Assessing the correlations and selection criteria between different traits in wheat salt-tolerant genotypes

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Article info

Article history:
Received 12 April 2021
Revised 26 May 2021
Accepted 27 May 2021
Available online 2 June 2021

Keywords:
Wheat
Salinity stress
Genetic relations
Mantel test
Path analysis

Abstract

Salinity is one of the largest stresses blocking horizontal and vertical expansion in agricultural lands. Establishing salt-tolerant genotypes is a promising method to benefit from poor water quality and salinized lands. An integrated method was developed for accomplishing reliable and effective evaluation of traits stability of salt-tolerant wheat. The study aims were to estimate the genetic relationships between explanatory traits and shoot dry matter (SDM), and determine the traits stability under three salinity levels. Morphophysiological and biochemical traits were evaluated as selection criteria for SDM improvement in wheat for salinity tolerance. Three cultivars and three high-yielding doubled haploid lines (DHLs) were used. Three salt (NaCl) levels (control (washed sand), 7 and 14 dS m −1) were applied for 45 days (at the first signs of death in the sensitive genotypes). All morphophysiological traits gradually decreased as salinity levels increased, excluding the number of roots. Decreases were more visible in sensitive genotypes than in tolerant genotypes. All biochemical traits increased as salinity levels increased. Variance inflation factors (VIFs) and condition number exhibited multicollinearity for membrane stability index and polyphenol oxidase activity. After their removal, all VIFs were <10, thereby increasing path coefficient accuracy. Total chlorophyll content (CHL) and catalase (CAT) provided significant direct effects regarding genetic and phenotypic correlations for the three salinity levels and their interactions in path analysis on SDM, indicating their stability. CHL and CAT had high heritability (>0.60%) and genetic gain (>20%) and highly significant genetic correlation, co-heritability, and selection efficiencies for SDM. CHL and CAT could be used as selection criteria for salinity tolerance in wheat-breeding programs. The tolerated line (DHL21) with the check cultivar (Sakha 93) can be also recommended as novel genetic resource for improving salinity tolerance of wheat.

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1. Introduction

Salinity is a serious abiotic stress and will remain a major concern of accessibility to credible screening criteria of salt tolerance in wheat (Triticum aestivum L.) genotypes for plant breeders and researchers in the field of plant physiology and biotechnology (Al-Ashkar et al., 2019, Al-Ashkar et al., 2021b). Many studies investigated the tolerance of wheat into the salinity and found that the tolerated genotypes can survive in the level of 10 dS m −1 NaCl (El-Hendawy et al., 2005, Al-Ashkar et al., 2019). Breeding strategies for wheat consist of segregating a large number of genotypes and crosses to derive new genotypes that are then compared and evaluated to obtain genotypes and commercial cultivars possessing the properties of high yield and tolerance to abiotic and/or bio-
tic stresses (Gutierrez et al., 2010, Al-Ashkar and El-Kafafi, 2014, Al-Ashkar et al., 2016, Barakat et al., 2020b). To achieve this goal, the selection of breeding lines for yield and salt tolerance in advanced growth media often needs repetition to validate the results; however, the repetitions sometimes produce inconsistent results because of the complicated genetic behavior of yield and salinity traits (Ball and Konzak, 1993). This methodology is time-consuming and expensive because it requires more than one field assessment, which must be conducted during different seasons and in various locations (Ureña-Gómez et al., 1996, Grzesiak et al., 2019). To reduce this difficult process of selection, preferably using rapid, convenient, and cost-neutral methods, heritability should have high genetic correlation and thereby be a selection tool using which breeders can screen genotypes and the selection process can proceed rapidly (Reynolds et al., 1999, Jackson, 2001, Al-Ashkar et al., 2021a).

Morphological and physiological traits can significantly influence the productivity of crops in direct and indirect pathways. Productivity can be particularly affected by environmental conditions when there are low heritability and a high genetic × environment interaction, which makes the selection of genotypes more difficult for a given environment, in addition to a high phenotypic coefficient of variation (Jackson et al., 1996, Barakat et al., 2020a). Testing the genotypes for salt tolerance under similar conditions in small-scale pot studies can serve as a useful indicator. The observed correlation for stress tolerance under both open field and laboratory conditions may be adequate (Kpoghomou et al., 1990, Watson et al., 2019). Selection for salt tolerance by measuring yield itself is a traditional approach, whereas selection based on shoot dry matter (SDM), considering it as an indirect trait that can substitute for grain yield, is another analytical approach (Richards, 1982, Prasad et al., 2007, Al-Ashkar et al., 2020b).

Comprehensive understanding and the integration of factors responsible for growth and development are required to identify an indirect selection tool to obtain further information and genetic gains to improve the salt tolerance of wheat genotypes (Richards, 1982). There are several plant traits in multiple mechanisms, such as morphophysiological and biochemical parameters, that may contribute to yield and salt tolerance improvement. Selecting potential targets can be a difficult and misleading process; however, some guidance is available to make the selection process more efficient (Pennacchi et al., 2018, Al-Ashkar et al., 2020a). The selection of target parameters of salt tolerance and yield by the plant breeder must be based on the correlation between the parameter and yield. Given the variation in the parameter among genotypes, the parameter stability (heritability), and the influence of the genetic × environment interaction on the parameter, it is necessary to conduct an assessment of multicollinearity to exclude explanatory traits that are highly correlated (Mir et al., 2012, Olivoto et al., 2017).

Although the selection of traits to focus on is a decisive step in breeding for yield and salt tolerance improvement, understanding the engagements and trade-offs between traits and their actions during the plant cycle are important factors for a rapid and efficient detection of high-yielding genotypes from a large number of lines for the advancement of genotypes (Pennacchi et al., 2018, Barakat et al., 2020b). Plant breeders make selections based on multiple traits; however, the advancement is complex and based on genetic correlations. If two traits are positively correlated, selection can improve both by closed selection, indirect selection, or a trait index (Bernardo, 2010, Al-Ashkar et al., 2020a). Conversely, negative correlations are also widespread and are often the bane of the breeder. Therefore, the heritability, the genetic gain of each parameter, and the genetic correlation between parameters, which determine the direct response to selection (Falconer and Mackay, 1996), are fixed parameters of genotypes. In addition, selection can be more accurate within established genotypes, and multi-trait genetic gain could be increased by developing better genotypes through an intentional selection of multi-trait with a more perfect mean, greater genetic gain, and higher positive genetic correlations (Neyhart et al., 2019).

