Effects of salinity stress on seedling biomass, physiochemical properties, and grain yield in different breeding wheat genotypes

Alireza Pour-Aboughadareh1 · Mohammad Reza Mehrvar1 · Sara Sanjani1 · Ashkboos Amini1 · Hamidreza Nikkhah-Chamanabad1 · Ameneh Asadi1

Received: 7 October 2020 / Revised: 1 May 2021 / Accepted: 28 May 2021 / Published online: 6 June 2021
© Franciszek Górski Institute of Plant Physiology, Polish Academy of Sciences, Kraków 2021

Abstract
The salinity tolerance of 17 breeding wheat genotypes along with three local varieties was evaluated under control and salinity stress (160 mM NaCl) conditions. At the seedling stage, several growth and physiological traits were measured. Moreover, the investigated genotypes were assessed in terms of grain yield across four saline regions during the 2018–2019 cropping seasons. Salinity treatment significantly decreased in the root and shoot dry weights (RDW and SDW), photosynthesis rate (PN), stomatal conductance (GS), transpiration rate (TE), shoot K+ content (SK), root K+/Na+ (RKN), root-to-shoot Na+ translocation (RTSN), and root-to-shoot K+ translocation (RTSK), but resulted in increased root Na+ content (RN), root K+ content (RK), and shoot Na+ content (SN). The results of additive main effects and multiplicative interaction analysis (AMMI) also indicated significant differences among test environments (E), genotypes (G), and their interaction effects (GEI). The PCA-based biplot revealed that grain yield strongly correlated with RKN and RK. Furthermore, the correlation among PN, GS, and TE traits was strong and positive and had a positive correlation with RWC, MSI, RDW, and SPAD index. Considering our results, RK and RKN were identified as useful physiological tools to screen salt tolerance at the early-growth stage. According to the ranking patterns obtained by the average sum of ranks method (ASR) and grain yield, we observed that genotype number G5 had considerable physiological potential at the early-growth stage and also responded well to soil salinity at the farm; thus, this genotype can be promoted for commercial production.

Keywords Salinity stress · Bread wheat · Photosynthesis properties · Root-to-shoot Na+ translocation · Ranking pattern

Introduction
Salinity is one of the most important soil edaphic stresses that negatively affect worldwide wheat productivity and furthermore contributes to food insecurity. Unfortunately, increased soil salinization in many regions worldwide caused by climate change and various human activities is progressively reducing agricultural productivity despite increasing food demand (Ahmadi et al. 2018; Isayenkov and Maathuis 2019). Under salinity conditions, Na+ is the main toxic ion that induces both osmotic and ionic toxicity (Hagemann and Erdmann 1997). Thus, maintaining low concentrations of Na+ is crucial for plant survival during salinity stress (Anil et al. 2007). Based on Munns’s et al. theory (1995), the response of plants to high salt levels is divided into two main phases, namely ion-independent (osmotic) and ion-dependent (ionic toxicity) phases. The osmotic phase initiates immediately after the accumulation of salts around the roots. The main consequence of this event is difficulty in extracting water from soil to roots, which ultimately reduces the rate of shoot growth. This situation reduces the mitigation of ion flux from root to shoot and closes the stomata (Hasegawa et al. 2000). The ionic toxicity phase, which occurs over days and even months, is related to the accumulation of cytotoxic ions (especially Na+) and is marked by reduction in plant metabolic processes, increased premature senescence, and finally cell death (Roy et al. 2014). Salinity stress commonly induces many metabolic changes in plants, such as reduction in photosynthetic pigments and carbon...
assimilation, decreased photosynthetic efficiency of photosystem II, ion toxicity, and induction of oxidative stress due to increased levels of reactive oxygen species (ROS) (Husain et al. 2003; Chen et al. 2001; Acosta-Motos et al. 2017). Plant tolerance to high concentrations of salts is a complex quantitative trait and all research thus far has focused on characterizing heritable tolerant variations and dissecting trait genetics (Liu et al. 2020). Therefore, many plant species have several important mechanisms that protect them to overcome negative effect of salinity conditions. Under salinity conditions, plants regulate stomatal conductance to decrease water loss through transpiration. In addition, partial stomatal closure may limit the photosynthetic rate, which results in enhancing ROS levels and maintaining or decreasing plant growth and productivity (Dadshani et al. 2019).

Photosynthetic activity is a key physiochemical mechanism for identifying a salt-tolerant plant. Previously, Kawasaki et al. (2001) and Geilfus et al. (2015) showed the considerable genotypic variability of photosynthetic activity and its related traits in several rice and fava bean genotypes, respectively. Panwar et al. (2016) also noted that the relative chlorophyll content can be used as a useful physiological index to determine the tolerance level in wheat. Inter cellular ion regulation is an important physiological mechanism for salinity tolerance. This mechanism includes excluding Na+ from root and shoot or reducing the uptake of Na+ into the root, minimizing salt concentration in the cytosol, and partitioning of Na+ into various tissues or cells (Arzani and Ashraf 2016). In recent years, research was mainly focused on the maintenance of K+/Na+ ratio as the useful physiological mechanism for salinity tolerance (Dadshahi et al. 2019). Ahmadi et al. (2018) evaluated a core collection of wheat germplasm under a severe salinity treatment and reported that the ability of wheat accessions to retain K+ was critical for their salt tolerance.

Bread wheat (Triticum aestivum L.) is an important cereal crop grown throughout most regions in the world. Its yield is affected by various environmental stresses, particularly drought and salinity (Maghsoudi et al. 2016). This cereal with a global production ~760 million tonnes (Food and Agriculture Organization 2020) supports well 20% of the daily calories requirement for 4.5 billion people worldwide (Singh et al. 2020). The global production volume of wheat is 763 million tonnes (Food and Agriculture Organization 2020) and supports 20% of the However, this crop suffers from considerable yield losses due to different environmental stresses. Although wheat is moderately tolerant to salinity stress, near to 40% grain yield losses have been reported in saline croplands (Qadir et al. 2014). In wheat, higher salt concentrations in soil or irrigation water dramatically affect different plant growth and development phases from germination to yield performance (Hasanuzzaman et al. 2017). Seedling stage is one of the most important phases for wheat growth and development. In this stage, seedlings are more sensitive to saline conditions, thus high concentration of salts may cause the death of them. Root and shoot biomasses, relative water content, leaf area, photosynthetic pigment concentrations, among other parameters, of both sensitive and tolerant genotypes decline under salt stress in wheat seedlings (Arfan et al. 2007). Several studies revealed that roots and shoots biomasses of wheat seedlings were negatively affected by salinity treatment (Athar et al. 2007; Afzal et al. 2008; Ghiyasi et al. 2008; Akbarimoghaddam et al. 2011). Reduction of photosynthetic processes and their related parameters under salinity conditions were also reported by Guo et al. (2015), Zou et al. (2016), and Ahmadi et al. (2020).

Genetic diversity is a basic component for the efficient breeding of salinity tolerance in wheat. Improvement of wheat varieties with high adaptation to saline environments through the use of local varieties or wild relatives in breeding programs is an accepted strategy to overcome the genetic bottleneck imposed by modern breeding programs (Nevo and Chen 2010). Bread wheat is the main crop cultivated in Iran as a staple food. In Iran, approximately 6.5 Mha of croplands are directly affected by salinity stress, which damages crop ecosystems [Agricultural Planning Economic and Rural Development Research Institute (APERDRI), 2020]. Based on the Stanford Iran 2040 Project report, many parts of the country are located in arid areas with >70% annual aridity index. Thus, wide areas of this country will encounter serious problems due to soil salinization in the near future. Therefore, any breeding program related to the development of new salt-tolerant varieties of wheat and increasing the area under cultivation of these varieties can help agricultural productivity. Nearly 3 decades of effort towards the improvement of wheat salinity tolerance have been invested in Iran, and thus far several commercial cultivars such as Narin, Bam, Arg, Sistan, and Barzegar have been introduced to farmers for use in saline regions. Here, we tested a set of new advanced wheat lines to determine if genetic variability exists among breeding genotypes for salinity tolerance in terms of physiological traits and grain yield and if a logical relationship among measured physiological traits exists at the seedling stage and grain yield at the end-of-life period of a wheat plant. Hence, this study was planned to test the 17 new breeding genotypes obtained from national breeding program crosses among Iranian local and foreign cultivars in terms of physiological traits and to identify superior genotypes that can be utilized for peer screening and to breed salt-tolerant varieties with acceptable stability and high performance.
Materials and methods

Plant materials

A set of 17 breeding lines from different crosses among Iranian local cultivars along with three control varieties (cv. Narin, Sistan, and Barzegar as the tolerant control) were tested under control and severe salinity stress conditions. More details on the pedigrees are found in Supplementary Table 1.

