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Impact of saline stress on the uptake of various macro and micronutrients and their associations with plant biomass and root traits in wheat

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Abstract: The associations among ion uptake, root development and biomass under salt stress have not been fully understood. To study this, a pot experiment was conducted with the objective to determine the concentrations of sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), zinc (Zn) and iron (Fe) and explore their associations with the biomass and root development by using eight wheat cultivars grown on control and salt stress treatments. About 6 folds increase Na^+/K^+ ratio in root, while 10 folds in the shoot were detected in salt stress compared to that for control. Ca, Mg, Zn concentrations in both root and shoot, and Fe concentration in the shoot were significantly changed by salt stress, except Fe concentration in the root. Principal component analysis revealed significant associations of these ions with the aboveground biomass and root traits. On salt stress treatment, the Na^+/K^+ ratio in shoot showed a significant negative correlation with root weight and aboveground biomass, while aboveground biomass correlated positively with lateral root length and root weight. A strategy towards manipulating the ion homeostasis, particularly Na^+/K^+ , combined with selecting genotypes with better salt tolerance is of promise to alleviate the effects of salt stress.

Keywords: salinity; *Triticum aestivum* L.; nutrition accumulation; ions uptake; saline soil

Since salt stress has a severe impact on crop productivity and the worldwide distributed agricultural saline land has been estimated to be around 830 million ha; therefore, targeted management is required to increase yield potential under such saline conditions (Minhas et al. 2020). Practical approaches to deal with salt stress include selecting/breeding crop genotypes

with better performance on salt-affected soil and manipulating the soil properties by adding appropriate nutrients and/or soil amendment (Chen et al. 2020). As a salinity measure, the electrical conductivity of soil increases with salt concentration, and the soil is considered saline when electrical conductivity reaches ≥ 4 dS/m (Marschner 1995). The physico-chemical

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properties of salt-affected soils can vary from site to site; soil with high salt concentration is usually referred to as "saline", "saline-sodic", or "salt-alkali". Based on extensive studies that have examined the physiological responses of plants to salt stress, the reduction in crop yield on saline conditions may be explained by ion toxicity, oxidative stress and osmotic stress (Yan et al. 2013).

Plants convert CO₂ and inorganic matters into biomass through photosynthesis and mineral metabolism, wherein ions homeostasis plays an important role in maintaining normal cell physiological functions required for assimilation. Due to the high Na⁺ concentration in saline soil, plant growth would experience an ion imbalance, which in turn leads to a change in nutrients concentration in the plant, compare to the normal conditions. Salt stress could result in an increase of Na⁺/K⁺ ratio; recent studies in rice and sorghum indicated that the difference in Na⁺/K⁺ ratio among genotypes was related to salt tolerance (Rasel et al. 2020, Rastogi et al. 2020). Calcium (Ca) and magnesium (Mg) in soil colloids could be replaced by sodium (Na) under salt stress, leading to a decrease in available Ca²⁺ and Mg²⁺, and hence partially contributing to impaired plant growth. Maintaining ion homeostasis is therefore regarded as a key strategy to adapt to salt stress. Early studies had shown strong indications that Ca²⁺ signals are involved in salt stress responses, i.e., plants exhibit a rapid increase in cytosolic Ca²⁺ concentration within seconds of being exposed to NaCl (Lynch and Läuchli 1988). In practice, applying gypsum (CaSO₄·2H₂O) as a source of Ca²⁺ to replace excess Na⁺ at the cation exchange sites is one of the most extensively used strategies to alleviate salt stress. Previous studies have shown that the application of exogenous Ca²⁺ could enhance the tolerance of wheat seedlings to salt stress (Tian et al. 2015). Besides Ca²⁺, zinc (Zn) might also have ameliorative effects on plants affected by salt stress, as Saeidnejad et al. (2016) has shown that the increased concentration of Na due to salt stress could be alleviated with the addition of Zn.

It has been well known that germination, root development, ions uptake, seedling growth, above-ground biomass and grain yield of wheat could be significantly affected under salt stress. On average, the electrical conductivity of the soil saturation extract (EC_e) of 13 dS/m would cause a 50% reduction in wheat yield (Minhas et al. 2020). The root is believed as the first organ that senses salt stress; it

can pass the stress signal to aboveground parts, which then subsequently induce an integral reaction at the whole-plant level. Robin et al. (2016) has suggested a reduction in root surface area as an important component of saline damage. Normal root growth requires the involvement of essential elements including Ca, Mg, iron (Fe), and Zn and these are affected during salt stress. Thus the reduction in root growth might have an impact on Ca, Mg, Fe, and Zn uptake. Ca, Mg, Fe, and Zn are essential nutrients for human nourishment, and wheat is a major cereal source for providing these essential nutrients worldwide. The associations among Ca, Mg, Fe, and Zn uptake, root traits and aboveground biomass in wheat have not been fully studied and understood yet; it is of great significance, therefore, to explore these important associations.

For this purpose, a pot experiment was conducted with the following objectives to (1) study the effects of salt stress on root development and Ca, Mg, Fe, and Zn uptake in wheat; (2) study the correlations among Na⁺/K⁺ ratio and Ca, Mg, Fe, and Zn uptake; (3) study the associations among Ca, Mg, Fe, and Zn uptake and biomass in saline conditions.

