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Impact of salt stress on physiological traits in tomato (*Lycopersicon esculentum* Mill.)

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Abstract

Salt stress is a major abiotic factor that limits plant growth and development globally, primarily due to the use of low-quality irrigation water and soil salinization caused by seawater intrusion. This study examines physiological parameters, antioxidant enzymes and the K/Na ratio in response to salt stress in various tomato genotypes at a salinity level of 8 dS m^{-1} during the vegetative stage. Specifically, it investigates superoxide dismutase activity, relative water content, electrolyte leakage, proline content, chlorophyll fluorescence and potassium and sodium ion content in roots, shoots and leaves. The results revealed significant variation in salt tolerance among the different genotypes. Genotypes LE-14 and LE-1 demonstrated superior performance under salt stress, displaying higher relative water content, reduced electrolyte leakage, increased superoxide dismutase activity, elevated proline content and favorable K/Na ratios. Principal component analysis showed significant eigenvalues, accounting for 72.5% of the total variability. These findings provide valuable insights into the mechanisms of salt tolerance in tomato crops and highlight the potential of LE-14 and LE-1 for cultivation in saline environments. The study emphasizes the importance of conducting field trials to validate these results for sustainable production in salt-affected areas.

Keywords

electrolyte leakage; Na and K content; proline; RWC; SOD; tomato (*Lycopersicon esculentum* Mill.)

Introduction

Tomato (*Lycopersicon esculentum* Mill.), a member of the Solanaceae family, is a vital and widely cultivated vegetable crop worldwide. As a day-neutral plant, tomatoes can be grown year-round in various climates. Although adaptable to nearly all soil types, tomatoes are particularly sensitive to moderate levels of soil salinity, which significantly reduces crop productivity (1). Vegetable crops generally exhibit low tolerance to salinity, classifying them as sensitive or moderately sensitive (2). In arid and semi-arid regions, high concentrations of soluble salts in the soil limit the cultivation of various crops. Like other crops, vegetable crops display a broad range of salinity tolerance: cabbage, broccoli, cauliflower, tomato, potato, eggplant, turnip, lettuce, radish, cucumber, pepper and pumpkin are moderately sensitive; red beet shows moderate tolerance, while onion, peas, carrot and okra are highly sensitive to salt (3). Research demonstrates notable variation in salinity response among tomato genotypes, emphasizing the value of genetic diversity in screening and breeding salt-tolerant varieties. Salinity affects multiple aspects of tomato plant physiology, hindering growth and development. One critical metabolic response to salt stress is the synthesis of compatible osmolytes, which play essential roles in adjusting osmotic potential, protecting cellular and subcellular structures and scavenging free radicals to prevent oxidative damage. Under salt stress, tomato plants produce osmotically active compounds such as sugars, sugar alcohols and amino acids to alleviate the osmotic stress induced by salinity.

Developing and breeding tomato cultivars that can thrive and yield well in saline conditions is a long-term, complementary strategy to reduce the adverse effects of salinity. The accumulation of solutes, such as proline, is crucial for helping plant systems adapt to saline environments. However, the physiological mechanisms underlying proline accumulation under salt stress remain incompletely understood. Additionally, sugar and other organic osmolytes significantly contribute to osmotic adjustment, accounting for up to 50% of the total osmotic potential in glycophytes exposed to saline conditions. Various plants have evolved different mechanisms to tolerate high salt concentrations (4, 5). The ability of plants to detect changes in ion levels and respond accordingly is crucial for their survival in saline environments (6). Tomato plants exhibit moderate salinity tolerance by maintaining water and ionic balance; however, high salinity negatively impacts seed germination, growth and fruit development in tomatoes (7). Most research on tomato salt tolerance has focused on comparisons between wild and domesticated species, with limited studies on commercial cultivars. This study aims to evaluate the effects of salt stress on physiological parameters across 12 tomato genotypes.