Multi-trait include several related traits that could be included in a multivariate analysis. However, there are computational obstacles to integrating all variables in a single model because of the strong interdependence among exploratory variables. This may cause overfitting of the analysis model and a broad probability of spurious errors (Sainani, 2014) because they collectively contribute to explain linear relationships. Principal component analysis (PCA) is a method that can narrow the number of correlated variables, wherein predictors are summarized into a new set of unrelated variables (principal components [PCs]) with minimal loss of data (Abdi and Williams, 2010, Al-Ashkar et al., 2021a). Therefore, PCA could be used as a method for data dimension reduction, which has been previously used in plant breeding with positive results (El-Dien et al., 2015). Multicollinearity is one of the outcomes of PCs that explain linear relationships in a multivariate analysis and are used when it is difficult to individually estimate the relationships of explanatory traits because they are associated and because they collectively contribute to explain linear relationships (Olivoto et al., 2017, Al-Ashkar et al., 2021a). When this problem is detected at moderate or high degrees, the variance accompanying the estimates of path coefficients reach very high values, reducing the credibility of the findings that are incompatible with biological expectation (Cruz et al., 2014). The problems associated with multicollinearity can be resolved by excluding the unlisted traits in the model.

This technique utilizes previous analysis of the correlation matrix among independent traits, adopts their findings, and gauges the level of existing multicollinearity. Moreover, it can perceive the traits that could cause problems (Mansfield and Helms, 1982, Montgomery et al., 2012). After excluding traits with multicollinearity, path coefficients can be evaluated without the negative effects of multicollinearity. Path analysis is a multivariate procedure that is used when there are several important traits. However, the trait is dependent and affected by explanatory traits; hence, the procedure presents the quantity and conceives the contributions among interpretive traits toward the dependent trait, which are essentially based on the principles of multiple regression. This method is based on ideas originally designed in biology and economics (Wright, 1934, Wold, 1954) and functions to partition the linear correlation coefficients into direct and indirect effects of numerous traits deemed as interpretive toward the distinct feature as the dependent trait. This technique has been quite useful in detecting the cause-and-effect associations to assist in indirect selection in plant-breeding programs (Bello et al., 2010, Nardino et al., 2016, Al-Ashkar et al., 2020b).

The objectives of the present study were to (1) compare the different physiological and biochemical traits of modern wheat lines and cultivars, (2) conduct path coefficient analysis to determine how various components affect the response variable and trait stability by including explanatory traits in a multivariate model, and (3) determine the genetic relationships including heritability, genetic gain, co-heritability, and selection efficiencies as an index of salt tolerance.
2. Materials and methods

2.1. Plant materials and experimental design

The experiment was conducted in the greenhouse at the Plant Production Department, College of Food and Agriculture Sciences, King Saud University, to investigate growth and physiological and biochemical changes of wheat plants developing under salt stress. Six wheat genotypes, including three cultivars, viz., Sakha-93 (salt-tolerant), Giza-168 (salt-moderate), and Gemmeiza-9 (salt-sensitive), and three DHLs, viz., DHL21, DHL7, and DHL2 (as novel high-yield genotypes), were used in this study. The grains of cultivars were obtained from the Agricultural Research Center, Egypt, and the grains of DHLs were obtained from the Department of Agronomy, Faculty of Agriculture, Al-Azhar University, Cairo, Egypt (El-Hennawy et al., 2011). Three salinity (NaCl) levels (control (washed sand), 7 and 14 dS m⁻¹) were used in this study. The grains of these six genotypes were germinated in freshwater to avoid an osmotic shock. Five plantlets from each genotype were planted under three salinity levels in plastic pots filled with sand. The field capacity 70% was achieved by adding tap water or salt solution to each pot. The nutrients were provided using 25% Hoagland’s nutrient solution. Growing conditions in the greenhouse were 23 ± 2 °C during the day and 16 ± 2 °C during the night, with a photoperiod cycle of 16-h light and 8-h dark and a light intensity of approximately 60 μmol m⁻² s⁻¹. Salinity levels were modified four times during the experiment period due to the uptake of salt by plants. A completely randomized design was used in the experiment. The experiment was replicated six times, with 30 grains for each of the six genotypes and replicates (n = 5 plants or samples per genotype in each treatment). The seedlings were harvested after 45 days from planting (at the first signs of death in the sensitive genotypes), and growth and physiological and biochemical measurements were recorded.

2.2. Growth measurements

Growth traits, including shoot length (SL, cm), root length (RL, cm), root number (RN), SDM (g), and root dry matter (RDM), were estimated at harvest. RDM and SDM were recorded after oven-drying at 70 °C for 48 h.

2.3. Determination of physiological parameters

Total chlorophyll content (CHL) was measured according to the method described by Hipkins and Baker (1986) and was expressed as μg g⁻¹ fresh weight (FW). Water status in the leaves was identified through two different measurements—relative water content (RWC %) and relative turgidity (RT%), as mentioned by Weatherley (1950) and Grzesiak et al. (2019). Membrane stability index (MSI, %) was measured based on the standard procedure described by Sairam et al. (2002).

2.4. Analysis of antioxidant enzyme activities

The activity of polyphenolPolyphenol oxidase (PPO) activity was measured as described by Duckworth and Coleman (1970) and was expressed as U g⁻¹ FW. Peroxidase (POD) activity was measured as described by Chance and Maehly (1955) and was expressed as U g⁻¹ FW. Catalase (CAT) activity was measured as described by Aebi (1984) and was expressed as U g⁻¹ FW.