Experiment setup at the seedling stage

A greenhouse experiment was carried out in the 2019–2020 cropping season at the Cereal Research Department, Seed and Plant Improvement Institute (SPII), Karaj, Iran. All genotypes were grown in a hydroponic system at optimal growing conditions. The photoperiod and temperature conditions were 16/8 h (light/dark) and 25/20 °C (day/night), respectively. Plant materials were sowed into tanks filled with 20 L of Hoagland nutrient solution consisting of macro- and microelements such as ammonium phosphate [(NH₄)₂HPO₄: 115 g L⁻¹], calcium nitrate [Ca(NO₃)₂·4H₂O: 236 g L⁻¹], potassium nitrate (KNO₃: 107 g L⁻¹), magnesium sulfate (MgSO₄·7H₂O: 246 g L⁻¹), boric acid (H₃BO₃: 0.38 g L⁻¹), zinc sulfate (ZnSO₄·7H₂O: 0.22 g L⁻¹), Fe-EDTA (5 g L⁻¹), manganese sulfate (MnSO₄·4H₂O: 1.02 g L⁻¹), ammonium heptamolybdate ((NH₄)₆Mo₇O₄·4H₂O: 0.02 g L⁻¹), and copper sulfate (CuSO₄·5H₂O: 0.08 g L⁻¹) (Hoagland and Arnon 1950). Two separated experiments were carried out based on a randomized block design (RCBD) with three replications. More details on the pedigrees are found in Supplementary Table 1.

Field experiment trials

The multi-location trials were performed at four saline regions of Iran (Yazd, Birjand, Esfahan, and Kerman) during the 2018–2019 cropping season. In all sites, the salinity level of soil and irrigation water was tested during the experimental period from seed sowing to harvesting. The mean salinity of soil and irrigation water was 12 and 10 dS m⁻¹, respectively. Fertilizer treatments of 100 kg P₂O₅ ha⁻¹ and 32 kg N ha⁻¹ were applied to the soil at the planting stage in

$$\text{RWC} \% = \frac{[\text{fresh weight} - \text{dry weight}]}{[\text{turgid weight} - \text{dry weight}]} \times 100.$$
each experiment. At each research station, genotypes were evaluated in a randomized complete block design (RCBD) with four replicates. Each experimental plot included eight 2.5-m-long rows with intra-row spacing of 0.15 m. Sowing was performed by an experimental plot planter (Wintersteiger, Austria) with a plant density of 450 seeds per m². The trials were kept weed-free by applying Puma-super (Fenoxaprop-p-ethyl) and Granstar (Tribenuron methyl DF-75%) as foliar contact and pre-emergence herbicides. At harvest time, plots were harvested using experimental combine (Wintersteiger, Austria). Finally, grain yields were measured and data were converted to tonnes per hectare.

Statistical data analysis

In the greenhouse experiment, a combined analysis of variance (ANOVA) was computed to test the stress treatments, genotypes, and their interaction. The relative change due to salinity stress (RC) was computed for each trait by the following equation:

$$RC\% = \left(\frac{MX_{\text{control}} - MX_{\text{stress}}}{MX_{\text{control}}}\right) \times 100,$$

where $MX_{\text{control}}$ and $MX_{\text{stress}}$ are the mean values of a trait in a given genotype under control and salinity conditions, respectively.

In the field experiment trials, the additive main effects and multiplicative interaction (AMMI) analysis was computed based on grain yield data as proposed by Zobel et al. (1988) using GenStat software (GENSTAT 2008). Differences among the environment and genotype means were tested by Duncan’s multiple range test. Principal component analysis (PCA) using the measurements recorded at the seedling stage and grain yield was computed using XLSTAT software. The ranking method was employed to select the most salt-tolerant genotype(s) through measured traits at the seedling stage and grain yield according to the approach described by Ketata et al. (1989). Accordingly, the best value of each trait received the minimum rank and thus the genotypes with the lowest ASR values were recognized as the salt-tolerant genotypes. Additionally, relationships among the measured traits and grain yield were tested by Pearson’s correlation.

Results

Root and shoot biomasses, leaf RWC and MSI

Under both conditions, the tested bread wheat genotypes significantly differed with respect to root and shoot biomasses (RDW and SDW), RWC, and MSI traits. Salinity stress also significantly affected these traits. However, the interaction effect between genotypes and salinity treatments was not significant for all of these traits (Table 1). Under salinity stress, the mean of RDW, SDW, RWC, and MSI for the 20 tested genotypes decreased by 24.44%, 49.98%, 3.38%, and 3.79%, respectively, compared with their respective values

| Table 1 | Analysis of variance of the measured traits in 20 bread wheat genotypes under control and salinity stress conditions |
| Traits | Salt treatment (S; df = 2) | Replication/S (df = 4) | Genotype (G; df = 19) | G × S (df = 19) | Error (df = 76) |
|--------|-----------------------------|-----------------------|----------------------|-----------------|----------------|
| Relative chlorophyll content (SPAD) | 8.64** | 9.51 | 19.51** | 2.08ns | 5.38 |
| Relative water content (RWC) | 289.6ns | 99.96 | 36.12** | 6.09** | 9.37 |
| Root dry weight (RDW) | 0.037** | 0.001 | 0.002ns | 0.003ns | 0.003 |
| Shoot dry weight (SDW) | 11.44** | 0.12 | 0.11*** | 0.013ns | 0.03 |
| Photosynthetic rate ($PN_0$) | 5521.63ns | 1461.05 | 120.65* | 0.013ns | 54.5ns |
| Stomatal conductance ($G_s$) | 0.001*** | 0.004 | 0.003* | 0.0001ns | 0.0001 |
| Transpiration rate ($TE$) | 1.25ns | 26.54 | 1.75** | 0.72ns | 0.678 |
| Membrane stability index (MSI) | 380.15* | 114.71 | 64.14** | 79.63ns | 78.85 |
| Root Na+ content (RN) | 21,385.92*** | 78.24** | 73.83ns | 80.61 |
| Root K+ content (RK) | 21.03* | 8.44 | 4.21ns | 3.82ns | 3.4 |
| Shoot Na+ content (SN) | 196.18*** | 24.64** | 17.69** | 7.43 |
| Shoot K+ content (SK) | 24.96*** | 5.09 | 1.28ns | 1.59 |
| Root K+/Na+ ratio (RKN) | 21.03* | 78.24** | 73.83ns | 80.61 |
| Shoot K+/Na+ ratio (SKN) | 5.04*** | 5.17* | 4.45* | 2.42 |
| Root-to-shoot Na+ translocation (RTSN) | 543.11*** | 6.09 | 5.17* | 2.42 |
| Root-to-shoot K+ translocation (RTSK) | 12.37** | 0.38 | 3.45* | 1.98ns | 2.11 |

ns not significant
*p < 0.05; ** p < 0.01; *** p < 0.001
in control conditions. Under control conditions, RDW varied between 0.08 and 0.21 g plant\(^{-1}\) with a mean of 0.14 g plant\(^{-1}\), and genotypes G7, G10, and G11 had the highest values (Table 2). Under salinity conditions, RDW varied between 0.08 and 0.15 g plant\(^{-1}\) with a mean of 0.11 g plant\(^{-1}\), and the control variety G2 followed by G14, G15, and G17 had the highest values. Most of the remaining genotypes had the RDW near the mean value. Under control conditions, SDW varied between 1.02 and 1.83 g plant\(^{-1}\) with an average of 1.24 g plant\(^{-1}\), and genotypes G3, G5, and G20 had the highest amounts. Under salinity conditions, SDW ranged from 0.51 to 0.91 g plant\(^{-1}\) with an average of 0.62 g plant\(^{-1}\). The genotypes G3, G17, and G20 showed the highest SDW, while G7, G8 and G9 produced the lowest shoot biomass. RWC varied between 88.36 and 95.61% in control conditions and from 84.65 to 95.10% in the salinity condition. The highest values for this trait in the control/salinity conditions were recorded for genotypes G10/G15, G15/G16, and G18/G17. Unlike other traits, MSI had a low variability in both the control and salinity conditions, ranging from 89.05 to 97.72% in the control and 82.99 to 96.29% in the salinity condition. Genotypes G8 and G10, along with the control variety G3, showed the highest MSI in the control and G17, G18, and G20 in the salinity condition (Table 2).