Materials and Methods

The experiment was conducted in 2020 at the Department of Vegetable Science, Horticultural College and Research Institute, Tamil Nadu Agricultural University, Coimbatore, using a pot culture approach. Twelve tomato genotypes were selected for study, including LE-1, Angarlata, LE-14, IIVR-EC-2798, PKM-1, EC-326146, Punjab Bagkoa, IIVR-EC-2495, IIVR-88783, H-24, LE-1020 and EC-326148. These genotypes were chosen based on their performance in a previous experiment with varying NaCl concentrations (2, 4, 6, 8, 10 and 12 dS m^{-1}). Among these, 8 dS m^{-1} was determined to be a critical threshold for tomato genotypes (8). In this experiment, 12 genotypes were grown under well-watered conditions as a control and with irrigated containing NaCl at 8 dS m^{-1} for salt stress treatment. A completely randomized block design with three replications was employed.

Seedlings, 25 days old, were transplanted into pots, with the control group irrigated with regular water and the stressed group with saltwater containing NaCl at 8 dS m^{-1}. Saltwater irrigation began three days after planting (DAP) and continued until harvest. Physiological parameters, such as superoxide dismutase (SOD) activity, relative water content (RWC), electrolyte leakage, proline content and Fv/Fm ratio, were measured 45 days after planting. Fully expanded, physiologically active young leaves (one leaflet) were collected for biochemical analysis. Additionally, sodium (Na) and potassium (K) content in the leaves, shoots and roots were assessed.

Relative water content (RWC: %)

The relative water content (RWC) was measured using the previously described method (9). Leaf discs were collected from physiologically active leaves and their fresh weight (FW) was recorded. These discs were then placed in petri dishes with water for 1 hr to allow water absorption. After soaking, any excess water was gently removed by blotting the discs with tissue paper and their turgid weight (TW) was recorded. The discs were then dried in a hot air oven at 80 °C for 24 hr to obtain their dry weight (DW). RWC was calculated using the formula:

$$RWC = (FW-DW)/ (TW-DW) \times 100 \qquad \text{(Eqn. 1)}$$

Electrolyte leakage assay (EL: %)

Electrolyte leakage (EL) was measured following the previously described method (10). Ten leaf discs, each 1 cm^2, were collected and placed in a flask containing 25 mL of deionized water. The flasks were then shaken for 20 hr and the initial electrical conductivity (EC) was recorded. Next, the flasks were place in a water bath at 80 °C for 1 hr, followed by an additional 20 hr of shaking. The final conductivity was measured and electrolyte leakage (%) was calculated using the formula:

$$EL (\%) = \text{Initial EC} / \text{Final EC} \times 100 \qquad \text{(Eqn. 2)}$$

Chlorophyll fluorescence parameter

Chlorophyll fluorescence (Fv/Fm ratio) was measured 60 days after sowing using a fluorometer (PEA, Hansatech Instrument Ltd., Version 1.21, UK), following the previously described method (11).

Proline determination

Proline content was determined according to previously described method (12). A 500 mg leaf sample was macerated with 3% sulphosalicylic acid and transferred to a centrifuge tube. The sample was then centrifuged at 3000 rpm for 20 min and the supernatant was collected. From this, 2 mL of the supernatant was mixed with 2 mL of glacial acetic acid and 2 mL of ninhydrin. The reaction mixture was boiled for 1 hr and then transferred to a separating funnel. After adding 20 mL of toluene, the reaction was completed and the lower pink-coloured phase was collected. Optical density (OD) values were measured at 520 nm using a spectrophotometer and the results were expressed as µg g^{-1} FW.

Determining K and Na content

Tomato plants were uprooted and thoroughly washed. The leaves, shoots and roots were separated and air-dried, followed by oven-drying at 70 °C for 24 hr. The dried leaf samples were ground into a fine powder. 1 g of this powder from each plant part was placed in a conical flask and 10 mL of diacid was added. The samples were left overnight in a fume hood for pre-digestion. They were then heated on a hot plate at 60 °C, then 120 °C for 30 min intervals and finally increased to 250 °C until the solutions became clear. After cooling, the samples were transferred to a 50 mL volumetric flask and filtered using Whatman No. 1 filter paper. The filtered solution was then analyzed for Na and K content using a flame photometer (13).