2.5. Data analysis

All the data of the examined traits were subjected to ANOVA in a completely randomized factorial design to determine the effects of salinity levels, genotypes, and their interaction on the examined traits. Duncan’s test was used to compare mean values at 95% or 99% levels of probability. Multicollinearity diagnosis was used to determine the source and magnitude of multicollinearity in a correlation matrix of explanatory traits. Two-way ANOVA, multicollinearity analysis, PCA, and Mantel test coefficient were conducted using the XLSTAT statistical package (Version 2018, Excel Add-ins soft SARL, New York, NY, USA). Phenotypic and genetic correlations between traits were calculated using Proc Mixed in the SAS software (Version 9.2, SAS Institute, Inc., Cary, NC, USA) as described by Singh and Chaudhary (1979). The following formulas were used to calculate the phenotypic (rₚ) and genetic (r₉) correlations:

\[ r_p = \frac{\text{cov}(\sigma_x^2 \times \sigma_y^2)}{\sqrt{\sigma_x^2 \times \sigma_y^2}} \]

\[ r_g = \frac{\text{cov}(\sigma_x^2 \times \sigma_y^2)}{\sqrt{\sigma_x^2 \times \sigma_y^2}} \]

where cov(σₓ²) and cov(σᵧ²) are phenotypic and genetic covariance, respectively, and σₓ² and σᵧ² are phenotypic variances, and σₓ² and σᵧ² are genetic variances of trait x and trait y, respectively.

Path analysis was conducted for each phenotypic and genetic correlation, dividing them into direct and indirect effects (Wright, 1934), with SDM being considered as a dependent variable, and SL, RL, RN, RDM, RWC, RT, CHL, POD, and CAT considered as causal variables. The residual value of the path analysis was obtained using the following expression:

\[ \text{Residual value} = \sqrt{1 - R^2} \]

where R² is the coefficient of determination.

Broad-sense heritability (h²), genetic gain (%), co-heritability, selection response (R), correlated response (CR), and relative selection efficiency (CR/R) were calculated using the following expressions:

\[ h^2 = \sigma_g^2 / \sigma_g^2 + \sigma_x^2 + \sigma_e^2 \]

\[ \text{Genetic gain} = \frac{((\sigma_g^2 / \sigma_p^2) \times \sqrt{\sigma_g^2 \times k})}{X} \times 100 \]

\[ \text{Co-heritability} = \frac{\text{cov}(\sigma_g^2 / \sigma_p^2) \times 100}{R} \]

\[ R = h_1^2 \sigma \]

\[ CR = h_1 h_2 \sigma \]

\[ CR/R = \frac{h_1}{h_2} \]

where σₓ² is the genotypic variance, σₑ² is the genotype x salinity levels, σᵣ² is the residual variance, 1 represents salinity levels, r is the number of replications, σₓ² is the phenotypic variance, k is the selection differential at 5% selection intensity, having a value of 2.06, X is the phenotypic mean for each trait, GA is the genetic advance, cov(σₓ²) is the genotypic covariance, cov(σₓ²) is the phenotypic covariance, h₁² is the heritability value for the trait, σₓ and σₑ are the phenotypic standard deviation values for causal and dependent traits, respectively, h₁ and h₂ are the square roots of the heritability.
of causal and dependent traits, respectively, and \( r_p \) is the genetic correlation between causal and dependent traits.

3. Results

3.1. Variation in genotypes and salinity levels for SDM and its explanatory traits

The results of ANOVA showed highly significant differences between salinity levels (L) and genotypes (G) for all the tested traits presented in Table 1. The \( L \times G \) interaction was also significant for RDM, SL, RT, CHL, POD, CAT, and SDM traits, whereas for RN, RL, RWC, MSI, and PPO, the interaction effect was nonsignificant. The effects of salinity were greater for the salt-sensitive cultivar Gemmeiza9 than for the salt-tolerant cultivar Sakha93, which exhibited more tolerance in most of the measurements. The differences in all parameters between all the examined genotypes were significant. The novel lines (DHL3 and DHL12) were more affected than the cultivar Gemmeiza9 compared to Sakha93, which was more resistant than for the salt-tolerant cultivar Sakha93. The interaction effect was nonsignificant for RDM, SL, RT, CHL, POD, CAT, and SDM traits, whereas for RN, POD, and SDM exhibited nonsignificant differences between control and 7 dS m\(^{-1}\) treatments (Table 1).

3.2. Mean performance and relative changes in wheat genotypes with different salinity levels

In the present study, the growth traits RN, RL, RDM, SL, and SDM were measured in the six genotypes of wheat while being cultivated under three salinity levels (Figs. 1 and 2). Minimum relative changes in RN and RL were observed in Sakha93 in the 7 and 14 dS m\(^{-1}\) treatments (RN: 0.43% and 6.86%; RL: 2.85% and 7.95%, respectively) compared to those in the control treatment (Fig. 1). The maximum relative change in RDM was observed in Sakha93 in the 7 and 14 dS m\(^{-1}\) treatments (14.81% and 18.82%, respectively) compared to that in the control treatment. The maximum relative change in RN and RL were observed in Giza168 and DHL3 in the control and 7 dS m\(^{-1}\) treatments (RN: 0.43% and 6.86%; RL: 2.85% and 7.95%, respectively) compared to that in the control treatment. In DHL21, both 7 and 14 dS m\(^{-1}\) treatments resulted in the maximum relative change in RN and RL (13.95% and 10.47%, respectively) compared to that in the control treatment. In DHL21, both 7 and 14 dS m\(^{-1}\) treatments resulted in the maximum relative change in RT (11.05% and 20.96%, respectively) compared to that without NaCl treatment. In Sakha93, both 7 and 14 dS m\(^{-1}\) treatments resulted in the minimum relative change in MSI (0.36% and 5.51%, respectively) compared to that in the control treatment. In DHL21, both 7 and 14 dS m\(^{-1}\) treatments resulted in the maximum relative change in CHL and POD (20.11% and 20.83%, respectively) compared to those without NaCl treatment. For biochemical traits (POD, PPO, and CAT), the maximum relative change was observed in Sakha93 and DHL21 when treated with 7 and 14 dS m\(^{-1}\) (Sakha93 [POD: 14.89% and 22.25%; PPO: 17.38% and 20.83%; CAT: 25.01% and 27.49%, respectively]; DHL21 [POD: 17.83% and 20.07%; PPO: 20.99% and 22.55%; CAT: 21.43% and 20.11%, respectively]) compared to those without NaCl treatment (Fig. 5).

