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Effect of salt stress on growth and physiological parameters of sorghum genotypes at an early growth stage

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Physiological regulation affects plant salinity tolerance. The objective of this research was to investigate the effect of salt stress on the physiological regulation in sorghum at early growth stage. Two sorghum genotypes (GT), Bayeqi (salt-tolerant) and PL212 (salt-sensitive), were grown in an artificial climate chamber with a nutrition solution containing 0，80, 160, and 240 mM NaCl. Results showed that salt-tolerant sorghum had enhanced activities of antioxidant enzymes including catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD), and increased stress-related osmolytes including free amino acids, and reducing and soluble sugars. Furthermore, ion regulation plays an important role in the osmotic adjustment. Results also suggest that K^+/Na^+ and Ca^{2+}/Na^+ ratios are associated with tolerance under salt-stressed environments and higher Na^+ and lower K^+ and Ca^{2+} concentrations are deleterious to sorghum growth. As a result, under salt-stressed environments, the salt-tolerant sorghum GT had better growth performance than salt-sensitive sorghum GT, which was evidenced by a greater plant high, leaf area, leaf fresh weight, and root fresh weight. Overall, under salt-stressed environments, the salt-tolerant sorghum GT had better growth performance including yield than salt-sensitive sorghum GT, which was evidenced by a greater plant high, leaf area, leaf fresh weight, and root fresh weight.

Keywords: Antioxidation, Ion regulation, Osmotic adjustment, Salinization, Sorghum

Salt stress is a serious agronomic problem that affects plant growth and limits crop productivity worldwide[1,2]. Salt stress may arise as a result of osmotic stress and ion accumulation imbalance in plants. It affects almost every aspect of plant physiology such as antioxidant enzyme activity, osmotic adjustment, and photosynthetic efficiency[3], and thus significantly reduces farmland productivity. Salinity stress is often more prominent in arid and semi-arid regions, where high temperature and limited rainfall associated with poor water supply is considered to be the principle threat to agricultural production[4,5].

Although sorghum (*Sorghum bicolor* L. Moench) is a moderately salt-tolerant crop, genotypic differences exist among cultivars[1]. Salt stress limits plant growth by disrupting physiological processes[2,3]. The declined plant growth rate under salinity stress has been associated with decreased photosynthetic rate and stomatal conductance (Cond)[4]. There are several methods for screening salt tolerance because the growth response and the majority of physiological processes, including photosynthesis and physiological parameters such as chlorophyll content and electrolyte leakage[5,6].

Accumulation of compatible organic solutes, which are also called osmolytes, in plant leaves is a common response to salt stress[7]. In alfalfa (*Medicage sativa* L.), lentil (*Lens culinaris* Medik.), rocket (*Eruca sativa* Mill.), and sunflower (*Helianthus* annuus L.)[8-11], salt-tolerant GT exhibited greater total free amino acids than salt-sensitive GT. The increase of proline content in plant leaves has also been documented under salt stress[12]. Moreover, soluble carbohydrates, organic acids, and reducing and soluble sugars increase under

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salt stressed environments[6]. These osmolytes may serve as reserve for plant metabolism or contribute to stabilization of protein molecules and cell membranes[13].

In addition to osmotic adjustment, salt stress causes oxidative stress due to the excessive formation of reactive oxygen species (ROS)[14]. To mitigate the oxidative damage, plants employed a complex antioxidant system, including antioxidant enzymes of catalase (CAT), superoxide dismutase (SOD), and peroxidases (POD)[15,16]. Effects of salt stress on antioxidant responses associated with ROS have been studied in many plant species, such as creeping bentgrass (*Agrostis stolonifera* L.), maize (*Zea mays* L.), and rice (*Oryza sativa* L.)[17-20]. It was noted that salt-tolerant plants increase their antioxidant enzyme activities and antioxidant components in response to salt stress, while salt-sensitive plants fail to do so. Antioxidative response is closely correlated with the tolerance of GT to salinity because the ability of these antioxidants removal of ROS[21].

Plant metabolic changes, including inorganic ion contents, occurred when plants suffered salt stress[22]. The deleterious effects of salt stress on plant growth are related to decreased osmotic potential of the ion toxicity[23]. One of the most prominent salt stress symptoms is a substantial K^+ efflux from cells to reduce the intracellular K^+ pool, affecting the cytosolic homeostasis of K^+[24]. The solutes response for increasing salinity in a plant's environment usually is Na^+[25].