### Chlorophyll content, \(P_N\), \(G_S\) and \(T_E\)

ANOVA indicated that salinity stress significantly affected \(P_N\) and \(G_S\) among genotypes (Table 1). However, significant differences for relative chlorophyll content (SPAD index), \(P_N\), \(G_S\), and \(T_E\) were observed among the tested genotypes. Salinity stress caused a 1.62% reduction in SPAD index compared to the control (range 29.80–37.13, average 33.17 in the control, range 29.93–36.60 with average 32.63 in the stress condition) (Table 2). Under control conditions, genotypes G16 and G17 and the control variety G1 had the

| Genotype code | RDW | SDW | SPAD | \(P_N\) | \(G_S\) | \(T_E\) | MSI | RWC |
|---------------|-----|-----|------|--------|-------|-------|-----|-----|
|               | C   | S   | C    | C      | S     | S     | S   | S   |
| G1            | 0.16| 0.11| 1.18 | 0.59   | 36.00 | 33.87 | 21.27| 0.023|
| G2            | 0.13| 0.15| 1.14 | 0.57   | 33.83 | 32.83 | 21.33| 0.017|
| G3            | 0.16| 0.11| 1.83 | 0.91   | 32.87 | 32.27 | 36.63| 0.030|
| G4            | 0.15| 0.11| 1.20 | 0.60   | 33.07 | 32.87 | 38.97| 0.026|
| G5            | 0.17| 0.09| 1.33 | 0.67   | 30.87 | 32.13 | 47.57| 0.016|
| G6            | 0.13| 0.09| 1.14 | 0.57   | 33.97 | 32.30 | 40.63| 0.020|
| G7            | 0.20| 0.10| 1.02 | 0.51   | 30.77 | 29.93 | 40.73| 0.009|
| G8            | 0.13| 0.08| 1.04 | 0.52   | 32.90 | 31.50 | 53.37| 0.023|
| G9            | 0.13| 0.10| 1.06 | 0.53   | 29.80 | 31.40 | 35.87| 0.015|
| G10           | 0.19| 0.12| 1.29 | 0.64   | 31.60 | 31.40 | 48.23| 0.021|
| G11           | 0.21| 0.09| 1.24 | 0.62   | 31.33 | 31.63 | 43.00| 0.040|
| G12           | 0.13| 0.10| 1.25 | 0.63   | 31.67 | 29.30 | 38.87| 0.023|
| G13           | 0.13| 0.10| 1.27 | 0.64   | 33.07 | 34.03 | 47.40| 0.020|
| G14           | 0.15| 0.14| 1.07 | 0.53   | 35.30 | 32.70 | 42.33| 0.030|
| G15           | 0.10| 0.14| 1.26 | 0.63   | 35.37 | 33.67 | 39.30| 0.019|
| G16           | 0.12| 0.09| 1.09 | 0.55   | 37.13 | 36.60 | 43.10| 0.037|
| G17           | 0.09| 0.14| 1.29 | 0.64   | 37.13 | 35.47 | 46.57| 0.024|
| G18           | 0.14| 0.11| 1.25 | 0.63   | 32.87 | 33.03 | 40.53| 0.024|
| G19           | 0.15| 0.09| 1.26 | 0.63   | 32.23 | 31.07 | 49.67| 0.030|
| G20           | 0.13| 0.13| 1.52 | 0.76   | 33.37 | 34.37 | 38.87| 0.028|
| Mean          | 0.14| 0.11| 1.24 | 0.62   | 33.17 | 32.64 | 42.20| 0.024|
| Std           | 0.006| 0.005| 0.03 | 0.02   | 0.37 | 0.31 | 1.51 | 0.002|
| \(\text{RCa}\) (%) | 24.44 | 49.98 | 1.62 | 32.15 | 44.63 | 14.25 | 3.80 | 3.38 |

See Table S1 for the definition of genotypes.

\(RDW\) root dry weight (g plant\(^{-1}\)); \(SDW\) shoot dry weight (g plant\(^{-1}\)); \(SPAD\) relative chlorophyll content; \(P_N\) photosynthetic rate (μmol CO\(_2\) m\(^{-2}\) s\(^{-1}\)); \(G_S\) stomatal conductance (μmol H\(_2\)O m\(^{-2}\) s\(^{-1}\)); \(T_E\) transpiration rate (μmol H\(_2\)O m\(^{-2}\) s\(^{-1}\)); \(MSI\) membrane stability index; and \(RWC\) relative water content; \(C\) control condition; \(S\) salinity stress.

* Relative change due to salinity stress compared to control conditions.
highest SPAD index, whereas the highest values in the stress condition were recorded for G16, G17, and G20. The pattern changes of data in tested genotypes showed that salinity stress caused a 32.15% reduction in $P_N$ compared to control conditions. This trait ranged from 32.47 to 53.37 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ with an average of 42.20 in the control and from 21.23 to 38.67 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ with an average of 28.64 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ in stress conditions. Genotypes G8, G10, and G19 in the control and G9, G10, and G16 in stress conditions were recognized as the best genetic materials with a high rate of $P_N$ compared with other genotypes (Table 2). Salinity stress considerably affected $G_S$, which decreased by 44.63% across the 20 genotypes from 0.024 $\mu$mol H$_2$O m$^{-2}$ s$^{-1}$ in the control to 0.013 $\mu$mol H$_2$O m$^{-2}$ s$^{-1}$ under salinity stress conditions (Table 2). Under control conditions, the highest $G_S$ values were recorded for genotypes G11, G12, and G16. Under stress conditions, G8, G14, and G16 had the highest stomatal conductance than others (Table 2). Salinity stress significantly decreased $T_E$ (approximately 15%) compared with control conditions (Table 2). Under control conditions, $T_E$ varied between 0.78 and 2.26 $\mu$mol H$_2$O m$^{-2}$ s$^{-1}$ with a mean of 1.43 $\mu$mol H$_2$O m$^{-2}$ s$^{-1}$, while under stress conditions $T_E$ ranged from 0.33 to 2.64 $\mu$mol H$_2$O m$^{-2}$ s$^{-1}$ with an average of 1.23 $\mu$mol H$_2$O m$^{-2}$ s$^{-1}$. Regarding mean values, two sets of triplet genotypes (G11, G16, G18 and G8, G11, G17) were selected as the best genotypes under both conditions, respectively (Table 2).