MATERIAL AND METHODS

Plant material. Eight commercially available wheat cultivars were selected and used in the current study. These cultivars include the widely grown cultivars in North China, Aikang 58, Bainong 207, Jimai 22, Liangxing 99, Lunxuan 987, Yannong 999, Zhoumai 22, and Zimai No 1 (purple grain).

Experimental setup. Germination of kernels was initiated in three days in the dark at room temperature (approximately 20 °C); the germinated kernels were then incubated at 4 °C for one week, then three seedlings of each genotype were transferred into a plastic pot (height: 18.0 cm; diameter: 16.0 cm) filled with a 2.5 kg mixture containing 1.5 kg soil and 1.0 kg river sand. Soil and sand mixture was used as a growth medium for both experimental control and saline stress treatment; this soil mixture had a pH 7.3, total N concentration of 0.65 g/kg, NaHCO₃-extractable phosphorus (Olsen-P) concentration of 3.5 mg/kg, and Zn as 35.7 µg/kg. Nutrients supply to plants was provided by irrigating 500 mL nutrients solution into each pot at the time of transplanting, then one week after transplanting and finally two weeks after transplanting. Components of nutrients solution were as following: 0.6 mmol KNO₃, 0.3 mmol

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MgSO₄, 0.3 mmol KH₂PO₄, 0.3 mmol KCl, 0.12 mmol CaCl₂, 1 μmol H₃BO₃, 50 nmol Na₂MoO₄, 0.2 μmol CuSO₄, 20 μmol ZnSO₄, 2 μmol MnSO₄, and 0.1 mmol FeNa-EDTA. Salt stress was applied gradually and stepwise by irrigating 300 mL of a salt solution mixture into each pot; the salt solution mixture of NaCl and NaHCO₃ (1:1) was prepared with a threshold concentration of 25 mmol for each NaCl and NaHCO₃ at transplanting, thereafter gradually increased to 100 mmol at two weeks after transplanting. For the control treatment, 300 mL distilled water was irrigated into each pot accordingly. After harvesting plant samples (20 days post transplanting), the soil mixture's electrical conductivity in control treatment was 0.4 dS/m and 4.5 dS/m in salt stress treatment. The plants were grown in a growth room with light and temperature conditions set to 16 h light at 25 ± 3 °C and 8 h dark at 18 ± 3 °C. Irradiation, which the plant canopy received was 5 W/m², while the photosynthetic photon flux density (PPFD) was 120 μmol/m²/s. Relative humidity during the growth period in the growth room ranged from 50% to 60%.

Measurements of aboveground biomass and root traits. Seedlings were harvested 20 days after transplanting; the soil was carefully washed away from the roots with tap water. Shoot and root were separated using a scissor; shoots were then oven-dried 72 h at 80 °C to obtain aboveground biomass, while root images were obtained using an Epson® Expression 10000XL scanner. The total axis root number was counted from the scanned image. Total axis root length (TARL), total lateral root length (LRL), and total root length (TRL) were determined using the WinRHIZO Root Analysis System (Regent Instruments, Montreal, Canada). Root weight (RW) of oven-dried roots was obtained for each root.

Elemental measurements. Shoot and root samples of the harvested seedlings were oven-dried and ground into a fine powder. For each shoot and root, a 30 mg sample was weighed out and digested with 13 mL nitric acid and 2 mL H₂O₂ using a microwave digestion instrument. Concentrations of Na, K, Ca, Mg, Zn, and Fe in both shoot and root were measured using an inductively coupled plasma mass spectrometer (ICP-MS, Thermo Fisher, Waltham, USA).

Association among different traits of interest. Given that salt stress could lead to an increased Na⁺/K⁺ ratio, Pearson correlation was used to explore the associations among Na⁺/K⁺ ratio and Ca, Mg, Fe, and Zn concentrations in both root and shoot. To further explore associations between ion uptake and biomass

(both root and shoot), twenty traits including twelve traits for elemental concentrations (Na, K, Ca, Mg, Zn, and Fe in both shoot and root), five root traits (ARN, ARL, LRL, TRL, RW), Na⁺/K⁺ ratio in both shoot and root, and aboveground biomass were analysed by Pearson correlation. Pearson correlation coefficient, which could reflect the strength of the correlation between two variables, was calculated based on the formula:

$$r = \frac{Cov(X, Y)}{\sqrt{Var(X)Var(Y)}}$$

wherein: *Cov*(*X*, *Y*) – covariance between *X* and *Y*, while *Var*(*X*) and *Var*(*Y*) were variances of *X* and *Y*, respectively.

Statistical analysis. Data normality was examined by the Kolmogorov-Smirnov test before being subjected to ANOVA. Two factors ANOVA was employed to examine the effects of factors, wherein control and salt stress treatment were considered as two levels of factor "salt stress", while eight cultivars were regarded as levels for factor "cultivar". Duncan's multiple comparisons among different cultivars were applied where the *F*-test for factor "cultivar" was significant (*P* < 0.05). Interaction between salt stress and cultivar was examined using the method proposed by Tukey (1949); multiple comparisons (Duncan) were performed for cultivar at a fixed salt stress level while the interaction was significant. Principal component analysis (PCA) was conducted using Origin software 2018 (Originlab, Northampton, USA) in order to extract valuable information from investigated traits, the principal components (eigenvectors) which determine the directions of the new feature space was a linear combination of the original variables, while eigenvalues determine their magnitude. The same twenty traits as in Pearson analysis, were used in PCA. ANOVA was conducted through SPSS 16.0 statistical software (Chicago, USA).