Statistical analysis

The data were statistically analyzed using a randomized block design and significance was determined with ANOVA tables at

$p<0.05$ (14). Correlation and principal component analysis were conducted using R studio version 4.3.1.

Results and Discussion

Salt stress is a significant abiotic factor that limits the growth and development of plants worldwide. It arises from the use of low-quality irrigation water and the intrusion of seawater, which leads to soil salinization. Salt stress adversely affects various physiological processes in plants, resulting in excessive accumulation of reactive oxygen species, ion toxicity, a weakened antioxidant defense system, impaired photosynthetic functions and imbalanced nutrient uptake. The response of tomato plants to salt stress is discussed in detail below.

Relative water content (RWC)

The RWC of leaves is a crucial indicator of water status and plant health. Salt stress significantly reduces RWC across all 12 tomato genotypes studied compared to the well-watered control plants. The well-watered plants maintained an RWC of nearly 85 to 90% in all genotypes. Under salt stress conditions, the most substantial reduction in RWC was observed at high salinity levels across all genotypes. Among these, LE-1 and LE-14 exhibited higher RWC percentages, followed by EC-326146. These plants maintained a high water status, indicating that well-hydrated cells could dilute the salt concentration, which prevented salt injury and demonstrated their salt tolerance. In contrast, the genotypes H-24, EC-326148 and LE-1020 showed the greatest reduction in RWC (Fig. 1a). The reduced water availability in the rooting medium led these plants to uptake more sodium, which increased the solute potential. This decline in RWC clearly indicates water stress, hampering water flow to areas of the plant where new cell elongation occurs, as observed in tomatoes and peaches (15, 16). This finding aligns with previous research, which reported that salt-sensitive plants exhibit a greater decrease in RWC compared to salt-tolerant plants (17). Similarly, another study found that RWC decreases with increasing salt concentration (18).

Electrolyte leakage

Leaf electrolyte leakage is a valuable metric for assessing membrane stability and salt stress tolerance. A reduction in cell volume increases the density and viscosity of cytoplasmic components, enhancing the likelihood of molecular interactions, which can lead to protein degradation and membrane damage. The leakage of electrolytes from plasma membranes serves as a key indicator of plant salt tolerance (19). Generally, electrolyte leakage increases under salt stress. In this experiment, LE-14 and Angarlata exhibited the most significant reduction in electrolyte leakage, followed by LE-1 (Fig. 1b), compared to the other tomato genotypes. This reduced leakage can be attributed to greater antioxidant activity, higher water status and lower sodium uptake in these genotypes. These findings align with previous studies (20, 21). High electrolyte leakage results from the rapid accumulation of reactive oxygen species (ROS), which induces oxidative stress due to an excess of energy being directed towards oxygen. This leads to lipid peroxidation, causing damage to lipids, proteins and nucleic acids in the cell membrane, ultimately resulting in electrolyte leakage and cell senescence (22, 23).

Superoxide dismutase activity (SOD)