3.3. Multicollinearity diagnosis and PCA

The tolerance level of the explanatory traits ranged from 0.244 to 0.060 (Table 2). Two variance inflation factors (VIFs) of >10 were observed (VIFs of >10 were 14.085 and 16.688 for MSI and PPO, respectively). Researchers must carefully choose the traits that need to be excluded because the exclusion of traits with high explanatory power could reduce the accuracy of the analysis. Important traits must be retained in the genetic breeding of wheat as they will contribute considerably to path coefficients and the coefficient of determination of the model. With the exclusion of the trait MSI, PPO provided a better response, which reduced the multicollinearity of the matrix. All the observed VIFs were <10, with the largest VIF being 8.674 related to CAT (Table 2), which should result in accuracy in the estimates of path coefficients. PCA is the process of computing the PCs and using them to perform a change of basis on the data, exploratory data analysis, and for making uncorrelated (orthogonal) predictive models that can minimize the number of variables to several prospective factors.

### Table 1

**Analysis of variance and effects of genotypes, salinity levels, and their interaction for 12 measured traits.**

| Sources | RN | RL | RDM | SL | RWC | RT | MSI | CHL | POD | PPO | CAT | SDM |
|---------|----|----|-----|----|-----|----|-----|-----|-----|-----|-----|-----|
| Genotypes (G) | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** |
| Salinity levels (L) | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** | *** |
| G \( \times \) L | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| Genotypes | DHL21 | 5.66 a | 8.71 ab | 0.037 a | 25.07 a | 90.57 ab | 85.06 d | 78.53 a | 90.876 b | 0.156 a | 0.028 b | 0.087 a | 0.399 a |
| Sakha93 | 4.78 b | 7.15 c | 0.031 c | 23.33 bc | 92.97 a | 88.92 c | 75.80 a | 829.01 b | 0.127 a | 0.029 a | 0.075 a | 0.305 b |
| Giza168 | 4.66 b | 8.25 ab | 0.034 b | 20.67 d | 90.55 ab | 95.92 a | 77.09 a | 618.93 d | 0.118 b | 0.034 a | 0.072 b | 0.332 a |
| DHL3 | 5.45 a | 7.85 bc | 0.036 a | 18.73 b | 92.93 c | 85.22 a | 60.12 c | 728.89 b | 0.127 a | 0.034 a | 0.072 b | 0.332 a |
| DHL21 | 4.56 b | 8.38 ab | 0.033 bc | 24.67 ab | 91.39 ab | 93.53 ab | 66.46 b | 680.41 cd | 0.152 a | 0.022 cd | 0.087 a | 0.399 a |
| Gemmeiza9 | 5.34 a | 9.35 a | 0.029 d | 19.73 d | 85.37 a | 92.74 b | 64.54 b | 679.14 cd | 0.106 a | 0.025 bc | 0.070 bc | 0.318 b |
| Salinity levels (L) | Control | 4.389 a | 9.709 a | 0.032 b | 24.87 a | 94.78 a | 96.35 a | 80.80 a | 788.74 a | 0.137 b | 0.025 b | 0.065 b | 0.372 a |
| 7 dS m\(^{-1}\) | 5.170 a | 8.280 b | 0.034 a | 24.33 a | 87.89 a | 90.53 b | 73.90 b | 712.84 b | 0.130 a | 0.028 ab | 0.075 a | 0.365 a |
| 14 dS m\(^{-1}\) | 5.665 a | 8.670 c | 0.034 a | 18.73 b | 85.73 b | 88.01 b | 60.12 c | 728.89 b | 0.127 a | 0.025 a | 0.075 a | 0.305 b |

*, **, *** denote significant at the 0.05 and 0.01 levels of probability. Root number (RN), root length (RL), root dry matter (RDM), shoot length (SL), shoot dry matter (SDM), g, relative water content (RWC, \%), relative turgidity (RT, %), membrane stability index (MSI, %), chlorophyll content (CHL, \( \mu g \) g\(^{-1}\) FW), peroxidase (POD, U g\(^{-1}\) FW ml\(^{-1}\)), polyphenol oxidase (PPO, U g\(^{-1}\) FW ml\(^{-1}\)), and catalase (CAT, U g\(^{-1}\) FW ml\(^{-1}\)) are measured in the six genotypes of wheat while being cultivated under three salinity levels (Figs. 1 and 2).
on each eigenvalue of >1 (Table 3), the analysis grouped the nine explanatory traits into two PCs (PC1 and PC2) that had contribution rates of 37.97% and 32.61%, respectively (with a cumulative total of 70.85%). PC1 compiled four traits (RDM, RT, CHL, and CAT), and PC2 compiled five traits (RN, RL, SL, RWC, and POD).

4. Relationship between genetic matrix and phenotypic matrix

The Mantel test was used to estimate the relationship between two matrices of quantitative variables (genetic matrix and phenotypic matrix) for the three salinity levels and their interaction on 10 examined traits (Tables 4–7). The Mantel test revealed a highly significant relationship (p < 0.0001, alpha = 0.01) between the genetic matrix and the phenotypic matrix when the plants were grown without NaCl (r = 0.899), 7 dS m⁻¹ (r = 0.914), and 14 dS m⁻¹ (r = 0.927). Furthermore, across the three salinity levels, the Mantel test revealed a highly significant relationship between the genetic matrix and the phenotypic matrix (r = 0.917, p < 0.0001, alpha = 0.01).