To our knowledge, there is a lack of comprehensive research on the effects of NaCl on sorghum photosynthesis and various physiological parameters. Here, we assessed select known physiological parameters associated with salinity tolerance in both salt tolerant and salt sensitive varieties of sorghum. We studied the photosynthetic system, antioxidant enzyme activity, electrolyte leakage, inorganic ion, lipid peroxidation, osmotic adjustment, and proline accumulation in both salt-tolerant and salt-sensitive sorghum GT for better understanding of the mechanisms of salt stress tolerance.

Materials and Methods

Study site

This research was conducted at Liaoning Academy of Agricultural Sciences in Shenyang, China from March to July 2017. Pots were placed in an artificial climate chamber set for 28/21°C day/night with an average irradiance of 1300 μmol m^{-1} s^{-1}, 50% relative humidity, and photoperiod of 12 h.

Plant material

A total of 686 grain sorghum cultivars cultivated in Northeastern China were examined and screened in a preliminary research for selecting two grain sorghum GT differing in NaCl tolerance. Two grain sorghum GT, Bayeqi (salt-tolerant) and PL212 (salt-sensitive) were selected and used in this research.

Experiment description

Sorghum seeds were surface-sterilized with 1% sodium hypochlorite for 5 min followed by rinsing three times with distilled water. Seeds were planted in plastic pots (20 cm diameter by 25 cm deep) filled with perlite. Hoagland solution was applied on alternate days to each pot. The test is completely random and repeated three times, seedlings were thinned to three per pot after emergence. Thereafter, seedlings were fertilized with 1/3 Hoagland nutrient solution containing 0, 80, 160, and 240 mM salinity level (SL) of NaCl. In an attempt to avoid osmotic shock, the salt concentration was increased stepwise in aliquots of 80 mM every day to attain an appropriate concentration[26]. Plants irrigated with NaCl-free nutrient solution were used as unstressed control. The electrical conductivity of nutrient solution for irrigating unstressed plants was 0.01 ds m^{-1}. Morphological and physiological measurements were conducted at 28 days after the final salt levels were reached (DAT).

Experimental design and statistical analysis

Experimental design was a randomized complete block. Two experimental runs were conducted twice over time. All measurements were replicated three times. Data were subjected to analysis of variance (ANOVA) in SAS (100 SAS Campus Dr., Cary, NC 27513). The significance of main effects was determined at the 0.05 probability level and treatment means were separated with Fisher's Protected Least significant difference (LSD) test at 0.05 probability level. Experiment by treatment interaction was not detected, and thus, data were pooled over experimental runs for analysis.

Results and Discussion

Plant growth parameters

Analysis of variance indicated that the effects of GT, SL, and their interactions were all significant for plant height, leaf area, and shoot fresh weight (Table 1). The effects of GT, SLand GT × SL interactions were significant for root fresh weight. As a result, salt stress decreased the plant height, leaf area, shoot fresh weight, and root fresh weight in both sorghum GT (Fig. 1). In addition, results showed that these growth parameters gradually reduced with an increase in NaCl conc. for both sorghum GT. The reductions were more pronounced for salt-sensitive plants, especially when plants were treated with 240 mM NaCl.

Relative water content

Variance of analysis showed that GT, SL, and their interactions had significant effects on leaf RWC. GT and SL had significant effects on root RWC (Table 2).

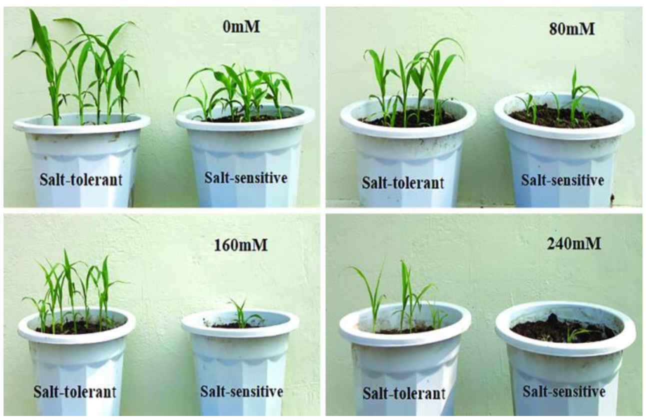

Fig. 1 — Effect of increasing concentrations of NaCl on plant height, leaf area, shoot fresh weight, leaf RWC, root fresh weight, and root RWC in salt-tolerant and salt-sensitive plants of sorghum.