RESULTS AND DISCUSSION

Aboveground biomass and root traits as affected by salt stress. ANOVA revealed a significant impact of salt stress (*F* = 419.66, *P* < 0.001), cultivar (*F* = 86.43, *P* < 0.001), and interaction between salt stress and cultivar (*F* = 22.37, *P* < 0.001) on aboveground biomass. All wheat cultivars showed a decrease in aboveground biomass in salt treatments compare to control (Figure 1). Genotypic differences in aboveground biomass were observed in both control conditions and salt stress treatment as Aikang 58, Bainong 207, and Zhoumai 22 had more biomass than that of others in control

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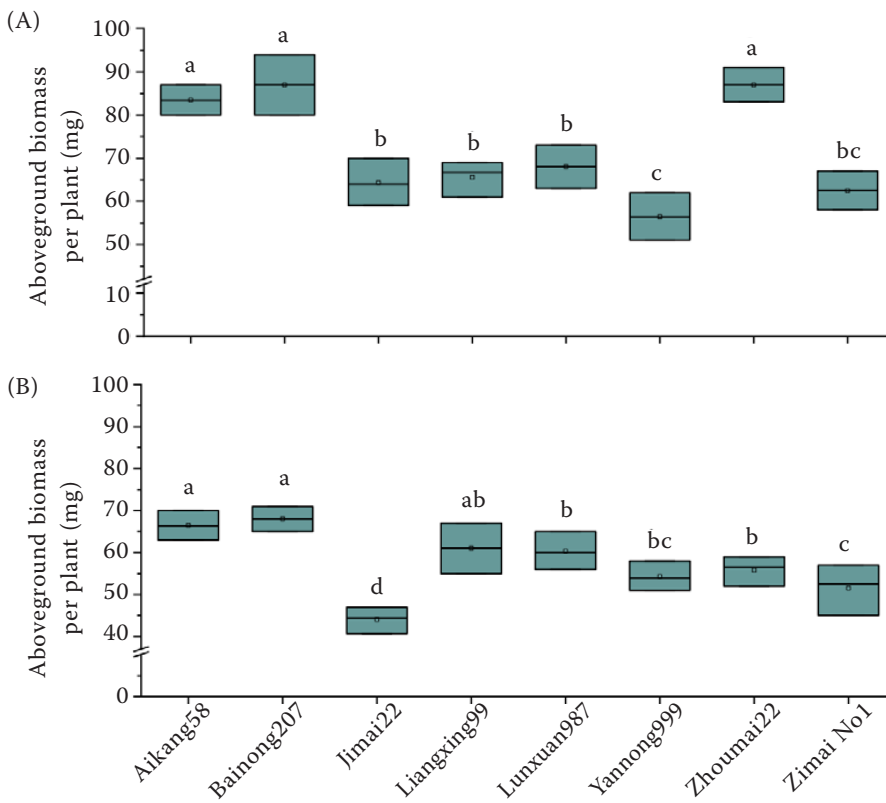


Figure 1. Comparison of aboveground biomass (dry weight) between cultivars in (A) control and (B) salt stress treatment. Different letters above the column indicate a significance at the 0.05 level

conditions (Figure 1A) while Aikang 58 and Bainong 207 exhibited more biomass compared to other cultivars in salt stress treatment (Figure 1B).

For root traits, there were also clear impacts of salt stress ($F = 458.31, P < 0.001$), cultivar ($F = 24.56, P < 0.001$), and interaction between salt stress and cul-

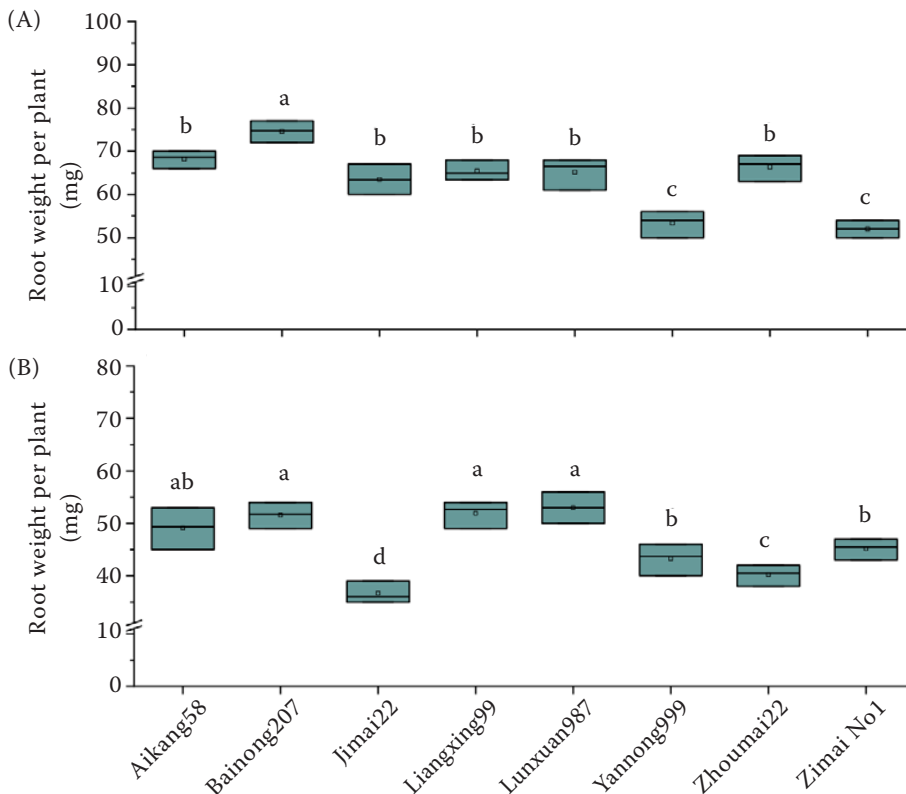


Figure 2. Comparison of root weight (dry weight) between cultivars in (A) control and (B) salt stress treatment. Different letters above the column indicate a significance at the 0.05 level