4.1. Direct effects and stable-measured traits

To determine the stable-measured traits and their contribution to SDM, the correlations between SDM and the nine explanatory traits were estimated for the three salinity levels and their interactions (Table 8). In the treatment without NaCl, the results revealed significant positive and negative correlations between SDM and RL (rg = 0.478), RDM (rg = 0.767 and rp = 0.715), SL (rg = 0.552), RT (rg = -0.579 and rp = -0.730), CHL (rg = 0.507 and rp = 0.810), POD (rg = 0.720 and rp = 0.499), and CAT (rg = 0.936). The traits SL and CHL exhibited the most significant direct effects in the path analysis for both the genetic and phenotypic correlations (Table 8).
The $R^2$ values were 0.952 and 0.904, with noise values of 0.218 and 0.310, for both the genetic and phenotypic correlations, respectively. In the 7 dS m$^{-1}$ treatment, the results showed significant positive and negative correlations between SDM and RDM ($r_g = 0.743$ and $r_p = 0.693$), SL ($r_g = 0.856$ and $r_p = 0.725$), RWC ($r_g = 0.640$), RT ($r_g = -0.721$ and $r_p = -0.883$), CHL ($r_g = 0.868$ and $r_p = 0.775$), POD ($r_g = 0.460$) and CAT ($r_g = 0.981$ and $r_p = 0.851$). The traits RT, CHL, and CAT showed the most significant direct effects in the path analysis for both the genetic and phenotypic correlations (Table 8). The $R^2$ values were 0.971 and 0.911, with noise values of 0.172 and 0.299, for both the genetic and phenotypic correlations, respectively.

In the 14 dS m$^{-1}$ treatment, the results showed significant positive and negative correlations between SDM and RDM ($r_g = 0.779$ and $r_p = 0.715$), RT ($r_g = -0.814$ and $r_p = -0.730$), CHL ($r_g = 0.920$ and $r_p = 0.810$), POD ($r_g = 0.538$ and $r_p = 0.499$), and CAT ($r_g = 0.903$ and $r_p = 0.936$). The traits CHL and CAT exhibited the most significant direct effects in the path analysis for both the genetic and phenotypic correlations (Table 8). The $R^2$ values were 0.885 and 0.835, with noise values of 0.340 and 0.407, for both the genetic and phenotypic correlations, respectively. Across the three salinity levels, the results showed significant positive and negative correlations between SDM and RN ($r_g = 0.798$ and $r_p = 0.298$), RL ($r_g = -0.527$), RDM ($r_g = 0.657$ and $r_p = 0.606$), SL ($r_g = 0.322$ and $r_p = 0.320$), RT ($r_g = -0.967$ and $r_p = -0.485$), CHL ($r_g = 0.918$ and $r_p = 0.641$), POD ($r_g = 0.401$), and CAT ($r_g = 0.771$ and $r_p = 0.653$). The traits CHL and CAT showed the most significant direct effects in the path analysis for both the genetic and phenotypic correlations (Table 8). The $R^2$ values were 0.911 and 0.877, with noise values of 0.298 and 0.351, for both the genetic and phenotypic correlations, respectively. These findings demonstrated that genetic correlations provided the largest coefficient of determination and the least noise among the investigated traits.

4.2. Heritability, genetic gain, selection response, CR, and relative selection efficiency

All traits provided moderate-to-high heritability values across the three salinity levels, which varied from 40.49 to 88.10. The genetic gain exhibited values ranging from 6.89 to 22.85 (Table 9). Although the explanatory traits provided variable phenotypic and genetic correlations across the three salinity levels, they exhibited high heritability. With SDM, heritability generally expressed the highest values across the three salinity levels. The response to selection (R) for SDM and its explanatory traits, RN, RL, SL, CHL, and CAT, exhibited a higher selection response and was significant compared to that of SDM and the other traits. The co-heritability between influential and affected traits (SDM) varied from 35.76 to 91.53. The CR was higher for RWC, RT, CHL, and CAT than for the other explanatory traits. The relative selection efficiency provided significant relationships for the explanatory traits, except for RWC and POD, for which the relationships were insignificant.
5. Discussion

Salinity tolerance and high yield correlated robustly with multiple traits related to light interception and conversion into biomass, with different traits contributing at the basic stages of the crop growth cycle. The selection of related traits for conversion efficiency is a current objective in crop breeding. The results obtained in this study support the use of multiple morphophysiological traits at the seedling stage as target traits for breeding salt-tolerant and high-yielding wheat cultivars. The superior lines had multiple strategies to achieve high yield, confirming the complicated nature of grain yield formation. The results are discussed with regard to the multiple correlations between traits and their effect on yield (Pennacchi et al., 2018, Barakat et al., 2020a). The results of ANOVA revealed highly significant differences between salinity levels (L) and genotypes (G) for all the evaluated traits (Table 1), indicating a genetic difference between the wheat genotypes used for salinity tolerance, and the interaction effect was significant for most of the traits.

Increased salinity in the growing medium was conducive to a significant reduction in plant growth and negatively affected their physiological state by causing water deficits, ion toxicity, and nutrient deficiencies (Munns et al., 2006, El-Hendawy et al., 2017, Al-Ashkar et al., 2019). In our study, plant growth traits such as RL, SL, and SDM and physiological traits such as RWC, RT, MSI, and CHL, and POD were gradually reduced with increased salinity levels (Table 1). Mean performance and relative change were more obvious in the traits of the salt-sensitive wheat genotypes such as Gemmeiza9 and DHL12 when treated with 7 and 14 dS m\(^{-1}\), respectively, compared to those without NaCl treatment. The decline was more obvious than that in the salt-tolerant genotype Sakha93 and DHL21 (Figs. 1 and 2). Other traits such as RN, RDM, PPO, and CAT gradually increased with increased salinity levels (Table 2). Mean performance and relative change were greater for these traits in the salt-tolerant wheat genotype Sakha93 and DHL21 when treated with 7 and 14 dS m\(^{-1}\), respectively, compared to those without NaCl treatment. The increase was greater than that in the salt-sensitive wheat genotype Gemmeiza9 and
DHL12, except for RN for the salt-sensitive genotype (Fig. 1). The increase in RN might be due to the salt stress that increased physiological drought. Plants might tend to grow more roots to absorb additional water under higher salt stress levels (Ahmad et al., 2013).

