

COMPARATIVE EFFECT OF SALINITY ON GROWTH, IONIC AND PHYSIOLOGICAL ATTRIBUTES OF TWO QUINOA GENOTYPES

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Soil salinization is a serious environmental menace that reduces the development, growth and yield of most of the plants. Growing halophyte crops such as quinoa (*Chenopodium quinoa* Willd.) is a promising way of productive utilization of saline soils. The present study was conducted during 2018-19, in which we investigated the comparative salt tolerance potential of two genotypes of quinoa (Puno and A1) on the basis of growth, ionic and physiological attributes. Five-week-old seedlings of both genotypes were exposed to different levels of salinity (0, 100, 200 and 400 mM NaCl) developed in Hoagland's nutrient solution. Results revealed that root and shoot growth, chlorophyll contents, membrane stability and relative water content remained unchanged at lower level of NaCl (100 mM). However, these attributes decreased significantly at higher level of NaCl (400 mM). The Na⁺ concentrations increased, whereas K⁺ concentrations and the ratio of K⁺: Na⁺ showed an inverse relation to the increasing salinity levels. The comparison of both genotypes indicated that physiological attributes and plant biomass were higher in A1 than Puno due to less uptake of Na⁺ ions and higher K⁺: Na⁺ ratio. Therefore, A1 is more suitable genotype than Puno to be grown on saline soils in arid regions of Pakistan.

Keywords: Quinoa, salinity, chlorophyll content, K⁺: Na⁺ ratio, genotypes

INTRODUCTION

Soil salinization is one of the serious environmental constraints distressing > 6% of the total land and >20% of the irrigated area globally (Qadir *et al.*, 2014). Pakistan is also facing this menace and approximately 12.9% of country's land (10 mha) is salt affected (FAO, 2008). Many crops show stunted growth and less yield on saline soils (Negrão *et al.*, 2017; Abbas *et al.*, 2018). On salt-affected soil, plants suffer from osmotic stress which causes water deficit in plants (Flowers and Colmer, 2015). This effect is followed by ionic toxicity and nutrient deficiency (Saqib *et al.*, 2013; Abbas *et al.*, 2015). Salinity also reduces leaf pigment contents, relative water contents (RWC) and gas exchange attributes (Amjad *et al.*, 2015; Abbas *et al.*, 2018). Ultimately, plant biomass, growth and productivity are severely decreased under salinity stress (Saqib *et al.*, 2005; Abbas *et al.*, 2018). The extent of salinity-induced alteration in plant's behavior is related to the type and amount of salts in growth medium, exposure duration, growth stages and highly on plant genotypes (Adolf *et al.*, 2012; Abbas *et al.*, 2018).

The most promising approach for counteracting soil salinity is the cultivation of halophyte plants (Shabala *et al.*, 2013). There is a great genetic variability among halophytes with respect to their salt tolerance potential (Ruiz-Carrasco *et al.*,

2011). Monocotyledonous halophytes show optimum growth around 50 mM NaCl concentration, whereas, dicotyledonous halophytes show maximum growth around 150 mM NaCl level (Glenn *et al.*, 1999; Flowers and Colmer, 2008). The most auspicious example of the dicotyledonous halophytes is quinoa. It is regarded as highly tolerant plant against salinity stress (Koyro and Eisa, 2008; Jacobsen, 2011), and combined stress of salinity and drought (Razzaghi *et al.*, 2011). It has the capacity to grow even at 400 mM salt concentration (Jacobsen *et al.*, 2003) and produces seeds of high nutritional quality (Jacobsen *et al.*, 2003; Ruiz-Carrasco *et al.*, 2016). According to Wilson *et al.* (2002), quinoa uses different tolerance mechanisms against salinity at different growth stages. During the initial growth stage, the salt tolerance is related to controlled metabolism in the form of osmolyte accumulation, osmotic adjustment and ion absorption (Ruffino *et al.*, 2010). In the later growth stages, cell turgor is maintained by adjusting leaf water potential and regulating the tissue ionic uptake (Hariadi *et al.*, 2010). When grown on saline soil, quinoa has the capability to accumulate organic solutes such as; soluble sugars and proline (Rosa *et al.*, 2009). Quinoa is an Andean native crop and it mainly cultivated for its edible seeds. Under the present changing climate scenario, this plant is considered very important with respect to food security due to its exceptional nutritional features (Stikic *et*

al., 2012). Recently, quinoa is widely cultivated in many countries worldwide and great variability has been noticed regarding its growth period and yield which are mostly due to difference in latitude (Christiansen *et al.*, 2010; Razzaghi *et al.*, 2015). Moreover, different genotypes of quinoa demonstrate considerable variability in morphophysiological responses when exposed to salinity stress (Adolf *et al.*, 2012). We want to grow two quinoa genotypes (A1 and Puno) on salt affected soils in Pakistan. Puno is a Danish variety, whereas A1 is originated from USA. The comparative potential of these genotypes to grow under salinity stress is unknown. The current study was therefore planned to determine the salinity tolerance potential of both these genotypes of quinoa by determining their growth, ionic and physiological attributes.