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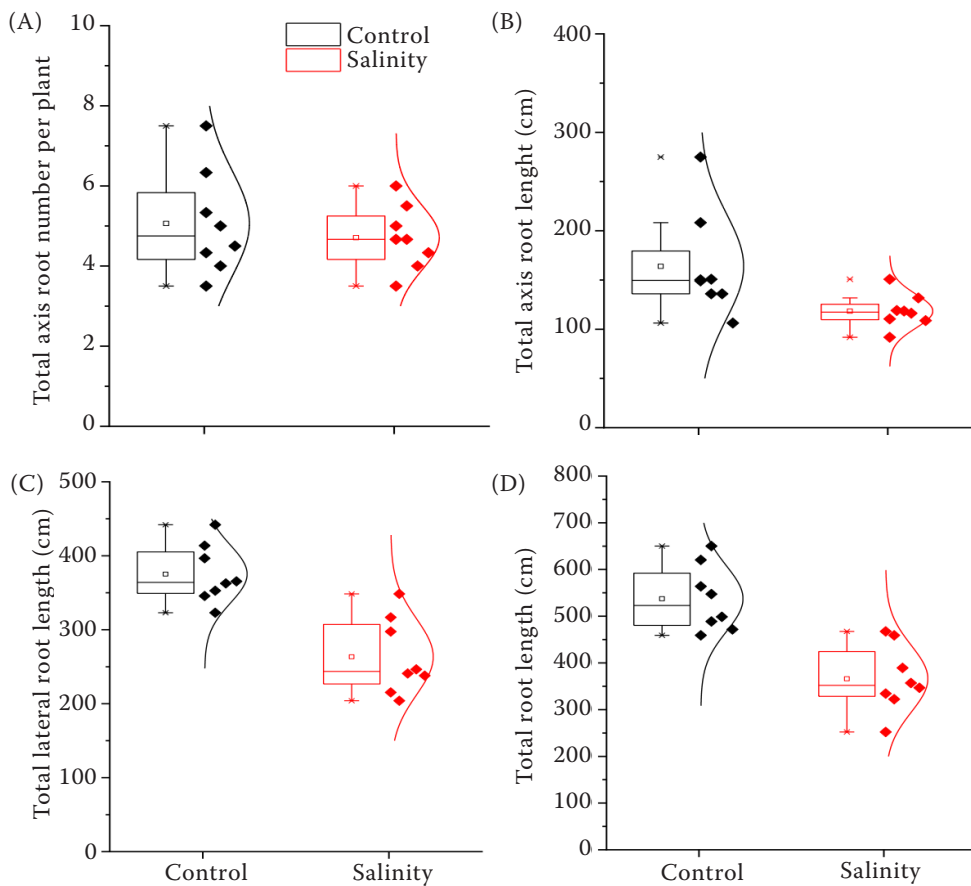


Figure 3. Comparison of (A) axis root number; (B) axis root length; (C) lateral root length and (D) total root length in control and salt stress treatment

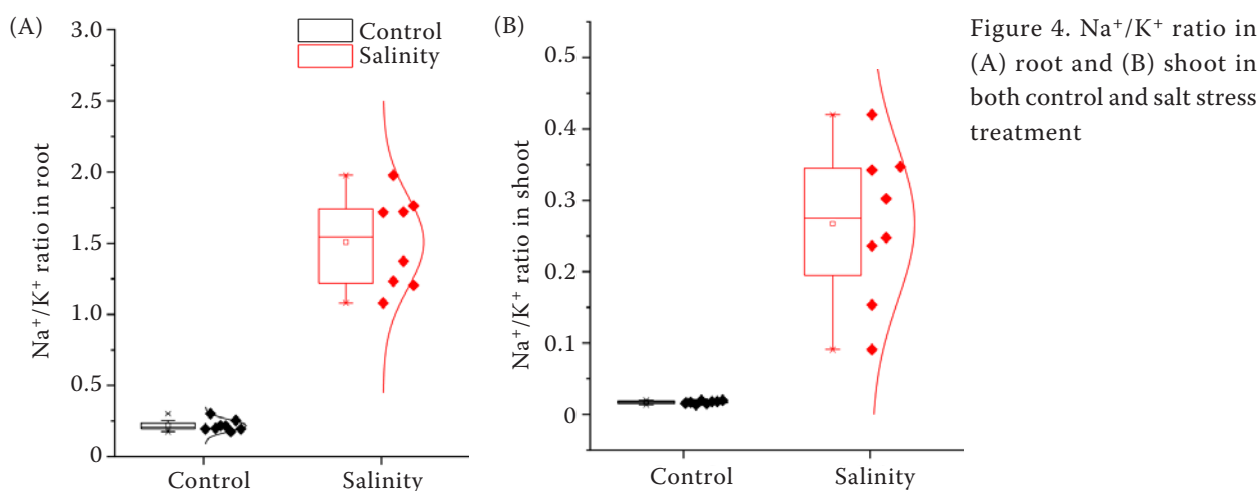
tivar ($F = 11.21, P < 0.001$) on root weight (Figure 2), genotypic differences for root weight were observed in both control and salt stress treatments (Figure 2). The axis root number was not different in both salt stress treatment and control ($F = 1.14, P = 0.29$), while axis root length ($F = 124.22, P < 0.001$), lateral root length ($F = 1.17 \times 10^3, P < 0.001$), and total root length ($F = 116.62, P < 0.001$) were sig-