Under abiotic stress conditions, such as drought, salinity, extreme temperatures and heavy metals, plants produce reactive oxygen species (ROS), including hydrogen peroxide, superoxide radicals and hydroxyl radicals. These ROS are highly reactive and can cause significant damage to cellular components such as lipids, proteins and nucleic acids, leading to oxidative stress. To combat this, plants have developed a sophisticated antioxidant defense system comprising both enzymatic and non-enzymatic components, which helps mitigate the damaging effects of ROS. The results of this study indicated that superoxide dismutase (SOD) activity was enhanced in all tomato genotypes under salt stress compared to the control. Notably, LE-14 exhibited significantly increased SOD activity, followed by Punjab Bagkoa (Fig. 1c). These results align with findings reported in the previous studies (24, 25). Superoxide dismutase is well-known as an oxygen scavenger within enzymatic scavenging systems and its action converts potentially harmful superoxide radicals into water and molecular oxygen (26). This study suggests that the high constitutive and induced levels of SOD in tomato genotypes may reflect an effective scavenging mechanism to mitigate oxidative damage within cells. Conversely, lower SOD activity was observed in the tomato genotype IIVR-88783, followed by EC326146 and PKM 1. This might be due to the increased accumulation of ROS and Na^{+} concentrations.

Proline content

Plants subjected to salt stress accumulate compatible solutes (27). In the 12 tomato genotypes studied, proline synthesis increases gradually and significantly, with the highest level observed in genotypes LE-14 and LE-1 (Fig. 1d) compared to the control. The increase in proline content under salt stress conditions enhances the plant's ability to tolerate salt stress, leading to improved seed germination, biomass, photosynthesis, gas exchange and overall yield. These advantages primarily arise from enhanced nutrient and water uptake, as well as biological nitrogen fixation. Proline accumulation represents a crucial response in plants for mitigating the effects of salt and water stress, as it helps regulate osmotic potential in the cytoplasm (28, 29). These findings support the notion that increased proline synthesis under salt stress is key to a plant's ability to tolerate salinity. Furthermore, enhanced proline accumulation may also regulate various processes essential for survival in salt-stressed conditions (30).

Fv/Fm ratio

Chlorophyll fluorescence is an extremely sensitive method for assessing stress-induced damage to PSII (31). According to previous study, the Fv/Fm ratio for an active leaf may vary, with a decline in this ratio indicating photo-inhibitory damage (32). In the current study, an increase in the Fv/Fm ratio was observed among the tomato genotypes 60 days after planting. Of the 12 genotypes analyzed, LE-14 exhibited the highest Fv/Fm ratio, followed by LE-1 and Angarlata (Fig. 2). Previous studies have noted that salt tends to accumulate primarily in older leaves, which ultimately fall off (2). This process allows photosynthesis to continue efficiently, as younger leaves remain relatively unaffected by the salt accumulation (33).