MATERIALS AND METHODS

Plant material and growth conditions: The current study was carried out in the wire house of the Department of Environmental Sciences, COMSATS University Islamabad, Vehari Campus (latitude 30.02° N, longitude 72.21° E, altitude 135 m, and average annual rainfall 127 mm), during 2018–2019. The climatic conditions during the study period were as: sunshine; 8 hours and 23 minutes, minimum temperature; 12 °C, maximum temperature; 25 °C, minimum relative humidity; 46%, and maximum relative humidity; 77%. The seeds of two quinoa genotypes (Puno and A1) were germinated in sand culture. Seeds of genotype Puno were obtained from the Department of Plant and Environmental Sciences, Faculty of Life Sciences, University of Copenhagen, Denmark, whereas the seeds of A1 (belongs to USA) genotypes were taken from Soil Salinity Research Institute Pindi Bhattian, Pakistan. Four-week-old uniform seedlings of both genotypes were transferred to Hoagland's nutrient solution contained in 10 L plastic tubs. There were three seedlings of each genotype in each tub. After establishment of plants for one week, sodium chloride (NaCl) was applied to develop 0, 100, 200, and 400 mM concentrations. The solution pH was adjusted with NaOH or HCl at 6.5 ± 0.2 on daily basis and the nutrient solution was changed on weekly basis. Each treatment was replicated thrice.

Chlorophyll content analysis: The uppermost fully expanded leaves were collected from each plant and were frozen using liquid nitrogen. Later on, about 1.0 g leaf samples were ground in darkness using acetone (80%). The samples were centrifuged at 3000 × g for 10 min and supernatant was collected. The absorbance of the obtained supernatant was noted using UV-Vis spectrophotometer (Lambda 25, PerkinElmer, Inc. USA), at 663.2 and 646.8 nm wavelengths. The extinction coefficients and equations given by Lichtenthaler (1987) were used for the estimation of chlorophyll content.

Membrane stability index (MSI): The procedure described by Sairam *et al.* (2002) was followed for measuring MSI. Electrical conductivity (EC) of leaf leachates in deionized water (DI) was measured at two different temperatures. Freshly harvested leaf samples (about 0.5 g) were shifted in 2 sets of test tubes having 10 mL of DI water. One set was heated in water bath at 40 °C for 30 min, and the other was heated for 10 min at 100 °C. Electric conductivities of both sets were measured as EC₁ and EC₂, respectively using EC meter. The values of MSI were calculated as per following equation;

$$MSI = 1 - \frac{EC_1}{EC_2} \times 100$$

Relative water content (RWC): The fully expanded leaf from the top (2nd leaf) of each plant was collected for determining RWC. Fresh weight (0.5 g) of these leaves was recorded immediately after harvesting. Turgid weight of these leaves was recorded after placing them in 100 mL distilled water for 4 h. The samples were then oven dried at 70 °C for 48 h to record dry weight. The equation given by Sairam *et al.* (2002) was used to estimate RWC.

$$RWC = \frac{\text{fresh weight} - \text{dry weight}}{\text{turgid weight} - \text{dry weight}} \times 100$$

Harvesting and growth measurements: After five-week exposure to treatments, shoots and roots were separately harvested. The fresh biomass and lengths of shoots and roots were measured immediately after harvesting. The samples were air dried for one week, then oven dried for 48 h at 70 °C and the weight was recorded.

Ionic concentrations: Roots and shoots were ground separately. The ground plant samples were acid digested with a diacid mixture (HNO₃ and HClO₄ in 2:1 ratio). The digestate were cooled, filtered and diluted up to 50 mL using DI water. The ionic concentrations (Na⁺ and K⁺) of the samples were measured using a flame photometer (BWB-XP5).

Statistical analysis: A complete randomized design with factorial arrangements was followed in the experiment. The obtained data were statistically analyzed by two-way analysis of variance (ANOVA). Least significant difference (LSD) test at 5% significance level was used for further comparison of genotypes and treatments (Steel *et al.*, 1997).

RESULTS

Plant growth: The growth of both genotypes was decreased with an increase in NaCl concentration except for 100 mM as shown in Table 1. Growth parameters of both genotypes were higher at the lower level of salinity (100 mM NaCl) in comparison with control. At higher level of NaCl (400 mM), root and shoot lengths were decreased by 46% and 52% in Puno, and 39% and 41% in A1, respectively as compared to controls. Similarly, fresh weights of root and shoot were decreased by 48% and 46% in Puno, and 39% and 38% in A1 as compared to controls. The respective decrease in root and shoot dry weights were 57% and 61% for Puno, and 44% and 49% in A1 over the controls.