able 1 — Analyses of variance of the effects of genotypes (GT) and salinity levels (SL) on *sorghum* growth traits, leaf and root RWC, electrolyte leakage, antioxidant enzymes, MDA, electrolyte leakage, stress-related osmolytes, and ion accumulation

Traits	Sources of variation (GT)	Traits	Sources of variation (GT)
Plant height	852.70**	Plant height	852.70**
Leaf area	1723.90**	Leaf area	1723.90**
Shoot fresh wt.	2315.17**	Shoot fresh wt.	2315.17**
Root fresh wt.	71.91**	Root fresh wt.	71.91**
Leaf RWC	2729.43**	Leaf RWC	2729.43**
Root RWC	55.25**	Root RWC	55.25**
CAT	353.36**	CAT	353.36**
POD	796.33**	POD	796.33**
SOD	597.24**	SOD	597.24**
MDA	9.62*	MDA	9.62*
Electrolyte leakage	765.77**	Electrolyte leak.	765.77**
Proline	506.25**	Proline	506.25**
Soluble sugar	205.29**	Soluble sugar	205.29**
Soluble protein	25.16*	Sol. protein	25.16*
Free amino acids	348.29**	Free AA	348.29**
Na^+	268.10**	Na^+	268.10**
K+	20.63*	K+	20.63*
Ca^{2+}	12.69*	Ca^{2+}	12.69*
K^+/Na^+	87.06**	K^+/Na^+	87.06**
Ca^{2+}/Na^+	15.65*	Ca^{2+}/Na^+	15.65*

[Level of significance: *$P \leq 0.05$; **$P \leq 0.01$, ns denotes a non-significant effect at the 0.05 significant level]

Although leaf RWC decreased in both sorghum GT, the reduction is more pronounced in salt-sensitive GT. RWC gradually decreased with an increase in NaCl concentration for both leaves and roots (Table 2). The reductions were more pronounced in salt-sensitive sorghum at 240 mM NaCl, although leaf and root RWC in both sorghum GT were restored at 28 DAT, salt-tolerant GT exhibited greater leaf and root RWC than salt-sensitive GT under salinity stress (Table 2 and Fig. 1).

The reduction of leaf RWC was more pronounced in salt-sensitive than salt-tolerant sorghum GT. The reduction in RWC suggested the loss of turgor of sorghum tissues under salinity stress. As a result, there was limited water availability for cell extensive process. Therefore, the growth inhibition of salt-stressed sorghum might be associated with the reduction of RWC induced by NaCl treatment.

Antioxidant enzymes, Lipid peroxidation, and Membrane permeability

Activities of selected ROS scavenging enzymes, including CAT, POD, and SOD, were measured in plant leaves. Variance of analysis showed that GT and SL had statistically significant effects on the POD activity (Table 1). GT, SL, and DAT, and most of their interactions had statistically significant effects on CAT, POD, and SOD activity. Overall, results showed that the activities of antioxidant enzymes including CAT, POD, and SOD significantly increased under salinity stress (Fig. 2). Salt-tolerant sorghum plants generally exhibited greater antioxidant activity as compared to salt-sensitive sorghum plants under salinity-stressed environments.

MDA levels in plant leaves were determined to evaluate lipid peroxidation. Analysis of variance showed that GT, SL, DAT, and their interactions had significant effects on lipid peroxidation (Table 1). As expected, MDA content was generally increased as

able 2 — The effect of increasing concentrations of NaCl on leaf and root relative water content (RWC) in a salt tolerant and salt sensitive sorghum plants

NaCl conc. /mM	Salt-tolerant		Salt-sensitive	
	Leaf RWC/%	Root RWC/%	Leaf RWC/%	Root RWC/%
0	82.57^{aA}	81.10^{aA}	83.47^{aA}	81.40^{aA}
80	80.67^{bB}	77.95^{bB}	79.12^{bB}	76.04^{bB}
160	79.49^{cB}	75.68^{cC}	73.36^{cC}	71.23^{cC}
240	79.47^{cB}	74.24^{dC}	56.01^{dD}	62.65^{dD}

[The English alphabets indicate the leaf RWC and root RWC in different NaCl concentrations in the same column; lowercase letters indicate 0.05 significance level and uppercase letters indicate 0.01 significance level] salinity stress increased (Fig. 2). At 28 DAT, MDA accumulated lower levels in salt-tolerant than salt-sensitive GT.