Based on the performance of the salt-tolerant genotypes indicated that they were less affected by salinity stress because of an increase in CAT activity and its ability to remove toxins, a modification in leaf morphology, chlorophyll composition, heat dissipation by xanthophyll pigments, electron transfer to oxygen acceptors other than water, and the biochemical activities that inhibited oxidative damage during photosynthesis. Moreover, it could probably be because of genotypic variation at the level of stomatal closure and responses that altered the rate of CO2 fixation (Munns and Tester, 2008, Foyer and Noctor, 2005, Zeeshan et al., 2020). As an interesting aspect, it should be noted that the effect of salinity on the growth of wheat and its productivity could not be excluded. To mitigate the negative effects of salinity, a more thorough understanding is needed on how salinity affects the growth of wheat plants and their productivity. This could be achieved by more robust real-time detection and surveillance and more effective diagnosis of multiple morph-physiological traits during phonological growth stages. Therefore, such methods are important tasks to be undertaken. Based on earlier studies, the osmotic and ionic stresses that were posed by salinity resulted in a massive alteration in multiple morph-physiological traits of the plants (Akca and Samsunlu, 2012, Zhang et al., 2014, Al-Ashkar et al., 2019).

Although the selection of traits upon which to be focused on is a decisive step in breeding for increased yield and salt tolerance, understanding the engagements and trade-offs between traits and their actions during the plant cycle play a vital role in a rapid and efficient detection of promising genotypes (Pennacchi et al., 2018). The selection of genotypes could be more accurate if multi-traits could be increased by developing better genotypes through the intentional selection of multi-traits with a more pre-
Fig. 5. Effect of control, 7 and 14 dS m\(^{-1}\) treatments on peroxidase (POD), polyphenol oxidase (PPO), and catalase (CAT) in different genotypes of wheat. Different letters above a column indicate significant differences between the genotypes of the same treatment. Numerical values above a column show the relative percentage of reduction or increase in the trait compared with control treatment.

Table 2
Multicollinearity diagnosis (tolerance and variance inflation factor) of Pearson product-moment correlation matrix for 12 explanatory traits.

| Statistic | RN    | RL    | RDM   | SL    | RWC   | RT    | MSI   | CHL   | POD   | PPO   | CTA   |
|-----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Before excluding traits |       |       |       |       |       |       |       |       |       |       |       |
| Tolerance | 0.219 | 0.122 | 0.164 | 0.146 | 0.131 | 0.244 | 0.071 | 0.235 | 0.180 | 0.060 | 0.194 |
| VIF       | 4.569 | 8.217 | 6.102 | 6.849 | 7.629 | 4.104 | 14.085| 4.261 | 5.569 | 16.667| 5.165 |
| After excluding traits |       |       |       |       |       |       |       |       |       |       |       |
| Tolerance | 0.225 | 0.259 | 0.261 | 0.207 | 0.302 | 0.268 | -     | 0.306 | 0.235 | -     | 0.115 |
| VIF       | 4.451 | 3.866 | 3.834 | 4.841 | 3.312 | 3.727 | -     | 3.272 | 4.256 | -     | 8.674 |

Root number (RN), root length (RL), root dry matter (RDM), shoot length (SL), shoot dry matter (SDM), relative water content (RWC), relative turgidity (RT), membrane stability index (MSI), chlorophyll content (CHL), peroxidase (POD), polyphenol oxidase (PPO), and catalase (CAT), variance inflation factor (VIF).
Table 3
Eigenvalues, proportion, and cumulative variance and eigenvectors for the three components for nine measured explanatory traits.

| Principal factor | Eigen value | Variability (%) | Cumulative% | Eigen vector |
|-----------------|-------------|-----------------|-------------|--------------|
|                 |             |                 |             | RN RL RDM SL RWC RT CHL POD CAT |
| PC1             | 3.417       | 37.971          | 37.971      | 0.235 -0.132 0.434 0.070 -0.258 -0.469 0.357 0.306 0.476 |
| PC2             | 2.935       | 32.613          | 70.583      | -0.437 0.378 0.031 0.522 0.362 0.110 0.315 0.386 0.037 |
| PC3             | 0.845       | 9.393           | 79.977      | -0.067 0.697 0.238 0.061 -0.542 0.157 -0.199 -0.250 0.172 |

Values in bold indicate the largest absolute value of each trait in all factors.

Table 4
Genetic matrix (upper diagonal) and phenotypic matrix (below diagonal) among nine explanatory traits and SDM as dependent variable obtained from the control treatment (n = 18).

|                | RN   | RL   | RDM  | SL   | RWC  | RT   | CHL  | POD  | CAT  | SDM  |
|----------------|------|------|------|------|------|------|------|------|------|------|
| RN             |      |      |      |      |      |      |      |      |      |      |
| RL             | -0.690 | 0.455 | 0.284 | 0.163 | -0.566 | 0.931 | 0.413 | 0.699 | 0.086 |
| RDM            | 0.321 | 0.202 | -0.297 | -0.938 | -0.757 | -0.277 | -0.469 | 0.952 | -0.478 |
| SL             | 0.183 | -0.200 | 0.698 |      | -0.074 | 0.266 | 0.262 | 0.980 | -0.108 | 0.552 |
| RWC            | 0.094 | -0.745 | -0.532 | -0.090 |      | 0.858 | -0.348 | -0.774 | -0.995 | -0.275 |
| RT             | -0.486 | -0.626 | -0.431 | 0.164 | 0.662 |      | -0.486 | 0.130 | -0.957 | -0.579 |
| CHL            | 0.682 | -0.291 | 0.683 | 0.240 | -0.205 | -0.436 |      | 0.628 | 0.515 | 0.507 |
| POD            | 0.305 | -0.319 | 0.702 | 0.838 | -0.277 | 0.065 | 0.520 |      | -0.957 | 0.720 |
| CAT            | 0.446 | 0.566 | 0.385 | -0.213 | -0.409 | -0.912 | 0.395 | -0.276 |      | 0.134 |
| SDM            | 0.039 | 0.241 | 0.715 | 0.328 | 0.116 | -0.730 | 0.810 | 0.499 | 0.936 |      |

Values in bold are different from 0 with a significance level of alpha = 0.05.