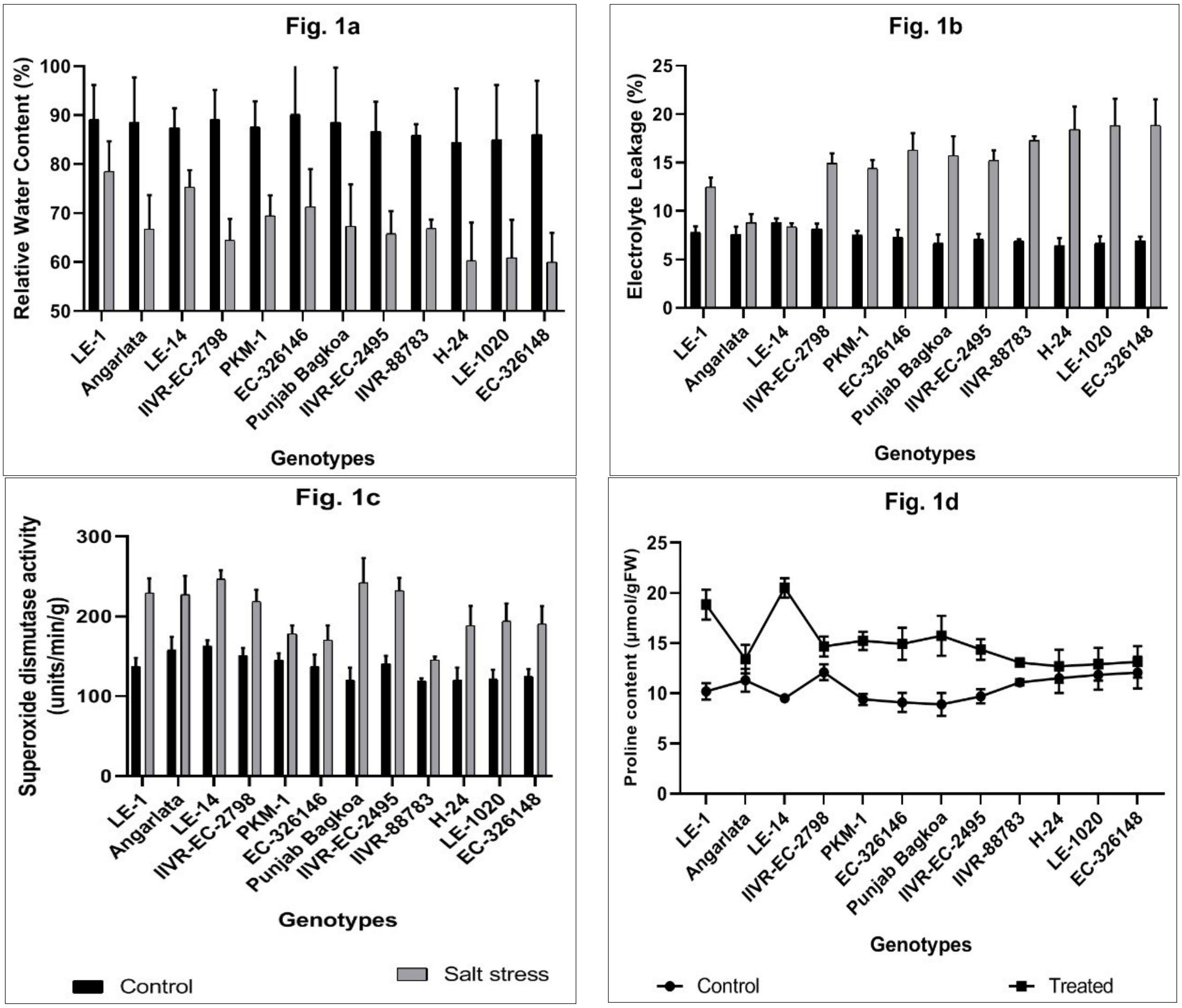

Fig. 1. Effect of salinity on relative water content, electrolyte leakage, proline content and superoxide dismutase activity.