All independent variables including GT, SL, and their interactions had significant effect on membrane permeability (Table 1). Salinity stress significantly increased membrane permeability in both sorghum GT, as indicated by increased electrolyte leakage (Fig. 2). At 28 DAT, data showed that the salt-tolerant plants grown at 80, 160, and 240 mM NaCl had 8, 35, and 157% more electrolyte leakages than the unstressed control, respectively, while the salt-sensitive plants grown at 80, 160, and 240 mM NaCl had 62, 156, and 225% more electrolyte leakages respectively than the unstressed control.

Stress-related osmolytes

Results of variance analysis showed that GT, SL, and their interaction had significant effects on free amino acids and proline contents in plant leaves (Table 1). GT, SL, and GT × SL interaction had significant effects on soluble sugar in plant leaves. GT, SL, and GT × SL interaction had significant effects on reducing sugar and soluble protein in plant leaves. Results showed that proline and soluble protein contents were statistically similar between the sorghum GT grown under unstressed condition (Fig. 3). Salinity stress generally increased the contents of all stress-related osmolytes including free amino acids, proline, soluble protein, and soluble sugar in both sorghum GT. However, the stress-related osmolytes of salt-tolerant sorghum are more responsive to salt stress and produced more free amino acids, proline, soluble protein, and soluble sugar than salt sensitive GT.

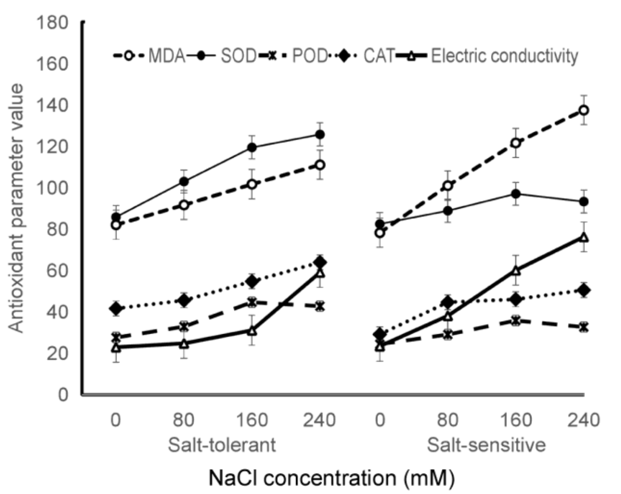

Fig. 2 — Effects of increasing concentrations of NaCl on antioxidant enzymes, lipid peroxidation, and membrane permeability in salt-tolerant and salt-sensitive sorghum genotypes. [X-axis represents genotypes with four NaCl concentrations i.e., 0, 80, 160 and 240 mM and Y-axis represents all measured ionic parameters. * and ** denotes significant effect at P = 0.05 and 0.01 level, The units were MDA, μmol/g DW;SOD, U/g protein;POD, U/(min/g) protein;CAT, U/(min/g) protein; APX U/g protein; and Electric conductivity, /%]

Inorganic ion

Variance analysis showed that all independent variables including GT, SL, DAT, and their interactions had significant effects on Na^+, K^+/Na^+, and Ca^{2+}/Na^+ (Table 1). Moreover, GT, SL, and DAT had significant effects on K^+ and Ca^+ accumulation in plants. Data showed that Na^+ concentration increased in leaves of both sorghum GT under salinity-stressed environments, especially in salt-sensitive GT. At 28 DAT, salt-tolerant GT grown at 80, 160, and 240 mM NaCl had 56, 91, and 161% more Na^+ than unstressed control, respectively, while salt-sensitive sorghum GT had 89, 151, and 217% more Na^+ than unstressed control, respectively. Compared to 21 DAT, Na^+ concentration reduced at 28 DAT in both sorghum GT. Salt tolerant sorghum GT grown at 80, 160, and 240 mM had 13, 33, and 69% more Na^+ than unstressed control, respectively, while salt-sensitive sorghum GT grown at 80, 160, and 240 mM had 69, 146, and 190% more Na^+ than unstressed control, respectively. Regarding the K^+ and Ca^+ concentrations, sorghum exhibited less K^+ and Ca^+ concentrations as NaCl concentration increased, and this effect was more pronounced in salt-sensitive sorghum GT. Leaf K^+/Na^+ and Ca^{2+}/Na^+ ratios were decreased as NaCl concentrations increased and were always higher in the