nificantly affected by salt stress (Figure 3). In the control treatment, axis root number ranged from 3 to 8 with an average of 4.9 while 3–7 with an average of 4.7 for that in salt stress treatment. Axis root length ranged from 108.0–276.7 cm, 93.4–153.8 cm for control and salt stress treatment, respectively. Lateral root length ranged from 324.3–453.8 cm in control while 205.8–360.1 cm in salt stress. Total

Table 1. Root traits of genotypes in both control and salt stress treatment

Genotype	ARN		ARL (cm)		LRL (cm)		TRL (cm)	
	CK	S	CK	S	CK	S	CK	S
Aikang 58	6.3 ^b	6.0 ^a	274.8 ^a	150.7 ^a	345.7 ^{cd}	316.7 ^{ab}	620.5 ^{ab}	467.5 ^a
Bainong 207	4.3 ^{bc}	4.7 ^{abc}	150.2 ^c	110.5 ^{bc}	413.7 ^{ab}	348.5 ^a	563.8 ^{abc}	459.0 ^a
Jimai 22	5.3 ^b	4.7 ^{abc}	150.7 ^c	119.0 ^b	396.7 ^{abc}	215.3 ^c	547.4 ^{bc}	334.3 ^b
Liangxing 99	5.1 ^{bc}	5.0 ^{abc}	149.0 ^c	118.4 ^b	323.0 ^d	204.1 ^c	459.0 ^c	322.4 ^b
Lunxuan 987	3.5 ^c	4.1 ^{bc}	134.0 ^c	91.8 ^c	352.7 ^{cd}	297.5 ^{ab}	488.7 ^c	389.3 ^b
Yannong 999	4.1 ^{bc}	4.3 ^{abc}	138.3 ^c	116.2 ^b	362.6 ^{bcd}	240.8 ^{bc}	498.6 ^c	357.0 ^b
Zhoumai 22	7.5 ^a	5.5 ^{ab}	208.3 ^b	131.8 ^{ab}	442.1 ^a	246.5 ^{bc}	650.2 ^a	252.2 ^c
Zimai No 1	4.5 ^{bc}	3.5 ^c	106.3 ^d	108.8 ^{bc}	365.0 ^{bcd}	238.0 ^{bc}	417.5 ^c	346.8 ^b

Different letters indicate significance at the 0.05 level. ARN – axis root number; ARL – axis root length; LRL – lateral root length; TRL – total root length; CK – control; S – salt stress



root length ranged from 463.9–652.8 cm in control while 257.2–469.1 cm in salt treatment. Multiple comparisons further revealed genotypic differences for ARN, ARL, LRL, and TRL in control and salt stress treatments (Table 1).

A stronger rooting system could probably lead to more aboveground biomass production on normal growth conditions or less yield penalty on drought and nutrient-deficient conditions. Root development requires uptake, translocation, and metabolism of essential nutrients; therefore, the development of root system architecture is a biological process that interacts tightly with ion homeostasis. In this study, the axis root number was not significantly affected, while root length was severely affected by salt stress. This may be due to the fact that root axis number is a strong genetically controlled trait, while the elongation of roots, particularly lateral roots at the

seedling stage, may prone to be affected by environmental factors such as salt stress. As a response to salt stress, therefore, the root adjusts its architecture mainly by tuning root length to adapt to saline stress.

Response of ions uptake to salt stress. Na⁺/K⁺ ratio in root was increased sharply in salt stress treatment as anticipated ($F = 3.35 \times 10^3$, $P < 0.001$, Figure 4), with an average increase of about 6-folds compare to that for control. Consistently, Na⁺/K⁺ ratio in shoot was also increased ($F = 4.25 \times 10^3$, $P < 0.001$), with an average increase of about 10 folds compare to that in control treatment. There was significant impact of salt stress on root Ca concentrations ($F = 47.29$, $P < 0.001$) and shoot Ca concentrations ($F = 315.98$, $P < 0.001$). Like Ca, Mg concentrations in both root ($F = 628.02$, $P < 0.001$) and shoot ($F = 404.3$, $P < 0.001$) and Zn concentrations in both root ($F = 65.76$, $P < 0.001$) and shoot ($F = 129.37$,

Table 2. The correlation coefficient among Na⁺/K⁺ ratio and Ca, Mg, Zn, Fe concentrations of the root in control and salt stress treatment

Trait	Treatment	Trait			
		CaCR	MgCR	FeCR	ZnCR
MgCR	CK	0.4209			
	S	-0.1459			
FeCR	CK	0.7746*	-0.0366		
	S	-0.0456	-0.3143		
ZnCR	CK	0.1727	0.6105	0.2542	
	S	-0.0899	0.5611	-0.0739	
NaKR	CK	0.3304	0.1065	0.2164	0.0854
	S	-0.0801	-0.3414	0.6081	0.1585