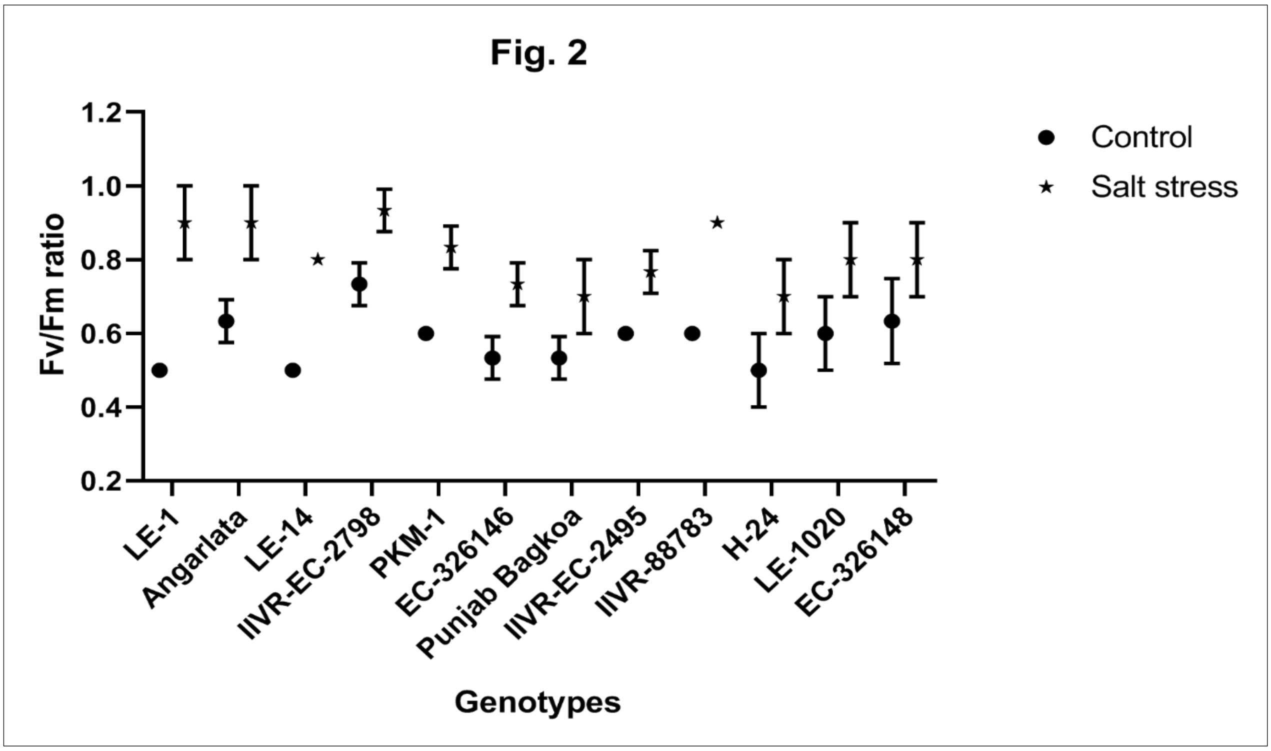

Fig. 2. Effect of salinity on Fv/Fm ratio on tomato genotypes.