Table 1. Effects of various levels of NaCl (mM) on root and shoot lengths, and root and shoot weights of two quinoa genotypes

Parameters	Genotypes	Control	100 mM NaCl	200 mM NaCl	400 mM NaCl
Root length (cm)	Puno	11.10±0.50 d	13.00±0.40 c	9.00±0.30 e	6.00±0.50 f
	A1	14.80±0.30 b	17.00±0.72 a	13.00±0.40 c	9.00±0.40 e
Shoot length (cm)	Puno	16.80±0.60 d	20.00±0.80 c	13.20±0.90 e	8.00±0.90 f
	A1	23.80±0.60 b	25.80±0.60 a	20.00±0.60 c	14.10±0.50 e
Root fresh weight (g plant ⁻¹)	Puno	0.48±0.03 d	0.60±0.04 cd	0.40±0.04 f	0.25±0.03 g
	A1	0.82±0.03 b	1.00±0.04 a	0.70±0.02 c	0.50±0.03 e
Shoot fresh weight (g plant ⁻¹)	Puno	2.80±0.20 e	5.00±0.40 c	2.10±0.30 f	1.50±0.20 g
	A1	6.50±0.30 b	8.90±0.30 a	5.00±0.40 c	4.00±0.40 d
Root dry weight (g plant ⁻¹)	Puno	0.07±0.01 d	0.10±0.01 c	0.06±0.00 e	0.03±0.00 f
	A1	0.16±0.01 b	0.22±0.01 a	0.14±0.01 b	0.09±0.01 c
Shoot dry weight (g plant ⁻¹)	Puno	0.51±0.08 d	0.72±0.05 c	0.52±0.04 d	0.20±0.04 e
	A1	1.17±0.05 b	1.72±0.04 a	1.10±0.06 b	0.60±0.04 cd

The values are mean of three replications ± SE. For each parameter, different lettering indicates the significant difference among treatment and genotypes at 5% probability level.

Chlorophyll content: At a level of 100 mM NaCl, the chlorophyll contents were significantly higher with respect to control in both genotypes (Fig. 1A, 1B, 1C). Even at 200 mM

NaCl, chlorophyll contents were at par with control treatment in both genotypes. However, at 400 mM NaCl, chl-a, chl-b and total chl contents of Puno were reduced by 48%, 55% and

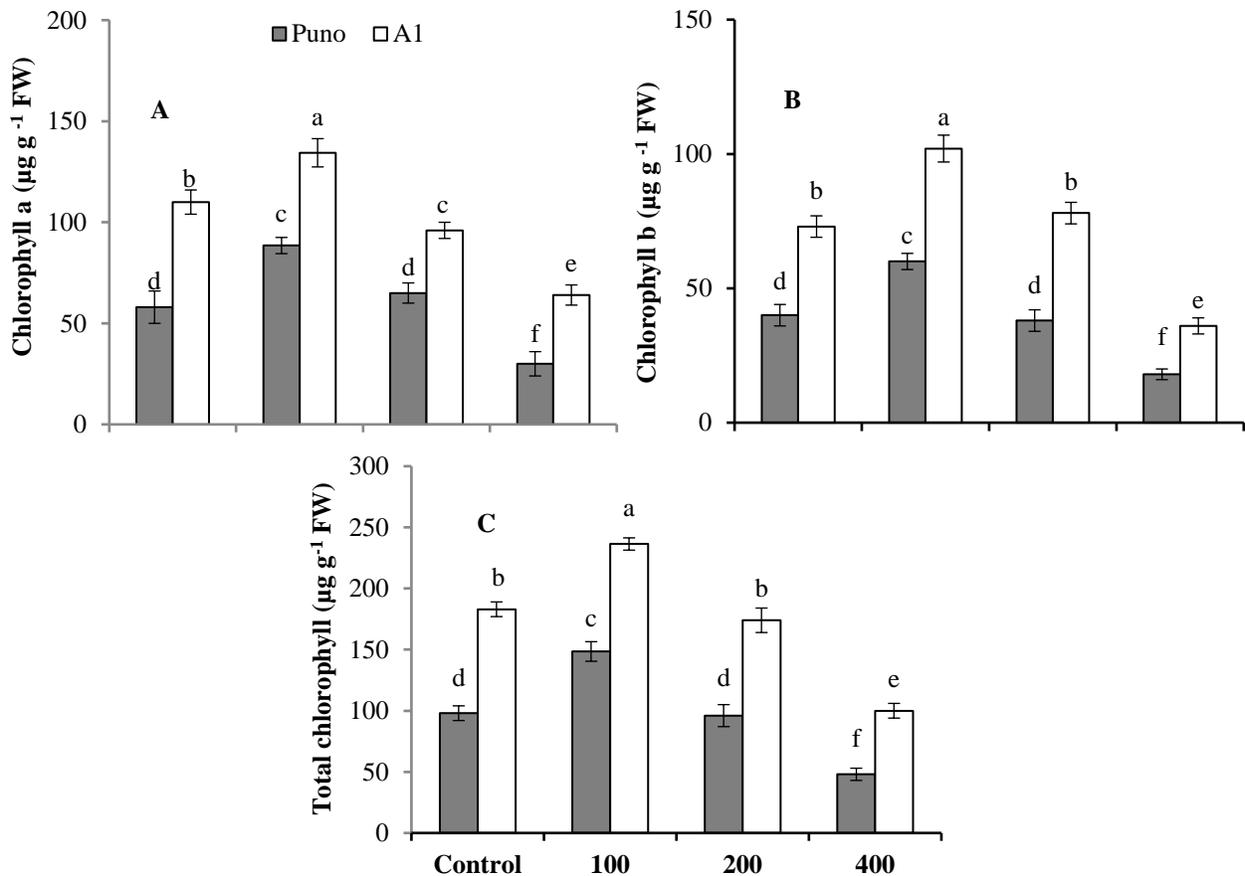


Figure 1. Effects of NaCl (mM) on chlorophyll a (A) chlorophyll b (B) and total chlorophyll (C) contents of two quinoa genotypes. Values are mean of three replications ± SE. For each parameter, values with different lettering indicate the significant difference among treatment and genotypes at 5% probability level.