*indicates that correlation is significant at the 0.05 level (2-tailed). No significant correlation was detected in salt stress treatment. MgCR – magnesium concentration in root; FeCR – iron concentration in root; ZnCR – zinc concentration in root; NaKR – Na⁺/K⁺ ratio in root; CaCR – calcium concentration in root; CK – control; S – salt stress

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Table 3. Correlations among Na^+/K^+ ratio and Ca, Mg, Zn, Fe concentrations of the shoot in control and salt stress treatment

Trait	Treatment	Trait			
		CaCS	MgCS	FeCS	ZnCS
MgCS	CK	0.679			
	S	0.172			
FeCS	CK	0.8962**	0.6524		
	S	0.6817	0.026		
ZnCS	CK	0.7524*	0.9617**	0.6908	
	S	0.8583**	0.4588	0.4348	
NaKS	CK	0.0812	0.1634	-0.1369	0.1791
	S	0.0638	-0.7001	-0.2848	-0.1136

**indicates that correlation is significant at the 0.01 level (2-tailed); *indicates that correlation is significant at the 0.05 level (2-tailed). MgCR – magnesium concentration in root; FeCR – iron concentration in root; ZnCR – zinc concentration in root; NaKR – Na^+/K^+ ratio in root; CaCR – calcium concentration in root; CK – control; S – salt stress

$P < 0.001$) were also significantly affected by salt stress treatment. For Fe concentrations, no significant difference was observed in root ($F = 0.95$, $P = 0.33$) but significant difference was detected in shoot ($F = 379.31$, $P < 0.01$).

In order to make a more clear relationship between Na^+/K^+ ratio and ion uptake, Pearson correlations among Na^+/K^+ ratio and Ca, Mg, Zn, Fe concentrations in root were conducted for control and salt stress treatment (Table 2). Ca concentration in root was significantly correlated with Fe concentration in root in the control treatment ($P < 0.05$), while no correlation was detected among Na^+/K^+ ratio and Ca, Mg, Zn, Fe concentrations in salt stress treatment. For the shoot in the control treatment, Pearson correlations revealed that Ca concentration was significantly correlated with Fe and Zn concentrations, and Mg concentration was significantly correlated with Zn (Table 3). In salt stress treatment, Ca concentration in the shoot was significantly correlated with Zn concentration (Table 3).

Adjustment of root length in salt stress probably offers partial feedback impact on ion uptake, consistently with this hypothesis, Ca, Mg, Zn concentrations in both root and shoot, and Fe concentration in the shoot were significantly changed by salt stress in the current study. These results clearly indicated that plants take advantage of the coordinate change in ion homeostasis and root architecture as a strategy to cope with increased Na^+/K^+ ratio in both shoot and root due to high pH and high salt concentrations. On the other hand, no correlation was detected between Na^+/K^+ ratio and Ca, Mg, Fe, and Zn concentrations

in both root and shoot, either in control or salt stress treatment, suggesting the variations of Ca, Mg, Fe, and Zn concentrations among genotypes could not be explained by variation in Na^+/K^+ ratio.

Association between ions uptake and biomass accumulation. To explore associations among ion uptake and biomass, PCA was performed using twenty traits, including elemental concentrations and root traits. In the control treatment, the PCA for these twenty traits in the 8 genotypes explained 64.74% of the variance in the first two components (Figures 5 and 6). The first component (PC1) represented 37.97% of the variability and accounted primarily for elemental concentrations in the root. The second component (PC2) represented 26.77% of the variability and accounted primarily for root length and biomass (root weight and aboveground biomass). In salt stress treatment, the first two components accounted for 56.12% of the variance (Figures 5 and 6). The first component (PC1) represented 28.97% of the variability and accounted primarily for elemental concentrations in both shoot and root, while the second component (PC2) represented 27.16% of the variability and accounted primarily for concentrations of Na^+ and K^+ , and Na^+/K^+ in both shoot and root.

To explore associations between ion uptake and biomass (both root and shoot), twenty traits used for PCA were further analysed by Pearson correlation. The associations among traits were obviously altered by salt stress (Figure 7). In control treatment, Na^+/K^+ ratio in root correlated positively with RW ($r = 0.7537$, $P < 0.05$) and ABG ($r = 0.7728$, $P < 0.05$), ABG correlated positively with TRL ($r = 0.8042$,