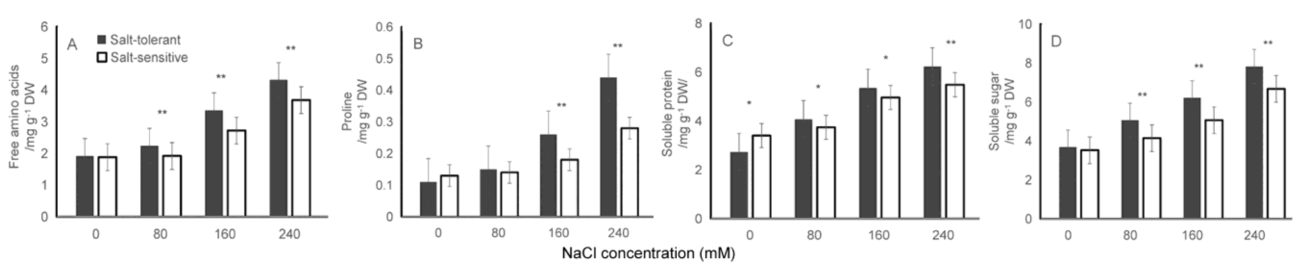

Fig. 3 — Effects of increasing concentrations of NaCl on osmotic adjustment in salt-tolerant and salt-sensitive sorghum plants

Table 3 — The effect of increasing concentrations of NaCl on ion accumulation in salt-tolerant and salt-sensitive *sorghum* plants

Cultivar	NaCl conc. (mM)	Na^+ (mg g^{-1} DW)	K^+ (mg g^{-1} DW)	Ca^+ (mg g^{-1} DW)	K^+/Na^+	Ca^{2+}/Na^+
Salt-tolerant	0	15.56^{cC}	90.24^{aA}	43.05^{aA}	5.80^{aA}	2.77^{aA}
	80	17.72^{bcC}	85.85^{abA}	39.14^{aA}	4.85^{bB}	2.21^{bAB}
	160	20.74^{bB}	81.71^{bcB}	41.10^{aA}	3.94^{cC}	1.98^{bB}
	240	26.36^{aA}	78.29^{cB}	33.27^{bB}	2.97^{dD}	1.26^{cC}
Salt-sensitive	0	12.78^{dD}	90.24^{aA}	48.92^{aA}	7.06^{aA}	3.83^{aA}
	80	21.61^{cC}	85.37^{bB}	41.10^{bB}	3.95^{bB}	1.90^{bB}
	160	31.55^{bB}	76.59^{cC}	31.31^{cC}	2.43^{cC}	0.99^{cC}
	240	37.17^{aA}	71.71^{dC}	29.35^{cC}	1.93^{dD}	0.79^{D}

[The English alphabets indicate the Na^+, K^+, Ca^+, K^+/Na^+ and Ca^{2+}/Na^+ in different NaCl concentrations in the same column; lowercase letters indicate 0.05 significance level and uppercase letters indicate 0.01 significance level]

salt-tolerant GT when plants suffered salinity stress (Table 3). Maximum reduction in K^+/Na^+ and Ca^{2+}/Na^+ ratios were observed in salt-sensitive GT at 28 DAT, with an averaged reduction of 73 and 79% at 240 mM NaCl, respectively.

Yield

Salinity stress had a significant effect on the yield of salt-tolerant and salt-sensitive sorghum, but the degree of impact differed on the two types of sorghum (Fig. 4). In addition, results indicated that with the increase of the degree of salt stress, the difference in yield between salt-tolerant sorghum and salt-sensitive sorghum increased significantly. When the phenotype encountered salt stress, salt-tolerant sorghum reduced the yield loss through a series of physiological adjustments, while salt-sensitive sorghum exhibited relatively poor self-physiological regulation ability.