Table 5
Genetic matrix (upper diagonal) and phenotypic matrix (below diagonal) among nine explanatory traits and SDM as dependent variable obtained from the 7 dS m⁻¹ treatment (n = 18).

|                | RN   | RL   | RDM  | SL   | RWC  | RT   | CHL  | POD  | CAT  | SDM  |
|----------------|------|------|------|------|------|------|------|------|------|------|
| RN             |      |      |      |      |      |      |      |      |      |      |
| RL             | 0.638 | 0.164 | -0.310 | -0.918 | -0.910 | -0.100 | -0.888 | 0.090 | 0.221 |
| RDM            | 0.202 | 0.045 | 0.578 | 0.394 | -0.717 | 0.423 | 0.312 | 0.651 | 0.743 |
| SL             | -0.199 | 0.047 | 0.473 | 0.898 | -0.877 | 0.906 | 0.982 | 0.777 | 0.856 |
| RWC            | -0.763 | -0.381 | 0.264 | 0.766 |      | -0.127 | 0.808 | 0.937 | 0.717 | 0.640 |
| RT             | -0.531 | -0.331 | -0.525 | -0.695 | -0.108 |      | -0.910 | -0.536 | -0.983 | -0.721 |
| CHL            | 0.035 | 0.188 | 0.424 | 0.964 | 0.578 | -0.839 |      | 0.773 | 0.705 | 0.868 |
| POD            | -0.506 | 0.051 | 0.294 | 0.885 | 0.899 | -0.321 | 0.761 |      | 0.584 | 0.460 |
| CAT            | 0.127 | 0.245 | 0.568 | -0.679 | 0.456 | -0.679 | 0.688 | 0.588 |      | 0.981 |
| SDM            | 0.272 | 0.026 | 0.693 | 0.725 | 0.352 | -0.883 | 0.775 | 0.412 | 0.851 |      |

Values in bold are different from 0 with a significance level of alpha = 0.05.
cise mean and greater positive genetic correlation (Neyhart et al., 2019). When the interrelationships of explanatory traits increase, the problem of evaluating their relative significance in the evaluation of the dependent trait is a substantial impediment (Hoerl and Kennard, 1981, Olivoto et al., 2017). Therefore, determining the degree of the interrelationships of explanatory traits and the degree of multicollinearity in the matrices of explanatory traits is a critical step to accomplish before estimating the path analysis. It was evident in our study that MSI and PPO exhibited detrimental effects of multicollinearity because of the large VIF values (VIFs > 10; Table 2). When MSI and PPO were excluded from the model, a considerable reduction in multicollinearity of the matrices was evident (VIFs < 10). Consequently, the degree of trustworthiness of the path coefficients depends on the ability of

Table 6
Genetic matrix (upper diagonal) and phenotypic matrix (below diagonal) among nine explanatory traits and SDM as dependent variable obtained from the 14 dS m$^{-1}$ treatment (n = 18).

|     | RN  | RL  | RDM  | SL  | RWC | RT | CHL | POD | CAT | SDM |
|-----|-----|-----|------|-----|-----|----|-----|-----|-----|-----|
| RN  | 0.398 | 0.097 | -0.518 | -0.937 | 0.123 | 0.057 | -0.671 | 0.094 | 0.063 |
| RL  | 0.234 | -0.021 | 0.350 | -0.049 | -0.927 | 0.893 | 0.605 | 0.884 | 0.166 |
| RDM | 0.096 | 0.292 | 0.724 | 0.456 | -0.631 | 0.608 | 0.489 | 0.703 | 0.779 |
| SL  | -0.453 | 0.132 | 0.697 | 0.860 | -0.634 | 0.503 | 0.851 | 0.436 | 0.404 |
| RWC | -0.745 | -0.077 | 0.387 | 0.743 | -0.153 | 0.067 | 0.900 | 0.276 | 0.101 |
| RT  | 0.080 | -0.557 | 0.599 | -0.583 | 0.149 | -0.907 | 0.616 | -0.905 | 0.814 |
| CHL | 0.016 | 0.552 | 0.559 | 0.484 | 0.013 | -0.990 | 0.628 | 0.950 | 0.920 |
| POD | -0.587 | 0.433 | 0.499 | 0.816 | 0.778 | -0.474 | 0.596 | 0.662 | 0.538 |
| CAT | 0.069 | 0.537 | 0.698 | -0.785 | 0.195 | -0.785 | 0.859 | 0.651 | 0.903 |
| SDM | 0.039 | 0.241 | 0.715 | 0.328 | 0.116 | -0.730 | 0.810 | 0.499 | 0.936 |

Root number (RN), root length (RL), root dry matter (RDM), shoot length (SL), shoot dry matter (SDM), relative water content (RWC), relative turgidity (RT), chlorophyll content (CHL), peroxidase (POD), catalase (CAT). Values in bold are different from 0 with a significance level of alpha = 0.05.

Table 7
Genetic matrix (upper diagonal) and phenotypic matrix (below diagonal) among nine explanatory traits and SDM as dependent variable obtained from across the three salinity levels (n = 54).

|     | RN  | RL  | RDM  | SL  | RWC | RT | CHL | POD | CAT | SDM |
|-----|-----|-----|------|-----|-----|----|-----|-----|-----|-----|
| RN  | 0.769 | 0.663 | 0.087 | -0.702 | -0.913 | 0.890 | -0.134 | 0.799 | 0.798 |
| RL  | 0.153 | -0.311 | -0.582 | 0.415 | 0.544 | -0.764 | -0.011 | -0.639 | 0.527 |
| RDM | 0.164 | 0.030 | 0.587 | 0.087 | 0.514 | 0.092 | 0.455 | 0.408 | 0.657 |
| SL  | 0.087 | -0.087 | 0.473 | 0.651 | 0.761 | 0.678 | 0.969 | 0.223 | 0.322 |
| RWC | -0.352 | -0.045 | 0.087 | 0.478 | -0.289 | 0.274 | 0.912 | 0.230 | 0.087 |
| RT  | -0.026 | 0.004 | 0.486 | -0.366 | -0.129 | -0.916 | -0.626 | -0.821 | -0.976 |
| CHL | 0.171 | 0.008 | 0.429 | 0.553 | 0.188 | -0.595 | 0.544 | 0.734 | 0.918 |
| POD | -0.140 | 0.267 | 0.520 | 0.627 | 0.477 | -0.295 | 0.608 | -0.347 | 0.159 |
| CAT | 0.160 | -0.332 | 0.410 | 0.283 | 0.151 | -0.449 | 0.610 | 0.544 | 0.771 |
| SDM | 0.298 | -0.107 | 0.606 | 0.320 | 0.073 | -0.485 | 0.641 | 0.401 | 0.653 |