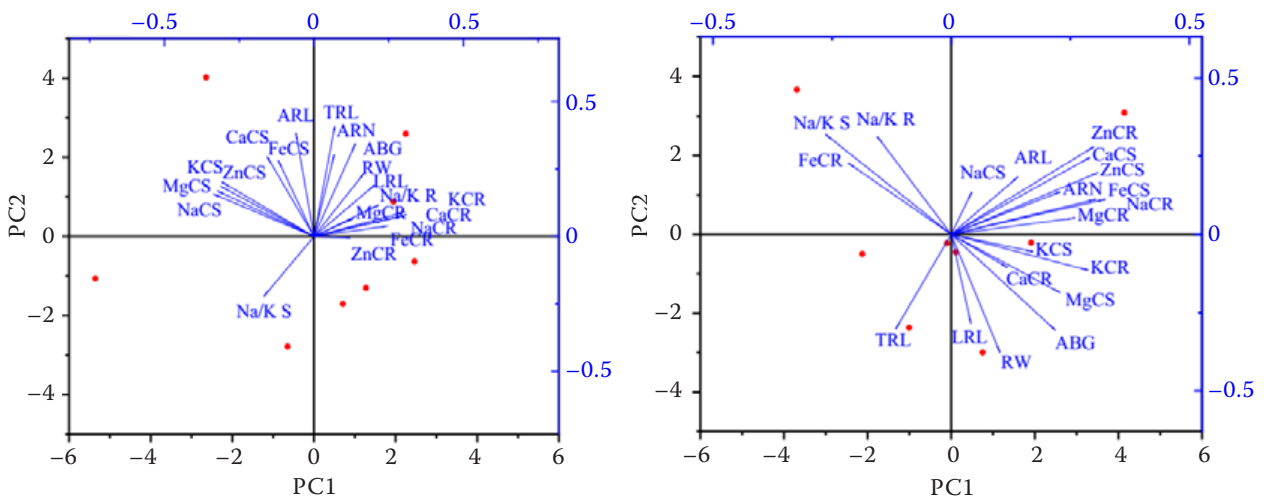


Figure 5. Principal component analysis for twenty traits of eight wheat genotypes in the control (left) and salt stress treatment (right). ABG – aboveground biomass; ARN – axis root number; ARL – axis root length; LRL – lateral root length; TRL – total root length; RW – root weight; CaCR – calcium concentration in root; FeCR – iron concentration in root; KCR – potassium concentration in root; MgCR – magnesium concentration in root; NaCR – sodium concentration in root; ZnCR – zinc concentration in root; Na/K R – Na⁺/K⁺ ratio in root; CaCS – calcium concentration in shoot; FeCS – iron concentration in shoot; KCS – potassium concentration in shoot; MgCS – magnesium concentration in shoot; NaCS – sodium concentration in shoot; ZnCS – zinc concentration in shoot; Na/K S – Na⁺/K⁺ ratio in shoot

$P < 0.05$) and RW ($r = 0.8478, P < 0.05$). In salt stress treatment, Na⁺/K⁺ ratio in shoot correlated negatively with RW ($r = -0.7720, P < 0.05$) and with ABG ($r = -0.7940, P < 0.05$); though not significant, Na⁺/K⁺ ratio in root correlated negatively with RW ($r = -0.6710, P = 0.07$) and ABG ($r = -0.6180, P = 0.10$). ABG correlated positively with LRL ($r = 0.7530, P < 0.05$) and RW ($r = 0.8210, P < 0.05$).

Leitão et al. (2019) have shown that nuclear Ca²⁺ signals are correlated with primary root development in *Arabidopsis*, highlighting the importance of Ca²⁺ in the formation of the root system architecture. Though not significant, positive correlations were observed for root Ca concentration vs. root weight and shoot Ca concentration vs. aboveground biomass in both control and salt stress treatment in the

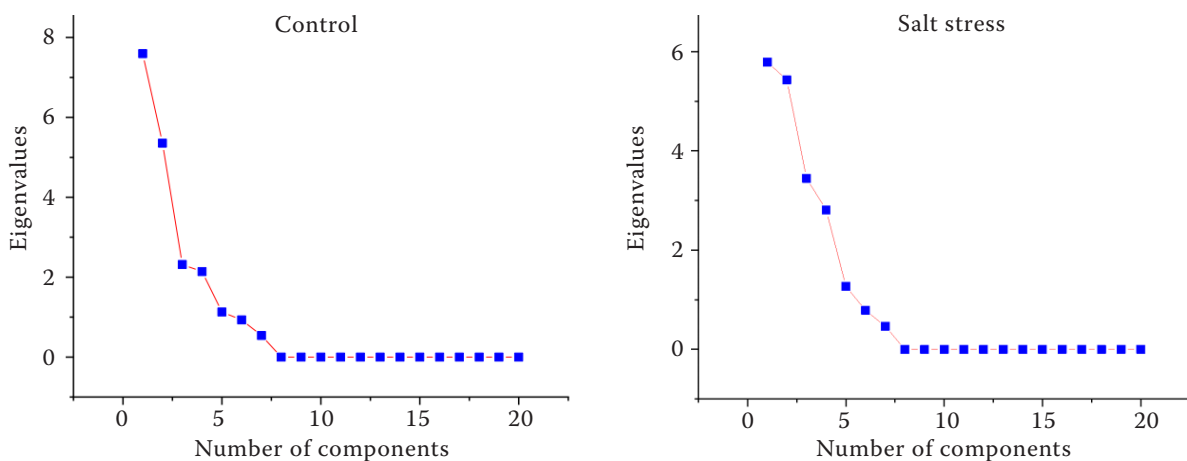


Figure 6. Eigenvalues of the principal components in both control (left) and salt stress treatment (right), wherein Eigenvalues determine the principle components' magnitude. The first two components of the PCA analysis based on twenty traits explained 64.74% of the variance for eight wheat genotypes in the control treatment. While the first two components of the PCA analysis based on twenty traits explained 56.12% of the variance for 8 wheat genotypes in the salt stress treatment