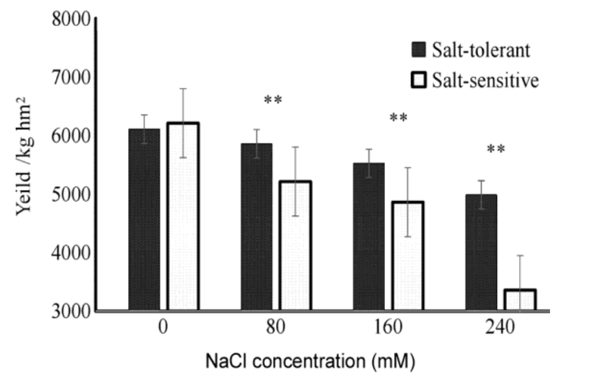

Fig. 4 — The effects of increasing concentrations of NaCl on yeild in salt-tolerant and salt-sensitive sorghum genotypes. [* and ** denotes significant effect at P = 0.05 and 0.01 level]

Discussion

Sorghum, a moderate salt tolerant crop, is often planted in semi-arid and arid regions where salinity is a major limitation for sorghum productivity[26]. Plant salt sensitivity varies with its growth stage with young plants at the seedling stages are generally more sensitive to salinity stress than at relative mature stages[27].

The present research showed that increasing salinity level of the growth medium caused a substantial reduction in the growth of both sorghum GT, as evident by plant height, leaf area, shoot fresh weight, and root fresh weight. These findings are in agreement with what have been previously reported in barley (*Hordeum vulgare* L.)[28], tomato[29], maize[30], and rice (*Oryza sativa* L.)[31]. The variation of measured plant growth parameters between the *sorghum* GT was observed in the present study. Results showed that salt-tolerant sorghum GT exhibited consistently better measured growth parameters than salt-sensitive sorghum GT under the salt stress environments. This result is in agreement with the previous findings in which significant genotypic differences with regard to salt tolerance at intra-specific level in turnip[26] and sorghum[32].

Maintenance of water status as reflected by leaf and root RWC is noted to be one of the most important adaptations to salt stress [26]. In the present research, sorghum leaf and root RWC decreased substantially as NaCl concentration increased, which may have been due to salt-induced water loss. Similar result has been previously reported in *Brassica napus* [33].

Changes in lipid peroxidation and index of membrane stability are correlated with oxidative damage under various abiotic stresses[16]. As a product of membrane lipid peroxidation, MDA content is noted a good indicator to indicate the oxidative damage of plant cells[34]. In the present study, MDA content is increased as salinity stress increased in both sorghum GT. Another physiological parameter that serves for assessment of membrane damage is membrane leakage, which indicates membrane dysfunction as the permeability and electrolyte leakage increase in plant cells[35]. Salinity stress increased MDA content and electrolyte leakage as the NaCl concentrations increased, suggesting the occurrence of membrane damage in sorghum seedlings.

The NaCl treatment caused an increase in stress-related osmolytes including free amino acids, proline, soluble protein, and reducing and soluble sugar contents in leaves of the salt-stressed sorghum seedlings. Results showed that the increase of free amino acids, proline, and soluble protein, and soluble sugar contents was positively correlated to the level of salt tolerance. The contrasting role of proline to osmotic adjustment has been previously documented and its specific roles as an adaptive process is still a matter of debate and varies according to the species[36]. For example, our finding is in contrast with those who noted that proline is not involved in the osmotic adjustment of sugar beet and rice[37], but is in agreement with those of Hajlaoui *et al*.[29] with maize (*Zea mays* L.). In previous investigations, proline accumulation in plant tissue under stressful conditions has been noted to be the result of an increased proline biosynthesis[38], and decreased proline degradation and utilization, as well as increased hydrolysis of proteins[39].

In previous research, Hajlaoui,*et al*.[29] noted that amino acids increasingly accumulated in leaves of maize with increasing salt stress. However, Chen *et al*.[40] reported that free amino acids increase at low salinity but decrease at high salinity stress. In the present research, free amino acids increased as salt stress increased. Additionally, salt-tolerant sorghum GT accumulated greater amount of amino acids compared to salt-sensitive sorghum GT under salinity-stressed environments. Previous research documented that the steady-state levels of free amino acids are dependent on the rate of protein degradation and the rate of efflux into growing structures[41].