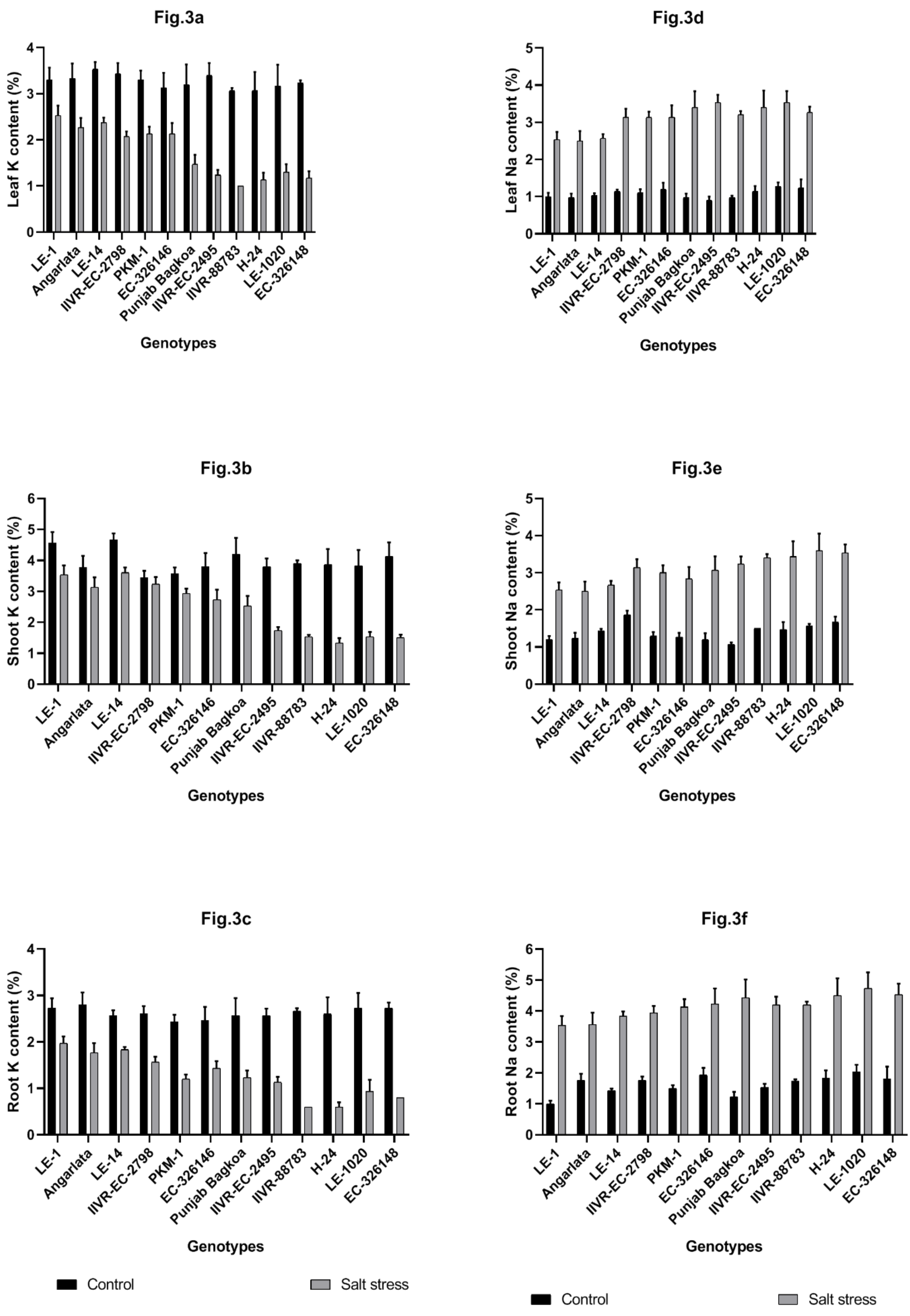

Fig. 3. Effect of salinity on leaf, shoot and root K content and leaf, shoot and root Na content.

Effect of salinity on leaf, shoot and root K content and leaf, shoot and root Na content

In this study, the potassium (K) and sodium (Na) contents in the leaves, shoots and root of 12 tomato genotypes were analyzed under both salt-stress and control conditions (Fig. 3) and a comparative performance analysis was conducted. Maintaining ion homeostasis through ion uptake and compartmentalization is essential for normal plant growth under salt stress. The genotypes showed significant variability in tolerance to NaCl levels of 8 dS m^{-1}, as determined by K/Na ratios in the leaves, shoots and roots, along with percentage reductions compared to the control treatment. Among the twelve cultivars, LE-14, LE-1 and Angarlata recorded the highest potassium content in leaves, shoots and roots, identifying them as the most salt-tolerant cultivars, followed by IIVR-EC-2789. These cultivars were less affected by salt treatment due to higher potassium levels, which supported better gas exchange through stomatal opening, improved transpiration, maintained cell hydration and regulated turgor pressure. Additionally, these genotypes maintained the lowest Na content across leaves, shoots and roots, with LE-1, LE-14 and Angarlata showing the highest salt tolerance, followed closely by EC-326146. Plants growing under saline conditions tend to accumulate more Na, leading to ionic imbalance. Reduced K uptake at higher Na concentrations hinders growth (7, 17). Excess Na in leaf tissues can disrupt metabolic processes, causing ion toxicity and osmotic stress, both of which severely impact plant growth (34, 35). In saline-treated plants, K deficiency was inversely related to increased Na accumulation, suggesting that Na and K ions compete for the same transport systems at the root surface (36).

When plants absorb and accumulate excessive Na, it becomes highly toxic at various physiological levels, causing issues like impaired potassium nutrition, water stress and oxidative cell damage (37). In our experiments with tomato cultivars under saline conditions of 8 dS m^{-1}, we observed reduced Na uptake, which led to lower Na ratios in roots, shoots and leaves. Some cultivars exhibited greater resilience to high salt concentrations, indicating their capacity to tolerate higher Na levels. For instance, LE-1, LE-14 and Angarlata showed higher K/Na ratios at 8 dS m^{-1}, maintaining growth even under high salt conditions and identifying them as the most salt-tolerant genotypes. Studies have shown that increased K concentrations in plants under salt stress can enhance growth and yield (38, 39). Reduced K content in plant tissues under high NaCl treatments is also well-documented in other plant varieties, including tomato, melon, eggplant (40), spinach, pepper (37) and squash (41).