**Root and shoot Na$^+$ and K$^+$ concentrations**

All traits related to root and shoot Na$^+$ and K$^+$ concentrations changed significantly under salinity stress. Significant differences were also observed among the tested bread wheat genotypes in the parameters shoot Na$^+$ concentrations (SN), shoot K$^+$/Na$^+$ ratio (SKN), root-to-shoot Na$^+$ translocation (RTSN), and root-to-shoot K$^+$ translocation (RTSK), but the interaction effect was not significant for all parameters (Table 1). The mean values for shoot K$^+$ concentrations (SK), root K$^+$/Na$^+$ ratio (RKN), SKN, RTSN, and RTSK decreased under stress conditions by 23.34%, 94.87%, 43.15%, 83.84%, and 31.14%, respectively, relative to control conditions. In contrast, salinity stress increased ionic concentration-based parameters across all genotypes, with the means of root Na$^+$ concentrations (RN), shoot Na$^+$ concentrations (SN) and root K$^+$ concentrations (RK) increasing by 2431.21%, 50.74%, and 29.38%, respectively, compared to control (Table 3). RN ranged from 0.65 to 1.73 (average 1.10 mmol g$^{-1}$ DW) under control conditions and from 14.82 to 44.77 mmol g$^{-1}$ DW (average 27.80 mmol g$^{-1}$ DW) under salinity stress. Under control conditions, the control varieties G1, G5, and G7 had the lowest RN content. Under salinity conditions, the control varieties G2, G9, and G12 had the lowest RN content (Table 3). RK contents varied between 1.48 and 4.47 mmol g$^{-1}$ DW (average 2.85) and between 1.23 and 7.13 mmol g$^{-1}$ DW (average 3.69) under control and stress conditions, respectively. Genotypes G11, G17, and G20 showed the highest K content in their root under control conditions, while under salinity stress the highest K content was observed in genotypes G5, G18, and G20 (Table 3). SN content ranged from 2.92 to 7.46 mmol g$^{-1}$ DW (average 5.04 mmol g$^{-1}$ DW) in the control conditions and from 3.22 to 15.52 mmol g$^{-1}$ DW (average 7.60 mmol g$^{-1}$ DW) under salinity stress. Under control conditions, G3, G15, and G20 had the lowest N content in the aboveground tissues, whereas G5, G15, and G16 had the lowest N content under stress condition (Table 3).

Values for SK content ranged from 2.71 to 5.47 mmol g$^{-1}$ DW (average 3.91 mmol g$^{-1}$ DW) and 1.71 to 3.60 mmol g$^{-1}$ DW (average 3 mmol g$^{-1}$ DW) under the control and stress conditions, respectively (Table 3). Under control conditions, RKN varied between 1.81 and 5.90 (average 2.67) and two control varieties G2 and G3 along with G8 had the highest ratio compared to other genotypes. Under stress conditions, this parameter varied between 0.08 and 0.27 (average 0.14) and the highest ratios were observed by genotypes G5, G7, and G9 (Table 3). Unlike RKN, the SKN showed a high range of variability among the investigated genotypes. This parameter varied between 0.64 and 1.79 (average 0.95) under control conditions and between 0.27 and 1.19 (average 0.54) under stress conditions. The highest values under the control/stress conditions were estimated for G9/G5, G12/G15, and G14/G16. RTSN showed a significant change due to salinity stress and its mean decreased by 83.84% across tested genotypes when compared with control conditions. This parameter ranged from 1.72 to 10.60 and from 0.17 to 1.15 under control and stress conditions, respectively. The G14, G17, and G20 genotypes in the control and G4, G5, and G20 under salinity stress showed the greatest ability in maintaining Na$^+$ ions in their roots (Table 3). Furthermore, RTSK varied between 0.62 and 8.21 (average 2.78) in control conditions and between 0.55 and 7.56 (average 1.91) under salinity stress. Due to the effect of salinity stress on this parameter, RTSK decreased by 31.14% across the 20 investigated genotypes. Based on genotypic means, G7, G10, and G14 under control conditions and G8 and G14 and the control variety G2 under stress conditions showed the best ability in the transfer of K$^+$ ions from root to shoot and mitigating salinity stress effects (Table 3).

**Grain yield**

The results of AMMI analysis indicated that the main effects due to environment (E), genotype (G), and GE interaction were significant (Table 4). The E, G, and GEI accounted for 40.57%, 26.64%, and 16.95% of the total
variation. This analysis further divided the interaction’s sum of squares into two interaction principal components (IPCA1 and IPCA2, respectively) and residual term. Both IPCAs were significant and explained 70.05% and 28.20% of the total variation due to the GE interaction, respectively. The mean grain yield (GY) of 20 investigated genotypes is presented in Table 5. The GY varied between 3.96 tonnes h⁻¹ at Yazd and 5.73 tonnes h⁻¹ at Birjand. The highest GY was observed in genotype G4, whereas genotype G16 had the lowest yield among all genotypes. However, there was crossover ranking across the tested locations. The highest-yield genotypes in Yazd, Kerman, Esfahan, and Birjand were G7, G5, G4, and G20, respectively, while genotypes G16, G19, G20, and G16, respectively, had the lowest yield at these locations. Means comparison revealed that genotype G4 followed by G9, G7, and G5 had the highest yield performance across four locations when compared with other genotypes (Table 5).

### Table 3 Mean values of ion content-related traits in the 20 bread wheat genotypes under control and salinity stress conditions

| Genotype code | RN C | RK C | SN C | SK C | RKN C | SKN C | RTSN C | RTSK C |
|---------------|-----|-----|-----|-----|------|------|--------|--------|
| G1            | 0.77| 33.25| 2.48| 4.36| 6.03 | 11.32| 3.00   | 2.76   |
| G2            | 0.85| 14.82| 3.15| 1.23| 4.06 | 5.49 | 4.44   | 3.26   |
| G3            | 1.02| 28.65| 3.17| 4.10| 3.56 | 6.41 | 4.04   | 3.22   |
| G4            | 0.78| 31.52| 1.48| 4.01| 7.46 | 4.95 | 2.87   | 1.71   |
| G5            | 0.75| 29.69| 2.23| 7.13| 5.19 | 4.03 | 4.29   | 3.51   |
| G6            | 0.78| 34.78| 2.63| 3.94| 5.29 | 7.04 | 4.43   | 2.58   |
| G7            | 0.65| 24.81| 2.04| 4.46| 3.60 | 5.58 | 3.73   | 2.80   |
| G8            | 0.85| 25.39| 2.40| 4.11| 7.30 | 15.52| 4.02   | 3.60   |
| G9            | 0.99| 19.18| 3.51| 4.08| 5.93 | 6.92 | 5.47   | 3.05   |
| G10           | 1.02| 28.47| 2.05| 3.96| 5.13 | 9.30 | 3.56   | 3.14   |
| G11           | 1.59| 33.59| 3.97| 3.54| 5.49 | 4.90 | 4.68   | 2.83   |
| G12           | 0.82| 17.01| 1.61| 1.68| 3.66 | 9.03 | 5.30   | 4.31   |
| G13           | 1.22| 27.49| 2.88| 3.45| 5.61 | 5.85 | 4.31   | 3.41   |
| G14           | 1.39| 19.33| 3.15| 1.96| 3.69 | 8.58 | 4.83   | 2.88   |
| G15           | 1.12| 26.95| 2.44| 1.92| 3.37 | 3.29 | 3.26   | 2.35   |
| G16           | 1.09| 21.37| 2.21| 2.32| 7.20 | 3.29 | 4.21   | 3.14   |
| G17           | 1.70| 32.83| 4.26| 2.86| 3.65 | 10.19| 2.71   | 3.07   |
| G18           | 1.36| 44.77| 3.07| 5.22| 5.34 | 14.09| 2.49   | 2.47   |
| G19           | 1.49| 33.04| 3.80| 4.29| 6.33 | 11.29| 3.77   | 3.12   |
| G20           | 1.73| 29.02| 4.47| 5.14| 2.92 | 4.90 | 2.79   | 2.71   |
| Mean          | 1.10| 27.80| 2.85| 3.69| 5.04 | 7.60 | 3.91   | 3.00   |
| Std           | 0.06| 1.65 | 0.21| 0.27| 0.31 | 0.57 | 0.21   | 0.13   |