51%, respectively compared with control. The respective decrease in chlorophyll contents of A1 was 42%, 51% and 45% over the control treatment.

Membrane stability index and relative water content: The MSI of both genotypes was not affected at lower level of

salinity (100 mM NaCl) (Fig. 2A). However, the higher salinity levels caused significant decrease in MSI of both genotypes. At the highest level of salinity (400 mM NaCl), MSI of Puno and A1 decreased by 44% and 30%, respectively in comparison to control treatments. Similarly, the RWC of

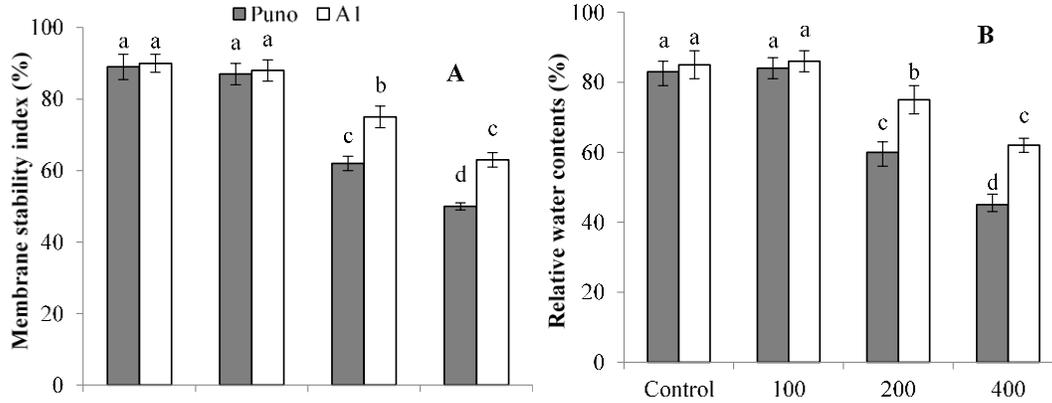


Figure 2. Effects of NaCl (mM) on membrane stability index (A) and relative water contents (B) of two quinoa genotypes. Values are mean of three replications \pm SE. For each parameter, values with different lettering indicate the significant difference among treatment and genotypes at 5% probability level.

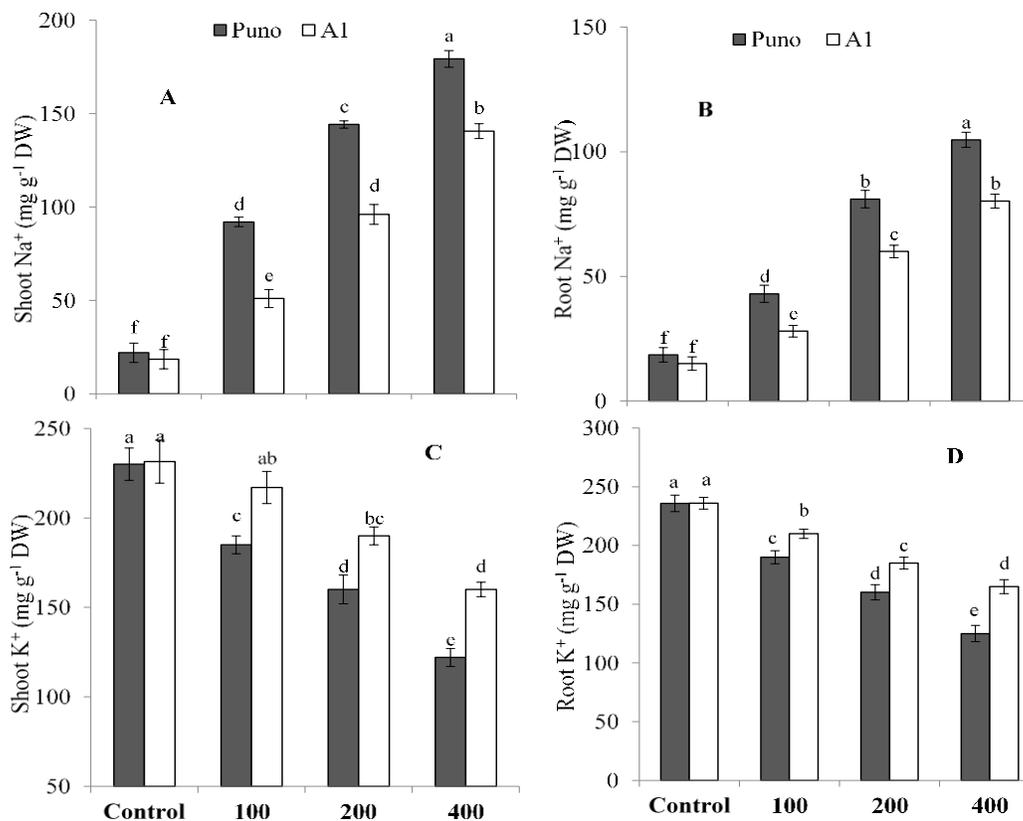


Figure 3. Effects of NaCl (mM) on shoot Na⁺ (A) root Na⁺ (B) shoot K⁺ (C) and root K⁺ (D) concentrations of two quinoa genotypes. Values are mean of three replications \pm SE. For each parameter, values with different lettering indicate the significant difference among treatment and genotypes at 5% probability level.

both genotypes was not significantly affected at 100 mM NaCl (Fig. 2B). However, RWC of both genotypes was significantly decreased at higher salinity levels. At 400 mM NaCl level, RWC of Puno and A1 decreased by 46% and 27%, respectively over the control.