In other *sorghum* GT, Lacerda*et al*.[42] reported that the salt-tolerant and salt-sensitive sorghum GT increasingly accumulated large amounts of carbohydrates during salt stress. The authors noted that the accumulation of carbohydrates during salt stress could be used for cell osmotic adjustment. Similar correlation between osmotic stress tolerance and sugar accumulation has been documented in maize[4]. Osmotic adjustment of reducing and soluble sugar contents is a vital mechanism for maintaining turgor and avoiding the adverse effects of salinity stress on vegetative and reproductive sorghum tissues. Therefore, our data suggest that the accumulation of reducing and soluble sugar is related to the salt tolerance of sorghum.

In this experiment, K^+ and Ca^{2+} concentrations significantly decreased in the leaves of salinized sorghum plants, especially in the salt-sensitive sorghum GT. K^+ plays a cofactor for many enzymes to maintain osmotic status, and Ca^{2+} protects plants against the adverse effects of Na^+ and enhances plant growth under saline condition. Therefore, plants require high levels of K^+ and Ca^{2+} under saline stress. Consequently, higher Na^+ and lower K^+ and Ca^{2+} concentrations are deleterious to sorghum growth, as observed in the present study. Our results showed that the K^+/Na^+ and Ca^{2+}/Na^+ ratios, which were high in the unstressed condition, decreased substantially in the sorghum leaves after the plants were suffered the high levels of NaCl, particularly in the salt-sensitive GT. The reductions in K^+/Na^+ and Ca^{2+}/Na^+ ratios were due to the increase in Na^+ concentration and decrease in K^+ and Ca^{2+} in salt-stressed sorghum seedlings. Similar results were reported in rice and sugar beet[43]. Overall, results suggest that higher K^+/Na^+ and Ca^{2+}/Na^+ ratios in sorghum contribute to the greater salt tolerance under saline conditions.

As In our study, Wang *et al*.[44] noted that amino acids increasingly accumulated in leaves of maize with increasing salt stress. However, Zhu *et al*.[9] reported that free amino acids increase at low salinity but decrease at high salinity stress. In the present research, free amino acids increased as salt stress increased. Additionally, salt-tolerant sorghum GT accumulated greater amount of amino acids compared to salt-sensitive sorghum GT under salinity-stressed environments. Selma *et al*.[45] documented that the steady-state levels of free amino acids are dependent on the rate of protein degradation and the rate of efflux into growing structures.

There have been many reports about changes in crop yields under salt stress, and it is generally believed that salt stress will cause serious crop yield reductions[44]. However, the results of this study show that salt stress exhibits minimal effect on the yield of salt-tolerant sorghum, but it has a significant effect on the yield of salt-sensitive varieties. The effect of salt stress on different types of sorghum varieties is quite different, which is basically consistent with the previous research, and clarifies the salt tolerance of sorghum to salt stress.

Conclusion

Investigation of salt stress effect on the growth and physiological parameters in sorghum GT with contrasting salt tolerance allows us to confirm that all of the growth traits , leaf and root RWC, electrolyte leakage, antioxidant enzymes, MDA, electrolyte leakage, stress related osmolytes and ion accumulation are affected by salt stress. Understanding these physiological parameters would be helpful for screening salt-tolerant sorghum GT in an effort of sorghum breeding. Physiologically, the tested sorghum accumulated more ROS and MDA contents under salt stress, but salt-tolerant sorghum had less electrolyte leakage and accumulated less ROS and MDA contents in leaves. We conclude that accumulation of inorganic ions plays an important role in the osmotic adjustment and high K^+/Na^+ and Ca^{2+}/Na^+ ratios in sorghum are associated with the greater salt tolerance under saline conditions. Further, the salt-tolerant sorghum had enhanced activities of antioxidant enzymes including CAT, POD, and SOD, and increased contents of stress-related osmolytes including free amino acids and reducing soluble sugars, leading to higher yield and greater salt tolerance.

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Conflict of interest

Authors declare no conflict of interests.

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