 Negative numbers indicate value higher than control conditions

See Table S1 for the definition of genotypes

RN root Na⁺ content (mmol g⁻¹ DW); RK root K⁺ content (mmol g⁻¹ DW); SN shoot Na⁺ content (mmol g⁻¹ DW); SK shoot K⁺ content (mmol g⁻¹ DW); RKN root K⁺/Na⁺ ratio; SKN shoot K⁺/Na⁺ ratio; RTSN root-to-shoot Na⁺ translocation; RTKN root-to-shoot K⁺ translocation; C control condition; S salinity stress

*Relative change due to salinity stress compared to control conditions

### Table 4 AMMI analysis of variance for grain yield of the 20 investigated bread wheat genotypes

| Source of variation | df | Ms  | F-value | % (G + E + GE) | % GE |
|---------------------|----|-----|---------|----------------|------|
| Treatments          | 79 | 2.9 | 10.61** | 26.64          |      |
| Genotype (G)        | 19 | 3.82| 13.97** | 50.74          |      |
| Environment (E)     | 3  | 36.85| 228.85** | 40.57          |      |
| Block               | 8  | 0.16| 0.59    |                |      |
| G × E interaction   | 57 | 0.81| 2.96**  | 16.95          |      |
| IPCA1               | 21 | 1.54| 5.62**  | 70.05          |      |
| IPCA2               | 19 | 0.48| 1.75*   | 28.20          |      |
| Residuals           | 17 | 0.38| 1.03    | 2.37           |      |
| Error               | 152| 0.27| 15.06   |                |      |

* p < 0.05; ** p < 0.01
Association among seedling-based physiological traits and grain yield under stress condition

The results of principal component analysis (PCA) revealed that the two first principal components (PCs) justified 46.64% of the total variation in data with eigenvalues of 4.37 and 3.56, respectively. PC1 explained 25.70% of the variation and was strongly correlated with PN, GS, TE, SN, RN, RTSN, and RTSK but was negatively correlated with SDW, RN, RK, RKN, and RSN. PC2 justified 20.93% of the total variation and was positively correlated with SPAD index, RWC, RDW, SDW, RN, MSI, and SKN but was negatively associated with RK, SN, SK, RKN, RTSN, RTSK, and grain yield (factor loadings not shown). As shown in Fig. 1, there is not a clear pattern of association between factor loadings and multiple traits, we selected tolerant genotypes for specific trait(s). Accordingly, the genotype numbers G5, G6, G7, and G10 along with two control varieties G1 and G3 were associated with RK, RKN, and grain yield. The genotypes G8, G11, and G12 were associated with SN, SK, RTSK, and RTSN traits. Among the measured traits, PN, GS, and TE discriminated the control variety G2 and G14 from other genotypes. The genotypes G15, G16, and G17 showed a strong association with RWC, MSI, SPAD index, and RDW. Other genotypes (G4, G13, G18, G19, and G20) were associated with RN, SDW, and SKN. Figure 1 also depicts a relationship among the measured physiological traits at the seedling stage and grain yield. A small angle between two trait vectors shows a strong positive correlation and a larger angle shows a weaker correlation. Moreover, the 90° and 180° angles would result if there were no correlation and a negative correlation between the traits, respectively. Accordingly, grain yield showed a positive and strong correlation with RKN and RK. Furthermore, grain yield had a positive but a weak correlation with SK, SN, and RTSN. This result was also confirmed by linear regressions among the ranking pattern for grain yields with RN, RK, SN, SK, RKN, and SKN (Fig. 2). The correlations among PN, GS, and TE traits were strong and positive and also they showed positive correlations with RWC, MSI, RDW, and SPAD index. RDW and SDW were positively correlated with RN, SKN, SPAD index, MSI, and RWC. The related-ion translocation parameters (RTSN and RTSK) were positively correlated with SN and SK but had a negative correlation with RN and RK. SDW positively correlated with SK and SKN but was negatively associated with SN.

| Genotype code | Yazd | Kerman | Esfahan | Birjand | Overall mean | ASR |
|---------------|------|--------|---------|---------|--------------|-----|
| G1            | 4.23 (6) | 4.33 (14) | 5.40 (12) | 5.08 (17) | 4.76 | B C D E F | 12.25 (13) |
| G2            | 3.59 (15) | 4.72 (11) | 5.36 (13) | 4.69 (19) | 4.59 | D E F | 14.50 (17) |
| G3            | 4.17 (9)  | 4.91 (9)  | 5.43 (11) | 5.75 (11) | 5.06 | A B C D | 10.00 (11) |
| G4            | 4.20 (8)  | 5.72 (2)  | 5.84 (1)  | 5.83 (9)  | 5.40 | D A | 5.00 (1)  |
| G5            | 4.16 (10) | 6.21 (1)  | 5.15 (15) | 5.74 (13) | 5.31 | A B C | 9.75 (10)  |
| G6            | 3.87 (13) | 4.95 (6)  | 5.69 (4)  | 6.19 (5)  | 5.18 | A B C D | 7.00 (6)   |
| G7            | 4.87 (1)  | 4.71 (12) | 5.49 (9)  | 6.40 (3)  | 5.37 | A B | 6.25 (5)   |
| G8            | 4.60 (4)  | 5.11 (3)  | 5.64 (7)  | 5.87 (8)  | 5.31 | A B C | 5.50 (2)   |
| G9            | 4.67 (3)  | 4.94 (8)  | 5.48 (10) | 6.46 (2)  | 5.39 | A | 5.75 (4)   |
| G10           | 4.85 (2)  | 4.91 (9)  | 5.60 (8)  | 5.75 (11) | 5.28 | A B C | 7.50 (7)   |
| G11           | 4.43 (5)  | 4.95 (6)  | 5.67 (5)  | 5.67 (15) | 5.18 | A B C D | 7.75 (8)   |
| G12           | 4.22 (7)  | 4.97 (5)  | 5.74 (3)  | 5.88 (7)  | 5.20 | A B C D | 5.50 (2)   |
| G13           | 3.99 (11) | 4.98 (4)  | 5.76 (2)  | 5.74 (14) | 5.12 | A B C D | 7.75 (8)   |
| G14           | 3.74 (14) | 4.47 (13) | 5.67 (5)  | 5.54 (16) | 4.86 | A B C D E | 12.00 (12) |
| G15           | 3.29 (18) | 4.09 (15) | 5.16 (14) | 6.34 (4)  | 4.72 | D E F | 12.75 (14) |
| G16           | 2.54 (20) | 3.22 (17) | 4.05 (18) | 4.63 (20) | 3.61 | B | 18.75 (20) |
| G17           | 3.10 (19) | 3.48 (16) | 4.20 (17) | 5.96 (6)  | 4.19 | P | 14.50 (17) |
| G18           | 3.89 (12) | 2.75 (19) | 4.80 (16) | 5.81 (10) | 4.31 | E F | 14.25 (16) |
| G19           | 3.38 (17) | 2.63 (20) | 3.94 (19) | 4.71 (18) | 3.67 | G H | 18.50 (19) |
| G20           | 3.58 (16) | 2.85 (18) | 3.91 (20) | 6.63 (1)  | 4.24 | F | 13.75 (15) |

Numbers in parentheses indicate the ranking pattern across all genotypes
See Table S1 for the definition of genotypes

Different letters in each row indicate significant differences at 0.01 probability level

Average of sum of ranks for each genotype across four test locations
Identification of superior salinity-tolerant genotypes

Due to the difficulty in identifying superior tolerant genotypes based on a single measured trait, we used the ranking method. In this way, the investigated genotypes received a rank from 1 (best mean value of each trait) to 20 (worst mean value of each trait); thus, the genotypes with the lowest average sum of ranks (ASR) values were selected as the superior genotypes. Genotypes G5, G13, G15, G16, G17, and G20 had the lowest ASRs and were considered the best genotypes (Supplementary Table S2). On the other hand, the ranking pattern of genotypes based on grain yield recognized G4, G5, G7, G8, and G9 as high-yield performance genotypes relative to other genotypes. Indeed, these results show that there is a strict correlation between tolerance pattern existence in the early growth stage and whole plant (Fig. 3). Thus, an increase in ASR value at the seedling stage is associated with reduced yield performance at the field stage. Based on these results, G5 may be a candidate as a superior salinity-tolerant genotype due to its high performance in the field and its response to a high level of salinity at the seedling stage.