Ionic concentrations: The Na^+ concentrations in shoot and root of the two genotypes were increased with an increase in salinity levels (Fig. 3A, 3B). The comparison of both genotypes indicated that Na^+ concentrations in plants were higher in Puno as compared to A1 for all treatments. At salinity level of 400 mM, shoot Na^+ concentrations in Puno and A1 were 179 and 140 mg g^{-1} DW, respectively. Whereas, root Na^+ contents were 105 and 80 mg g^{-1} DW in Puno and A1, respectively. The K^+ concentrations of plants (shoot and root) decreased in both genotypes as a result of increasing NaCl in the growth medium (Fig. 3C, 3D). The K^+ concentrations were considerably higher in A1 as compared to Puno for all the treatments. At the highest levels of salinity, shoot K^+ concentrations in Puno and A1 were 122 and 160 mg g^{-1} DW, respectively. While, root K^+ concentrations were 125 and 165 mg g^{-1} DW in Puno and A1, respectively.

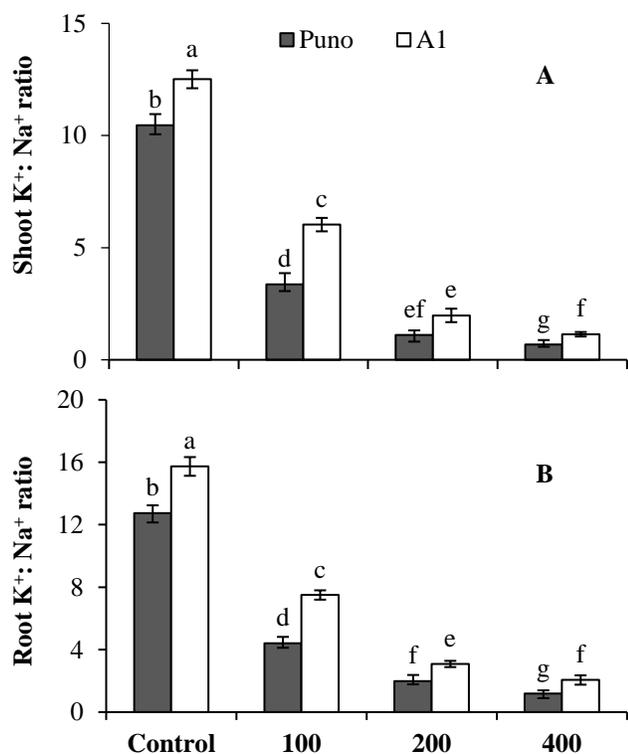


Figure 4. Effects of NaCl (mM) on shoot K^+ : Na^+ ratio (A) and root K^+ : Na^+ ratio (B) of two quinoa genotypes. Values are mean of three replications \pm SE. For each parameter, values with different lettering indicate the significant difference among treatment and genotypes at 5% probability level.

The ratios of K^+ : Na^+ in plants decreased considerably in both genotypes with an increase in the salt stress (Fig. 4A, 4B). These ratios were at peak in control plants and least in 400 mM NaCl treated plants. The genotype A1 had higher ionic ratio in root and shoot of plants as compared to Puno.

DISCUSSION

The current study was carried out to compare the salinity tolerance potential of two quinoa genotypes having different origin. The genotype Puno is a Danish variety, whereas A1 is originated from USA. When exposed to salinity stress, both genotypes showed typical halophytic nature and showed higher growth and biomass at lower salinity level (100 mM NaCl) in comparison to control treatment. Similarly, an enhancement in growth of different quinoa genotypes under NaCl level of 150 mM has been previously observed (Hariadi *et al.*, 2010). Survival of quinoa even at 500 mM NaCl was also observed in a Peruvian variety by Koyro and Eisa (2008). We also found that both genotypes survived at NaCl level of 400 mM, but there was a considerable decrease in growth and biomass of both genotypes. Our results revealed that growth and biomass of genotype A1 was less decreased as compared to Puno, indicating greater salinity tolerance potential of A1 genotype. Similarly, Ruiz-Carrasco *et al.* (2011) explored the salt tolerance potential of four genotypes of quinoa originating from different locations at 150 and 300 mM NaCl levels. They concluded that based on relative decrease in root length and plant biomass, the genotype PRJ was the most tolerant and BO78 the most sensitive one among the four tested genotypes. Plant shows different responses under the salt stress conditions and it involves changes in uptake and metabolic pathways which are activated at the cellular homeostasis. All these changes lead to different type and degree of adaptation, and these changes results in the altered growth patterns of root and shoot (Patterson *et al.*, 2009).