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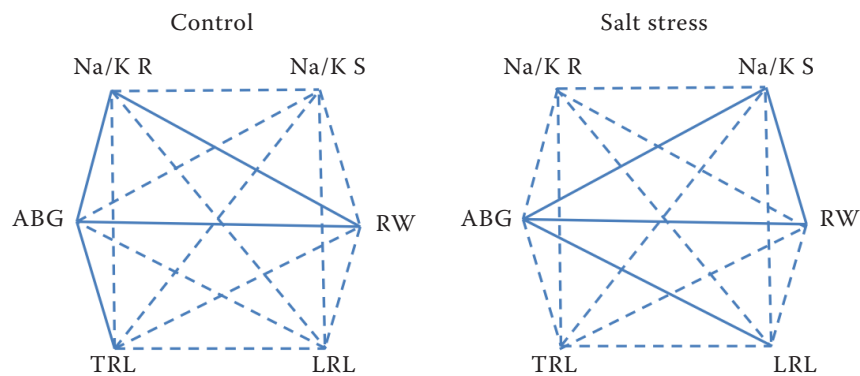


Figure 7. Correlations among Na^+/K^+ ratio in the root (R), Na^+/K^+ ratio in the shoot (S), aboveground biomass (ABG), root weight (RW), total root length (TRL), lateral root length (LRL) in control (left) and salt stress (right). The bold line indicates a significant correlation, while the dashed line non-significant

current study, suggesting Ca^{2+} might have played a positive role in regulating root architecture and an efficient translocation of Ca^{2+} from root to shoot would lead to a beneficial effect on aboveground biomass accumulation.

The content of Ca^{2+} ion in most non-saline soils is sufficient to maintain normal plant growth, while symptoms of Ca deficiency could occur in saline soil due to the decrease in the content of available Ca^{2+} by roots absorption. Under salt stress, Ca^{2+} content may be one of the important factors limiting crop growth; hence, management practices that replace Na^+ from cation exchange sites with Ca^{2+} can ameliorate high Na^+ and its adverse effects (Bronick and Lal 2005). Adding an appropriate amount of Ca^{2+} has been shown to be a beneficial approach for alleviating salt stress on plant growth caused by Na or sulfate (Tian et al. 2015, Reich et al. 2018). However, contrary results of Severino et al. (2014) suggest that Ca does not alleviate the toxic effects of Na on the emergence and initial growth of castor, cotton, and safflower. Joshi et al. (2012) has observed beneficial effects of supplemental Ca^{2+} for castor plants in soil with 4.1 dS/m when the $\text{Ca}^{2+}:\text{Na}^+$ was raised to 0.25:1, but further increments of Ca^{2+} caused reductions in plant growth. Ameliorative effects of adding Ca^{2+} to deal with salt stress require a balance between the antagonism with Na^+ and an improvement in the plant's nutritional status (Severino et al. 2014).

Mg^{2+} plays a key role in photosynthesis: such as partitioning of carbohydrates and dry matter production between roots and shoots as suggested by Cakmak and Kirkby (2008); higher Mg levels enabled an increase in net photosynthetic rate (Bhuiyan et al. 2015). However, the results of Severino et al. (2014) do not support that Mg^{2+} could alleviate the toxic

effects of Na; they suggested ameliorative effects of Mg^{2+} requires a balance of the effects of added Mg functioning as nutrition or as a kind of salt stress. In the current study, significant differences were detected in Mg^{2+} concentrations for both root and shoot between control plants and salt stress-treated plants, Mg^{2+} concentration in the shoot of control showed a weak negative correlation, while that in salt stress treatment showed a positive correlation with root weight and aboveground biomass. These results support the hypothesis that uptake and translocation of Mg^{2+} could play a positive role in alleviating the toxic effects of Na.

Poaceae plants, including wheat, deal with Fe deficiency by increasing the secretion of phytosteroids to target the reduced available Fe concentration in soil (Römheld and Marschner 1986, Grillet and Schmidt 2019), possibly by transforming insoluble Fe-containing compounds into soluble Fe. However, a high Fe concentration was present in the nutrients solution used in the current study, and thus the plants should have not been subjected to Fe deficiency. There was no difference for root Fe concentration, but a decreased shoot Fe concentration was detected between control and salt stress treatment, suggesting that Fe translocation from root to shoot was down-regulated by salt stress treatment.

A previous study by Saeidnejad et al. (2016) suggested adding Zn can alleviate the increased Na concentration due to salt stress. For Zn biofortification in practical crop breeding, one concern is to what extent salt stress would affect Zn uptake. Zn deficiency in the crop is prone to occur, particularly in alkaline soils and sandy soils (Cakmak 2002, Alloway 2009). Here in the current study significant difference was observed between control and salt

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stress treatment for Zn concentration in both root and shoot, while genotypic differences among tested cultivars in both control and salt stress treatment were also observable. Linking to the work which detected sizable genotypic difference of Zn uptake in 112 wheat genotypes (Zhao et al. 2020), breeding new cultivars with higher Zn concentration under salt stress is of promise.

In conclusion, increased Na^+/K^+ ratio in the shoot has an apparent impact on biomass accumulation of root and aboveground parts under salt stress. A strategy towards manipulating the ion balance combined with selecting suitable genotypes to improve ion uptake promises to alleviate the effects of salt stress imposed on biomass. The genotypic difference of root traits and Fe and Zn uptake in salt stress response offers a potential strategy towards breeding new wheat cultivar with better suitability and nutritional value on saline soils.

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