Discussion

Crops commonly encounter environmental stresses. Among these, salinity is a major stress that limits plant growth and its productivity globally (Long et al. 2020). These negative effects may be attributed to the imbalance of various ions and ion toxicity, reduction in carbon fixation, stomatal conductance and photosynthesis rate, and nutritional imbalances (Sadak 2019). In the present study, 17 advanced genotypes of bread wheat along with three local check varieties were evaluated in terms of several plant growth and physiological traits under two optimal and salinity stress treatments to reveal tolerance mechanisms that may be useful for the identification of ideal genotypes at the seedling stage. Furthermore, the yield performance of the investigated bread wheat genotypes was compared with each other and the control varieties across four salinity regions. Our findings indicated that the effect of salinity stress on the response of wheat plants was significantly dependent on the genetic background of the investigated genotypes, as significant differences were observed for SDW, RWC, G\textsubscript{S}, T\textsubscript{E}, SN, SKN, RTSN, and RTSK (Table 1). Salinity stress significantly reduced the SKN (94.87%), RTSN (83.84%), SDW (49.98%), G\textsubscript{S} (44.63%), SKN (43.15%), P\textsubscript{N} (32.15%), RTSK (31.14%), RDW (24.44%), SK (23.34%), and T\textsubscript{E} (14.25%) when compared with control conditions (Tables 2, 3). In contrast, salinity stress significantly increased RN (2431.21%), SN (50.74%), and RK (29.38%).

Our results showed that the percentage of reduction of SDW is more than RDW under salinity stress conditions compared to control conditions (Table 2). Generally, a negative effect of salinity stress on root and shoot biomasses is in agreement with the results of a study conducted by Islam et al. (2015), who indicated that a decrease in these growth parameters was associated with a reduction in the net photosynthesis that results in reduced plant biomass. Furthermore, we found that genotypes G15 and G17 had the highest root and shoot biomasses than the other investigated bread wheat genotypes (Table 2). These genotypes also showed an increasing pattern in root biomass due to salinity stress compared to control conditions (45.37 and 60.81%, respectively). This increasing trend under salinity conditions is a possible stress-avoidance mechanism. In addition to root and shoot dry biomass, salinity stress had an adverse effect on ion concentrations and many physiological traits; the rate of reduction or increase in the various measured traits in different crop plants was significantly associated with an increase in salt concentration (Sadak 2019; Ahmadi et al. 2018, 2020; Ebrahim et al. 2019; Zeeshan et al. 2020). Loss of intracellular water content is identified as one of the main consequences of salinity stress. The water status of plant cells is an important factor for plant growth and development (Islam...
et al. 2016). RWC is a physiological parameter that measures the water content of a leaf and the maximum amount that can take under full turgidity (Qin et al. 2010). Through RWC analysis, we observed that there were no noteworthy differences between levels of salinity treatments, although salinity caused an approximate 4% reduction of RWC compared to control conditions (Table 2). This finding may be supported by the effect of higher osmolyte concentration, which may be reflected by the maintenance of higher RWC. However, this result is inconsistent with other studies, which have reported that salinity stress can decrease the water content level in plants (Suriya-Arunroj et al. 2004; Suarez and Medina 2008; Qin et al. 2010).

MSI is another physiological parameter that is considered an indicator of stress tolerance and is widely used to measure potential salinity tolerance in different plant species (Sairam et al. 2002; Senguttuvel et al. 2014; ElBasyoni et al. 2017; Ebrahim et al. 2019). Farooq and Azam (2006) also noted that MSI is an effective physiological character in screening tolerant genotypes at the seedling stage. Under salinity stress conditions, there is a direct association between MSI and lipid peroxidation caused by reactive oxygen species (ROSs) that results in the production of malondialdehyde (MDA) (Ahmed et al. 2013). Furthermore, this is a quantitative trait, which through moderate heritability has a significant genetic association with grain yield (Asif and Kamran 2011; Ali et al. 2009; Hemantaranjan 2014; Talukder et al. 2014). Our results showed that when plants were exposed to salinity stress, the MSI changed modestly relative to control conditions (Table 2). As a result, several genotypes showed the highest MSI parameters. G17 and G20, along with G18, G19, and the control salt-tolerant genotype G1 showed an increasing trend in response to salinity stress. Plants have evolved different protective mechanisms either to overcome excess salts within their cells or to exclude salts from their cells (Carillo et al. 2011). One of the main protective mechanisms is the ability to control the balance of K⁺ and Na⁺ accumulation in different plant tissues. In other words, the assessment of root and shoot K⁺ and Na⁺ contents is needed to infer salt-tolerance mechanisms (Islam et al. 2016).
A marked reduction in GS, PN, TE, and SPAD parameters was observed in the investigated bread wheat genotypes (Table 2). These reductions are possibly due to either inhibition of metabolic phenomena or increased ROSs (Neill et al. 2002). The regulation of gas exchange between the inner and outer space of the leaf is controlled by two symmetric guard cells. Several phenomena and events such as stomatal density and status of its pore, and the water-transport capacity of the guard cells on the leaf surface controlled stomatal conductivity (G₅) (Zhu et al. 2018). This parameter estimates the rate of CO₂ and transpiration using stomata is determined due to the degree of physical resistance to gas transport between the inner and outer space of the leaf (Pietragalla and Pask 2012; Pour-Aboughadareh et al. 2017). In our study, salinity stress decreased G₅ by 44.63% compared with the control conditions (Table 2). This finding is consistent with a research conducted by Mahlooji et al. (2018) where a reduction in G₅ occurred due to salinity stress. In this case, genotypes G8, G11, G14, G16, and G17 had the highest G₅ values (Table 2). G8, G14, and G16 had a relatively smaller reduction or even an increasing trend in stomatal conductivity than the other genotypes and the control varieties (Table 2).

Similar to other physiological and biochemical traits, photosynthesis is also decreased due to salinity stress (Misra et al. 1997). Na⁺ accumulation affects photosynthetic components such as enzymes, chlorophylls, and carotenoids. It has been reported that there is a direct relation between reduction of photosynthetic rate and increases in the accumulation of ROSs (Davenport et al. 2005). In this study, when compared with control conditions, Pₐ values of salt-treated seedling plants were relatively low. Salinity reduced Pₐ values by 32.15% when averaged across all the tested genotypes (Table 2). Under salinity stress, the trend of photosynthesis rate was G10 > G9 > G16 > G8 > G14 > other genotypes and the control varieties (Table 2). According to our results, the transpiration rate was also affected by salinity stress; the average of this parameter across all genotypes was reduced by 14.25% compared with the control. Genotypes G14, G8, G11, G17, and G16 had the highest values (Table 2). These results revealed that there is a strong association among Gs, Pₐ, and Tₑ, as among the selected genotypes and SKN (Table 3). In addition to the reduction in root and shoot biomass, a marked reduction in Gₛ, Pₐ, Tₑ, and SPAD parameters due to salinity stress was recorded in the investigated wheat genotypes (Table 2). These reductions are possibly due to either inhibition of metabolic phenomena or increased ROSs (Neill et al. 2002). The regulation of gas exchange between the inner and outer space of the leaf is controlled by two symmetric guard cells. Several phenomena and events such as stomatal density and status of its pore, and the water-transport capacity of the guard cells on the leaf surface controlled stomatal conductivity (Gₛ) (Zhu et al. 2018). This parameter estimates the rate of CO₂, and transpiration using stomata is determined due to the degree of physical resistance to gas transport between the inner and outer space of the leaf (Pietragalla and Pask 2012; Pour-Aboughadareh et al. 2019, 2020). In this way, the best genotypes received the minimum rank for each trait or parameter. Thus, our results showed that genotypes G₅, G₁₃, G₁₅, G₁₆, G₁₇, and G₂₀ had the lowest ASRs and were therefore identified as the best genotypes compared with the control varieties and other genotypes (Supplementary Table S2).