Leaf chlorophyll contents and RWC were not decreased at lower salt level (100 mM), and were rather increased in both genotypes, confirming the salt loving nature of both genotypes. Panda *et al.* (2017) noticed that the chlorophyll contents in halophyte *Suaeda maritima* seedlings were not affected even at 400 mM NaCl level. However, we found that at a higher level of salinity these attributes were decreased in both quinoa genotypes as noticed in many other quinoa genotypes (Takagi and Yamada, 2013; Amjad *et al.*, 2015). Reduction in chlorophyll contents in quinoa at higher salinity level might be due to degradation of chlorophyll structure (Rangani *et al.*, 2016). These attributes were decreased to greater extent in Puno than A1 indicating higher stability of chlorophyll structure in A1 than Puno. Reduction in the stability of cell membrane of both genotypes under higher salt stress is an indicator of the oxidative stress due to the overproduction of reactive oxygen species (ROS). Salinity-induced membrane damage due to ROS has been widely

reported in various plants including quinoa (Amjad *et al.*, 2015; Rehman *et al.*, 2019). The relatively less decrease in MSI in case of A1 confirms its greater tolerance against salinity induced oxidative stress.

We noticed an increasing trend in Na⁺ concentration in tissues of both genotypes with increasing salt concentrations in the medium. Plants can cope with the potential Na⁺ toxicity by four ways; (a) reduced uptake of Na⁺ by roots (b) limiting Na⁺ translocation from root to shoot (c) re-transporting Na⁺ from the shoots (d) vacuolar sequestration of Na⁺ ions (Munns and Tester, 2008). A remarkable variability in these strategies has been observed among different plant species and genotypes (Munns and Tester, 2008; Abbas *et al.*, 2018). Shabala *et al.* (2013) explored the genotypic differences regarding salt tolerance among fourteen quinoa genotypes on the basis of shoot Na⁺ uptake. According to their findings, the three most tolerant varieties accumulated very small amount of Na⁺ and hence they exhibited the exclusion strategy. The remaining eleven varieties accumulated relatively higher quantities of Na⁺ and sequestered it into vacuoles. In our study, although both genotypes differed considerably regarding the amount of Na⁺ uptake, however, both genotypes followed the same strategy for dealing with excessive Na⁺ in the medium. Both genotypes accumulated higher Na⁺ in shoot than in roots, so they probably sequestered the excessive Na⁺ into their leaf vacuoles. In case of quinoa, mostly it has been found that the Na⁺/H⁺ exchangers are more up regulated in leaves than in roots. It suggests that the most prominent mechanism of salinity tolerance in quinoa is vacuolar Na⁺ compartmentation rather than root exclusion (Maughan *et al.*, 2009; Shabala *et al.*, 2013).

In halophytes, inorganic mineral ions are used to sustain the cell turgidity under saline conditions (Parida *et al.*, 2016). We observed that with increasing the salinity stress, K⁺ concentration was lessened in both genotypes. Under salinity stress, Na⁺ ions use cations channels to enter into the cell (Flowers and Colmer, 2015). Consequently, with an increase in Na⁺ concentration, the concentration of K⁺ is decreased (Amjad *et al.*, 2015; Abbas *et al.*, 2017) leading to K⁺ deficiency (Munns and Tester, 2008).

We found that K⁺: Na⁺ ratio decreased in both genotypes with an increase in level of salinity. This ratio is an important element elucidating the salt tolerance potential of quinoa (Adolf *et al.*, 2013). Potassium is an essential macro nutrient involved in activation of more than 50 enzymes (Marschner, 1995; Shabala, 2003) including the enzymes involved in biosynthesis of chlorophyll. Both Na⁺ and K⁺ ions have very similar ionic radius and hydration energy. Therefore, under saline conditions, Na⁺ enters the cell by using K⁺ channels located at cell membranes (Marschner, 1995). The higher cytoplasmic concentration of Na⁺ leads to lower K⁺: Na⁺ ratio, which ultimately affects plant metabolism. Moreover, loss of K⁺ from leaf mesophyll cells under salinity (Shabala *et al.*, 2005) causes the activation of many proteases which initiate

the programmed cell death (Shabala, 2009). Hence, the capability of the plants to limit K⁺ loss and maintenance of high ionic ratio (K⁺: Na⁺) in cytoplasm is an indication of their salt tolerance potential (Adolf *et al.*, 2012). We noticed considerably higher K⁺: Na⁺ ratio in A1 genotype than Puno, due to which the former genotype showed greater salt tolerance potential and produced more biomass.

Conclusion: The study elaborated that plant growth, chlorophyll and membrane stability of quinoa genotypes remained undamaged up to 100 mM NaCl level. However, at higher salinity level these attributes were decreased significantly. The comparison of both genotypes indicated that physiological attributes and plant biomass were higher in A1 than Puno due to less buildup of Na⁺ and greater uptake of K⁺ ions. Therefore, A1 is more suitable genotype than Puno to be grown on saline soils in arid regions of Pakistan.

