9.
- Vijitha, R. and S. Mahendran. 2010. Effect of moisture stress at different growth stages of tomato plant (*Lycopersicon esculentum* Mill.) on yield and quality of fruits. *J. Sci. Univ. Kelaniya*, 5: 1-11.
- Vossen, H.A.M. R. Nono-Womdim and C.M. Messiaen. 2004. *Lycopersicon esculentum* Mill. In: (Eds.): Grubben, G.J.H. & O.A. Denton. *PROTA 2: Vegetables/Legumes*. PROTA, Wageningen, Netherlands.
- Wakeel, A., A. Sumer, S. Hanstein, F. Yan and S. Schubert. 2011. *In vitro* effect of different Na⁺/K⁺ ratios on plasma membrane H⁺-ATPase activity in maize and sugar beet shoot. *Plant Physiol. Biochem.*, 49: 341-345.
- Wang, M., Q. Zheng, Q. Shen and S. Guo. 2013. The critical role of potassium in plant stress response. *Int. J. Mol. Sci.*, 14: 7370-7390.
- Watad, A.E., P.A. Pesci, L. Reinhold and H.R. Lerner. 1986. Proton fluxes as a response to external salinity in wild type and NaCl adapted Nicotiana cell lines. *Plant Physiol.*, 81: 454-459.
- Yuncaï, H. and U. Schmidhalter. 2005. Drought and salinity: A comparison of the effects of drought and salinity. *J. Plant Nutr. Soil Sci.*, 168: 541-549.
- Zhu, J.K. 2002. Salt and drought stress signal transduction in plants. *Annu. Rev. Plant Biol.*, 53: 247-273.
- Zhu, J.K. 2003. Regulation of ion homeostasis under salt stress. *Curr. Opin. Plant Biol.*, 6: 441-445.