In the present study, results of AMMI model revealed significant differences among the test genotypes and locations (Table 4). These findings show that there is a considerable genetic variation for grain-yield performance across the 20 investigated bread wheat genotypes in response to salinity conditions. From the mean comparison, the highest mean grain yields were recorded for genotypes G₄, G₅, G₇, and G₉ (Table 5). The PCA-based biplot revealed a considerable association between grain yield and some of the physiological traits at the early growth stage. Grain yield positively and significantly correlated with RK and RKN (Fig. 1). Indeed, this result supports the fact that selection in the early stage may lead to achieving tolerant and high-yield genotypes, and furthermore,

![Fig. 3](image-url) Relationship between ranking patterns obtained from grain yield and 16 measured traits under salinity stress conditions. See Table S1 for the definition of genotypes. The ranking pattern obtained from grain yield is opposite to the ASR method. Thus, the highest grain yield and lowest ASR values have received the minimum and maximum ranks, respectively.
these traits can be served as useful physiological tools to select salt-tolerant genotypes at the early growth stage. Our results also indicated an association between the ranking patterns for grain yield and ASR-based all measured traits (Fig. 3). Considering our results, genotype G5 showed an acceptable ASR value and high-yield performance. The pedigree of this promising genotype is “Arg/5/Seri*3//RL6010/4*VYR/3/Pastor/4/Bav92” in which cultivar “Arg” contributed as one of the Iranian landraces that is considered as the best salinity-tolerant parent in crossing programs. Cultivar “Arg” was formerly obtained from a hybridization between an Iranian landrace and international parent (cv. Inia from CIMMYT). This cultivar, with a productivity of 5.5 tonnes per hectare, is still favored by some farmers as it can tolerate a high level of soil and water salinity (12 and 10 dS m⁻¹, respectively) in the saline regions of Iran. Due to these features, we surmise genotype G5 is expected to perform successfully in target regions and to be adopted by farmers as its progenitor. Furthermore, the presence of “Pastor” as one of the main parents in this pedigree may have contributed to improved field resistance to stripe rust. We can conclude that genotype G5 can be recommended as a superior bread wheat genotype for cultivation in saline environments.

**Conclusion**

Our results revealed significant genotypic differences among breeding bread wheat genotypes for salinity tolerance in terms of several physiological traits at the early growth and grain yield. As a result, our findings indicate there is a positive correlation between salinity tolerance at the early growth stage and grain-yield performance at the adult phase. This result may allow for a reconsideration of the associations between tolerance at the seedling and adult phases of growth and of the complex connections among different physiological and photosynthesis parameters in resistance to salinity stress. The increased tolerance of genotype G5 was due to the higher root and shoot K⁺/Na⁺ ratios and lower concentration of Na⁺ in its root and shoot tissues. In addition, this genotype had high-yield performance in different saline regions of Iran. Hence, further study is needed to discover the underlying physiological and molecular mechanisms and to investigate its yield stability and adaptation in severe saline environments.

**Author contribution statement** AP conceived and designed the experiment. AA (the fourth author) provided the seeds of breeding genotypes. The experiment was performed by AP and AA (the sixth author). AP, HN, MM, SS and AA (the sixth author) collected the experimental data. AP performed the analysis and wrote the manuscript. MM and SS provided comments and edits. All authors read and approved the final manuscript.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s11738-021-03265-7.

**Acknowledgements** The authors acknowledge the lab facilities support (No. 2-03-03-236-980895) from the Seed and Plant Improvement Institute (SPII), Agricultural Research, Education and Extension Organization (AREEO), Iran. The authors thank the reviewers and the editor of Acta Physiologiae Plantarum for providing helpful comments and corrections on earlier drafts of this manuscript. Also, the first author is grateful to Dr. Peter Poczai, from the Botany Unit, Finnish Museum of Natural History, University of Helsinki, for his fruitful comments and improve the langue of the manuscript. Furthermore, the authors acknowledge the Research Square for sharing our manuscript as a preprint (https://doi.org/10.21203/rs.3.rs-158975/v1) before the final publishing.

**Declarations**

**Conflict of interest** The authors declared no conflict of interest.

**References**

[References]
Arzani A, Ashraf A (2016) Smart engineering of genetic resources for enhanced salinity tolerance in crop plants. Crit Rev Plant Sci 35:146–189. https://doi.org/10.1080/07352689.2016.1245056

Asif M, Kamran A (2011) Plant breeding for water-limited environments. Crop Sci 51:2911–2912. https://doi.org/10.2135/crops ci2011.12.0004br

Athar HUR, Khan A, Ashraf M (2007) Exogenously applied ascorbic acid alleviates salt-induced oxidative stress in wheat. Environ Exp Bot 63:224–231. https://doi.org/10.1016/j.envexpbot.2007.10.018

Blum A (2010) Plant breeding for water-limited environments. Springer, New York

Carillo P, Grazia Annunziata M, Pontecorvo G, Fuggi A, Woodrow P (2011) Salinity stress and salt tolerance. In: Shanker A (ed) Abiotic stress in plants—mechanisms and adaptations. IntechOpen, UK, pp 21–38

Chen F, Dahal P, Bradford KJ (2001) Two tomato expansin genes show divergent expression and localization in embryos during seed development and germination. Plant Physiol 127:928–936. https://doi.org/10.1104/pp.104.057307

Ebrahim F, Arzani A, Rahimmalek M, Sun D, Peng J (2019) Salinity stress and cell membrane stability. J Plant Physiol 127:928–936. https://doi.org/10.1016/j.jplph.2015.04.008

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000a) Plant cellular and molecular responses to high salinity. Annu Rev Plant Physiol Plant Mol Biol 51:463–499. https://doi.org/10.1146/ annurev.arplant.51.1.463

Hemantaranjan A (2014) Heat stress responses and tolerancetolerance. Adv Plants Agric Res 1:1–10. https://doi.org/10.15406/ apar.2014.01.00012

Hoagland DR, Arnon DI (1950) The water-culture method for growing plants without soil. California Agricultural Experiment Station, Circular No. 374. The College of Agriculture, University of California, USA

Husain S, Munns R, Condon AG (2003) Effect of sodium exclusion trait on chlorophyll retention and growth of durum wheat in saline soil. Aust J Agric Res 54:589–597. https://doi.org/10.1071/AR03302

Isayenkov SV, Matthuis FJM (2019) Plant salinity stress: many unanswered questions remain. Front Plant Sci 10:80. https://doi.org/10.3389/fpls.2019.00080

Islam F, Yasmeen T, Ali S, Ali B, Farooq MA, Gill RA (2015) Priming-induced antioxidative responses in two wheat cultivars under saline stress. Acta Physiol Plant 37:153. https://doi.org/10.1007/s11738-015-1897-5

Islam F, Yasmeen T, Arif MS, Ali S, Ali B, Hameed S, Zhou W (2016) Plant growth promoting bacteria confer salt tolerance in Vigna radiate by up-regulating antioxidant defense and biological soil fertility. Plant Growth Regul 80:23–36. https://doi.org/10.1007/s10725-015-0142-y

Kawasaki S, Borchert C, Deyholos M, Wang H, Brazile S, Kawai K, Galbraith D, Bohnert HJ (2001) Gene expression profiles during the initial phase of salt stress in rice. Plant Cell 13:889–905. https://doi.org/10.1105/tpc.13.4.889

Ketata HY, Yau SK, Nachit M (1989) Relative consistency performance across environments. In: International Symposium on physiology and breeding of winter cereals for stressed Mediterranean environments. Montpellier, July 3–6, pp 391–400

Liu S, Constable G, Stilller W (2020) Using leaf sodium concentration for screening sodicity tolerance in cotton (Gossypium hirsutum L.). Field Crop Res 46:107678. https://doi.org/10.1016/j.fcr.2019.107678