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REFERENCES

- Abbas, G., M. Saqib and J. Akhtar. 2015. Interactive effects of salinity and iron deficiency on different rice genotypes. *J. Plant Nutr. Soil Sci.* 178:306-311
- Abbas, G., M. Saqib, J. Akhtar and G. Murtaza. 2017. Physiological and biochemical characterization of *Acacia stenophylla* and *Acacia albida* exposed to salinity under hydroponic conditions. *Can. J. Forest Res.* 47:1293-1301.
- Abbas, G., Y. Chen, F. Khan, Y. Feng, J. Palta and K. Siddique. 2018. Salinity and low phosphorus differentially affect shoot and root traits in two wheat cultivars with contrasting tolerance to salt. *Agron.* 8:155.
- Adolf, V.I., S. Shabala, M.N. Andersen, F. Razzaghi and S.E. Jacobsen. 2012. Varietal differences of quinoa's tolerance to saline conditions. *Plant Soil.* 357:117-129.
- Adolf, V.I., S.E. Jacobsen and S. Shabala. 2013. Salt tolerance mechanisms in quinoa (*Chenopodium quinoa* Willd.). *Environ. Exp. Bot.* 92:43-54
- Amjad, M., S.S. Akhtar, A. Yang, J. Akhtar and S.-E. Jacobsen. 2015. Antioxidative Response of Quinoa Exposed to Iso-Osmotic, Ionic and Non-Ionic Salt Stress. *J. Agron. Crop Sci.* 201:452-460.
- Christiansen, J.L., S.E. Jacobsen and S.T. Jørgensen. 2010. Photoperiodic effect on flowering and seed development in quinoa (*Chenopodium quinoa* Willd.). *Acta Agric. Scand. B.* 60:539-544.
- FAO. 2008. Land and plant nutrition management service. FAO Rome, Italy. <http://www.fao.org/ag/agl/agll/spush>

- Flowers, T.J. and T.D. Colmer. 2008. Salinity tolerance in halophytes. *New Phytol.* 179:945-963.
- Flowers, T.J. and T.D. Colmer. 2015. Plant salt tolerance: adaptations in halophytes. *Ann. Bot.* 115:327-331.
- Glenn, E.P., J.J. Brown and E. Blumwald. 1999. Salt tolerance and crop potential of halophytes. *Crit. Rev. Plant Sci.* 18:227-255.
- Hariadi, Y., K. Marandon, Y. Tian, S.E. Jacobsen and S. Shabala. 2010. Ionic and osmotic relations in quinoa (*Chenopodium quinoa* Willd.) plants grown at various salinity levels. *J. Exp. Bot.* 62:185-193.
- Jacobsen, S.E., A. Mujica and C. Jensen. 2003. The resistance of quinoa (*Chenopodium quinoa* Willd.) to adverse abiotic factors. *Food Reviews Inter.* 19:99-109.
- Jacobsen, S.E. 2011. The situation for quinoa and its production in southern Bolivia: from economic success to environmental disaster. *J. Agron. Crop Sci.* 197:390-399.
- Koyro, H.-W. and S.S. Eisa. 2008. Effect of salinity on composition, viability and germination of seeds of *Chenopodium quinoa* Willd. *Plant Soil.* 302:79-90.
- Lichtenthaler, H.K. 1987. Chlorophylls and carotenoids: chlorophylls of photosynthetic biomembranes. In: *Methods in enzymology*. Academic Press, United States. 148:350-382.
- Marschner, H. 1995. The soil root interface (rhizosphere) in relation to mineral nutrition. *Mineral nutrition of higher plants*, 2nd Ed. Academic Press, London. pp. 537-595.
- Maughan, P., T. Turner, C. Coleman, D. Elzinga, E. Jellen, J. Morales, J. Udall, D. Fairbanks and A. Bonifacio. 2009. Characterization of Salt Overly Sensitive 1 (SOS1) gene homoeologs in quinoa (*Chenopodium quinoa* Willd.). *Genome.* 52:647-657.
- Munns, R. and M. Tester. 2008. Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol.* 59:651-681.
- Negrão, S., S. Schmöckel and M. Tester. 2017. Evaluating physiological responses of plants to salinity stress. *Ann. Bot.* 119:1-11.
- Panda, A., J. Rangani, A. Kumari and A.K. Parida. 2017. Efficient regulation of arsenic translocation to shoot tissue and modulation of phytochelatin levels and antioxidative defense system confers salinity and arsenic tolerance in the halophyte *Suaeda maritima*. *Environ. Exp. Bot.* 143:149-171.
- Parida, A.K., S.K. Veerabathini, A. Kumari and P.K. Agarwal. 2016. Physiological, anatomical and metabolic implications of salt tolerance in the halophyte *Salvadora persica* under hydroponic culture condition. *Front. Plant Sci.* 7:351.
- Patterson, J.H., E. Newbigin, M. Tester, A. Bacic and U. Roessner. 2009. Metabolic responses to salt stress of barley (*Hordeum vulgare* L.) cultivars, Sahara and Clipper, which differ in salinity tolerance. *J. Exp. Bot.* 60:4089-4103.
- Qadir, M., E. Quillérou, V. Nangia, G. Murtaza, M. Singh, R.J. Thomas, P. Drechsel and A.D. Noble. 2014. Economics of salt-induced land degradation and restoration. *Natural Resources Forum.* 38:282-295.
- Rangani, J., A.K. Parida, A. Panda and A. Kumari. 2016. Coordinated changes in antioxidative enzymes protect the photosynthetic machinery from salinity induced oxidative damage and confer salt tolerance in an extreme halophyte *Salvadora persica* L. *Front. Plant Sci.* 10:7-50.
- Razzaghi, F., S.H. Ahmadi, V.I. Adolf, C.R. Jensen, S.-E. Jacobsen and M.N. Andersen. 2011. Water relations and transpiration of quinoa (*Chenopodium quinoa* Willd.) under salinity and soil drying. *J. Agron. Crop Sci.* 197:348-360.
- Razzaghi, F., S.E. Jacobsen, C.R. Jensen and M.N. Andersen. 2015. Ionic and photosynthetic homeostasis in quinoa challenged by salinity and drought—mechanisms of tolerance. *Funct. Plant Biol.* 42:136-148.
- Rehman, S., G. Abbas, M. Shahid, M. Saqib, A.B.U. Farooq, M. Hussain, B. Murtaza, M. Amjad, M.A. Naeem and A. Farooq. 2019. Effect of salinity on cadmium tolerance, ionic homeostasis and oxidative stress responses in conocarpus exposed to cadmium stress: Implications for phytoremediation. *Ecotoxicol. Environ. Safet.* 171:146-153.
- Rosa, M., M. Hilal, J.A. Gonzalez and F.E. Prado. 2009. Low-temperature effect on enzyme activities involved in sucrose–starch partitioning in salt-stressed and salt-acclimated cotyledons of quinoa (*Chenopodium quinoa* Willd.) seedlings. *Plant Physiol. Biochem.* 47:300-307.
- Ruffino, A.M.C., M. Rosa, M. Hilal, J.A. González and F.E. Prado. 2010. The role of cotyledon metabolism in the establishment of quinoa (*Chenopodium quinoa*) seedlings growing under salinity. *Plant Soil.* 326:213-224.
- Ruiz-Carrasco, K., F. Antognoni, A.K. Coulibaly, S. Lizardi, A. Covarrubias, E.A. Martínez, M.A. Molina-Montenegro, S. Biondi and A. Zurita-Silva. 2011. Variation in salinity tolerance of four lowland genotypes of quinoa (*Chenopodium quinoa* Willd.) as assessed by growth, physiological traits, and sodium transporter gene expression. *Plant Physiol. Biochem.* 49:1333-1341.
- Ruiz-Carrasco, K., S. Biondi, E. Martínez, F. Orsini, F. Antognoni and S.E. Jacobsen. 2016. Quinoa—a model crop for understanding salt-tolerance mechanisms in halophytes. *Plant Biosys.* 150:357-371.
- Sairam, R.K., K.V. Rao and G.C. Srivastava. 2002. Differential response of wheat genotypes to long term salinity stress in relation to oxidative stress, antioxidant activity and osmolyte concentration. *Plant Sci.* 163:1037-1046.
- Saqib, M., C. Zörb, Z. Rengel and S. Schubert. 2005. The expression of the endogenous vacuolar Na⁺/H⁺ antiporters in roots and shoots correlates positively with