Root number (RN), root length (RL), root dry matter (RDM), shoot length (SL), shoot dry matter (SDM), relative water content (RWC), relative turgidity (RT), chlorophyll content (CHL), peroxidase (POD), catalase (CAT). Values in bold are different from 0 with a significance level of alpha = 0.05.
Table 8

| Traits                  | Control (n = 18) | Across the salinity levels (n = 54) |
|------------------------|------------------|-----------------------------------|
|                        | Direct           | Indirect                          | Direct           | Indirect                          |
|                        | effects          | effects                           | effects          | effects                           |
| RN                     | 0.086            | 0.001                             | 0.39             | 0.001                             |
| RL                     | 0.478            | 0.072                             | 0.872            | 0.072                             |
| RDM                    | 0.376            | 0.059                             | 0.241            | 0.059                             |
| RT                     | 0.673            | 0.051                             | 0.151            | 0.051                             |
| RWC                    | 0.579            | 0.024                             | 0.810            | 0.024                             |
| CHL                    | 0.307            | 0.020                             | 0.810            | 0.020                             |
| CAT                    | 0.704            | 0.096                             | 0.765            | 0.096                             |
| Residual effect        | 0.218            | 0.352                             | 0.193            | 0.352                             |

The correlation value is divided into direct and indirect effects by path analysis. Indirect effects may occur because of several traits, but direct effects are important for plant breeders in the selection of traits. The traits CHL and CAT showed the most significant direct effects in the path analysis for both the genetic and phenotypic correlations for the three salinity levels and their interactions in most of the cases (Table 8), which supported their importance. They could be used as criteria for a thorough selection for salinity tolerance in wheat (Khan et al., 2004, Nguyen, 2012). Despite the fact that the traits RDM and POD showed a significant correlation in most of the treatments, their direct effects were low, which suggested that they had devolved into indirect effects. These findings demonstrated that genetic correlation provided the largest coefficient of determination and the lowest noise among the examined traits. Heritability is the proportion of the phenotypic variance derived from genetic effects, which has the ability to be passed from parents to descendants, and could serve as an indicator of traits with strong genes (Falconer, 1989, Zhang et al., 2000, Shi et al., 2017). If one trait has high heritability (>0.60%) and genetic gain (>20%) and also a highly significant genetic correlation for its direct effect and co-heritability with the dependent trait, it
could serve as a significant indicator of successful selection in breeding programs (Jing, 1999, Gutierrez et al., 2010, Shi et al., 2017). However, if one of these factors is lost, it will not be a good indicator.

The Co-heritability indicates the genetic linkages per two of quantitative traits. Hence, co-heritability is a relevant component of the genetic cause for the phenotypic correlation between traits, which can be used to simplify the analysis of the genetic correlation coefficients (Janssens, 1979, Singh and Narayanan, 2000), and the results are indicative of this fact (Table 9). In this study, the relative efficiency of selection was calculated based on heritability and genetic correlation between traits. The ratio between correlated responses for the dependent trait and independent traits and the responses to selection for the independent traits is a measure of the relative selection efficiency (Falconer, 1989, Gutierrez et al., 2010, Shi et al., 2017). CHL and CAT showed selection efficiencies that were higher than the remainder of the traits. They also had higher co-heritability. This indicates that the selection of these traits could achieve better salinity tolerance in breeding programs.

6. Conclusions

Our study results confirmed the importance of excluding the effects of multicollinearity and emphasized the importance of CHL and CAT in providing significant direct effects in the path analysis for both the genetic and phenotypic correlations for the three saline levels and their interactions, which reflected their stability. The results also demonstrated the significance of genetic relationships, such as heritability, genetic gain, co-heritability, and selection efficiencies, for evaluating trait stability for saline levels and their interactions.

Funding

The authors extend their appreciation to the Deanship of Scientific Research at King Saud University for funding this work through Research Group No. (RG-1440-054).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors extend their appreciation to the Deanship of Scientific Research at King Saud University for funding the work through the research group project No RG-1440-054 and the Researchers Support & Services Unit for their technical support.

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Table 9

| RN | RL | RDM | SL | RWC | RT | CHL | POD | CAT | SDM |
|----|----|-----|----|-----|----|-----|-----|-----|-----|
| Genetic parameters for each trait | Heritability | 73.02 | 63.98 | 74.69 | 60.07 | 88.10 | 73.02 | 65.50 | 40.49 | 76.42 |
| Genetic gain | 14.49 | 12.25 | 20.48 | 12.99 | 6.89 | 8.94 | 17.49 | 21.19 | 15.73 | 22.58 |
| R | 0.554** | 0.827** | 0.004 | 0.761** | 0.055 | 0.094 | 0.351** | 0.055 | 0.342** | 0.324* |
| Genetic parameters for each trait with SDM (as correlative traits) | Co-heritability | 85.10 | 65.93 | 86.70 | 66.24 | 58.51 | 91.53 | 85.19 | 35.76 | 88.17 |
| CR | 0.003 | –0.002 | 0.003 | 0.001 | 0.357** | –0.448** | 0.397** | 0.004 | 0.347** | – |
| CR/R | 0.836** | –0.600** | 0.664** | 0.347** | 0.089 | –0.844** | 0.832** | 0.124 | 0.761** | – |

Root number (RN), root length (RL), root dry matter (RDM), shoot length (SL), shoot dry matter (SDM), relative water content (RWC), relative turgidity (RT), chlorophyll content (CHL), peroxidase (POD), catalase (CAT). * and ** indicate significance at p < 0.05 and 0.01, respectively.