Long M, Shou J, Wang J, Hu W, Hannon F, Mwamba TM, Farooq MA, Zhou W, Islam F (2020) Ursolic acid limits salt-induced oxidative damage by interfering with nitric oxide production and oxidative defense machinery in rice. Front Plant Sci 11:697. https://doi.org/10.3389/fpls.2020.00697

Maghsoudi K, Emmam Y, Pessarakli M (2016) Effect of silicon on photosynthetic gas exchange, photosynthetic pigments, cell membrane stability and relative water content of different wheat cultivars under drought stress conditions. J Plant Nutr 39:1001–1015. https://doi.org/10.1080/01904167.2015.1109108

Mahlooji M, Seyed Shariﬁ R, Razmjoo M, Sabzalian MR, Sedghi M (2018) Effect of salt stress on photosynthesis and physiological parameters of three contrasting barley genotypes. Photosynthetica 56:549–556. https://doi.org/10.1007/s11099-017-0699-y

Misra A, Sabu AN, Misra M, Singh P, Meera I, Das N, Kar M, Sahu P (1997) Sodium chloride induced changes in leaf growth, and oxidative damage by interfering with nitric oxide production in wheat (Triticum aestivum L.). Physiol Plant 107:328–334. https://doi.org/10.1111/j.1399-3054.1997.tb02046.x

Misra A, Sabu AN, Misra M, Singh P, Meera I, Das N, Kar M, Sahu P (1997) Sodium chloride induced changes in leaf growth, and oxidative damage by interfering with nitric oxide production in wheat (Triticum aestivum L.). Physiol Plant 107:328–334. https://doi.org/10.1111/j.1399-3054.1997.tb02046.x
Neill SJ, Desikan R, Clarke A, Hurst RD, Hancock JT (2002) Hydrogen peroxide and nitric oxide as signaling molecules in plants. J Exp Bot 53:1237–1247. https://doi.org/10.1093/jxbot/53.372.1237

Nevo E, Chen G (2010) Drought and salt tolerances in wild relatives for wheat and barley improvement. Plant Cell Environ 33:670–685. https://doi.org/10.1111/j.1365-3040.2009.02107.x

Panwar M, Tewari R, Gulati A, Nayyar H (2016) Indigenous salt-tolerant rhizobacterium Pantoea dispersa (PSB3) reduces sodium uptake and mitigates the effects of salt stress on growth and yield of chickpea. Acta Physiol Plant 38:278. https://doi.org/10.1007/s11738-016-2284-6

Pietragalla J, Pask AJD (2012) Physiological breeding II. In: Pietragalla H, Pask AJD, Mullan D, Reynold MD (eds) A field guide to wheat phenotyping. CIMMYT, Mexico, pp 15–17

Pour-Aboughadareh A, Ahmadi J, Mehrabi AA, Etminan A, Moghaddam M, Siddique KHM (2017) Physiological responses to drought stress in wild relatives of wheat: Implications for wheat improvement. Acta Physiol Plant 39:106. https://doi.org/10.1007/s11738-017-2403-z

Pour-Aboughadareh A, Etminan A, Abdelrahman M, Siddique KHM, Tran LSP (2020) Assessment of biochemical and physiological parameters of durum wheat genotypes at the seedling stage during polyethylene glycol-induced water stress. Plant Growth Regul. https://doi.org/10.1007/s10725-020-00621-4

Pour-Aboughadareh A, Omidi M, Naghavi MR, Etminan A, Mehrabi AA, Poczai P, Bayat H (2019) Effect of water deficit stress on seedling biomass and physio-chemical characteristics in different species of wheat possessing the D genome. Agronomy 9:522. https://doi.org/10.3390/agronomy9050522

Qadir M, Quillero E, Nangia V, Murtaza G, Singh M, Thomas RJ, Drechsel P, Noble AD (2014) Economics of salt-induced land degradation and restoration. Nat Resour Forum 38:282–295. https://doi.org/10.1111/1477-8947.12054

Qin J, Dong WY, He KN, Yu Y, Tan GD, Han L, Dong M, Zhang YY, Zhang D, Li AZ, Wang ZI (2010) NaCl salinity induced changes in water status, ion contents and photosynthetic properties of Shepherdia argentea (Pursh) Nutt seedlings. Plant Soil Environ 56:325–332. https://doi.org/10.17221/209/2009-PSE

Rahnama A, Fakhrri S, Meskarbasheem M (2019) Root growth and architecture responses of bread wheat cultivars to salinity stress. Agron 111:2991–2998. https://doi.org/10.2134/agronj2018.12.0795

Roy SJ, Negrao S, Tester M (2014) Salt resistant crop plants. Curt Opin Biotechnol 26:115–124. https://doi.org/10.1016/j.copbio.2013.12.004

Sadak M (2019) Physiological role of trehalose on enhancing salinity tolerance of wheat plant. Bull Natl Res Cent 43:53. https://doi.org/10.1186/s42269-019-0098-6

Sairam RK, Veerabhadrudu R, Srivastava GC (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. https://doi.org/10.1016/S0168-9452(02)00278-9

Saqib M, Zorb C, Rengel Z, Schubert S (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. https://doi.org/10.1016/j.plantsci.2005.07.001

Senguttuvil P, Vijayalakshmi C, Thiyagarajan K, Kannanbanu JR, Kota S, Padmavathi G, Geetha S, Srinatharan N, Viraktamath BC (2014) Changes in photosynthesis, chlorophyll fluorescence, gas exchange parameters and osmotic potential to salt stress during early seedling stage in rice (Oryza sativa L.). SABRAO J Breeding Genet 46:120–135

Singh P, Mahajan MM, Singh NK, Kumar D, Kumar K (2020) Physiological and molecular response under salinity stress in bread wheat (Triticum aestivum L.). J Plant Biochem Biot 29:125–133. https://doi.org/10.1007/s15562-019-00521-3

Suarez N, Medina E (2008) Salinity effects on leaf ion composition and salt secretion rate in Avicennia germinans (L.) Braz J Plant Physiol 20:131–140. https://doi.org/10.1590/S1677-0420200800200005

Suriya-Arunroj D, Supapeoj N, Toojinda T, Vanavichit A (2004) Relative leaf water content as an efficient method for evaluating rice cultivars for tolerance to salt stress. Sci Asia 30:411–415. https://doi.org/10.2306/scienceasia1513-1874.2004.30.411

Talukder SK, Babar MA, Vijayalakshmi K, Poland J, Prasad PVV, Bowden R, Fritz A (2014) Mapping QTL for the traits associated with heat tolerance in wheat (Triticum aestivum L.). BMC Genet 15:1–13. https://doi.org/10.1186/s12863-014-0097-4

Xu Y-F, An D-G, Liu D-C, Zhang A-M, Xu H-X, Li B (2012) Mapping QTLs with epistatic effects and QTL× treatment interactions for salt tolerance at seedling stage of wheat. Euphytica 186:233–245. https://doi.org/10.1007/s10681-012-0647-7

Zeeshan M, Lu M, Sehar S, Holford P, Wu F (2020) Comparison of biochemical, anatomical, morphological, and physiological responses to salinity stress in wheat and barley genotypes deferring in salinity tolerance. Agronomy 10:127. https://doi.org/10.3390/agronomy10010127

Zhu X, Cao Q, Sun L, Yang X, Yang W, Zhang H (2018) Stomatal conductance and morphology of arbuscular mycorrhizal wheat plants respond to elevated CO2 and NaCl stress. Front Plant Sci 9:1363. https://doi.org/10.3389/fpls.2018.01363

Zobel RW, Wright MJ, Gauch HG (1998) Statistical analysis of yield trials. Agron J 80:388–393. https://doi.org/10.2134/agronj1998.00021962000000300002x

Zou P, Li K, Liu S, He X, Zhang X, Xing R, Li P (2016) Effect of sulfated chitoiosogascharides on wheat seedlings (Triticum aestivum L.) under salt stress. J Agri Food Chem 64:2815–2821. https://doi.org/10.1021/acs.jafc.5b05624

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.