- the salt resistance of wheat (*Triticum aestivum* L.). *Plant Sci.* 169:959-965.
- Saqib, M., J. Akhtar, G. Abbas and M. Nasim. 2013. Salinity and drought interaction in wheat (*Triticum aestivum* L.) is affected by the genotype and plant growth stage. *Acta Physiol. Plant.* 35:2761-2768.
- Shabala, S. 2003. Regulation of potassium transport in leaves: from molecular to tissue level. *Annals Bot.* 92:627-634.
- Shabala, S., L. Shabala, E. Van Volkenburgh and I. Newman. 2005. Effect of divalent cations on ion fluxes and leaf photochemistry in salinized barley leaves. *J. Exp. Bot.* 56:1369-1378.
- Shabala, S. 2009. Salinity and programmed cell death: unravelling mechanisms for ion specific signalling. *J. Exp. Bot.* 60:709-712.
- Shabala, S., Y. Hariadi and S.E. Jacobsen. 2013. Genotypic difference in salinity tolerance in quinoa is determined by differential control of xylem Na⁺ loading and stomatal density. *J. Plant Physiol.* 170:906-914.
- Steel, R.G.D., J.H. Torrie and D. Dickey. 1997. *Principles and Procedures of Statistics: A Biometrical Approach*, 3rd Ed. McGraw Hill Book Co. Inc., New York.
- Stikic, R., D. Glamoclija, M. Demin, B. Vucelic-Radovic, Z. Jovanovic, D. Milojkovic-Opsenica, S.-E. Jacobsen and M. Milovanovic. 2012. Agronomical and nutritional evaluation of quinoa seeds (*Chenopodium quinoa* Willd.) as an ingredient in bread formulations. *J. Cereal Sci.* 55:132-138.
- Takagi, H. and S. Yamada. 2013. Roles of enzymes in anti-oxidative response system on three species of chenopodiaceous halophytes under NaCl-stress condition. *Soil Sci. Plant Nutr.* 59:603-11.
- Wilson, C., J.J. Read and E. Abo-Kassem. 2002. Effect of mixed-salt salinity on growth and ion relations of a quinoa and a wheat variety. *J. Plant Nutr.* 25:2689-2704.

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