Principal component analysis

Control: In this principal component analysis (PCA), the principal components (PC) with eigenvalues greater than 1 are PC1 (7.978) and PC2 (1.303). PC1 explains 72.5% of the variance, with positive correlations observed for root, shoot and leaf K content, SOD activity, proline content, RWC and Fv/Fm ratio, while negative correlations are observed with electrolyte leakage and root, leaf and shoot Na content. PC2 accounts for 11.8% of the variance, showing positive correlations with SOD, EL, RWC, leaf and shoot K content, root, shoot and leaf Na content and proline content, whereas the Fv/Fm ratio is negatively correlated. Root, leaf and shoot K content, along with proline, RWC and SOD, show positive correlation in both PC1 and PC2. Additionally, root, leaf and shoot K content, along with RWC, are correlated with PKM1, while root, leaf, shoot Na content and electrolyte leakage correlate with IIVR-EC-295. The genotypes Punjab Bagkoa, LE-14, IIVR-88783 and LE-1 are outliers, not correlating with any other parameters.

Salt stress: In this PCA, eigenvalues greater than 1 are PC1 (7.978) and PC2 (1.303). PC1 accounts for 72.5% of the variance, showing positive correlation with K content in roots, shoots and leaves, as well as with SOD, proline, RWC and Fv/Fm. Conversely, it displays negative correlations with EL and Na content in roots, leaves and shoots. PC2 explains 11.8% of the variance, exhibiting positive correlations with SOD, EL, RWC, K content in leaves, Na content in roots, shoots and leaves, proline and K content in shoots, while Fv/Fm is negatively correlated. Both PC1 and PC2

Table 1. Principal component analysis of the first four principal components of various traits of tomato genotypes under control and salt stress

Characters	Control					Salt stress				
	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4	PC5
SOD	**0.995**	-0.092	0.039	-0.027	0.001	**0.995**	-0.092	0.039	-0.027	0.001
RWC	0.060	**0.880**	0.303	-0.356	-0.018	0.060	**0.880**	0.303	-0.356	-0.018
EL	-0.069	-0.325	**0.901**	-0.044	0.156	-0.069	-0.325	**0.901**	-0.044	0.156
Proline	0.045	0.284	0.229	**0.885**	-0.151	0.045	0.284	0.229	**0.885**	-0.151
Fv/Fm	0.000	0.003	-0.016	-0.007	-0.016	0.000	0.003	-0.016	-0.007	-0.016
K leaf	0.009	0.073	-0.071	0.154	**0.512**	0.009	0.073	-0.071	0.154	**0.512**
K shoot	0.015	0.102	-0.102	0.148	**0.688**	0.015	0.102	-0.102	0.148	**0.688**
K root	0.010	0.046	-0.053	0.029	0.338	0.010	0.046	-0.053	0.029	0.338
Na leaf	-0.004	-0.058	0.082	-0.136	0.190	-0.004	-0.058	0.082	-0.136	0.190
Na shoot	-0.007	-0.066	0.073	0.013	-0.172	-0.007	-0.066	0.073	0.013	-0.172
Na leaf	-0.008	-0.072	0.106	-0.148	0.193	-0.008	-0.072	0.106	-0.148	0.193

SOD: Superoxide dismutase activity, RWC: Relative water content, Fv/Fm: Fluorescence parameter, Pro: Proline content, EL: Electrolyte leakage, Na leaf: Leaf sodium content, Na shoot: Shoot sodium content, Na root: Root sodium content, K leaf: Leaf potassium content, K shoot: Shootpotassium content, K root: Root potassium content

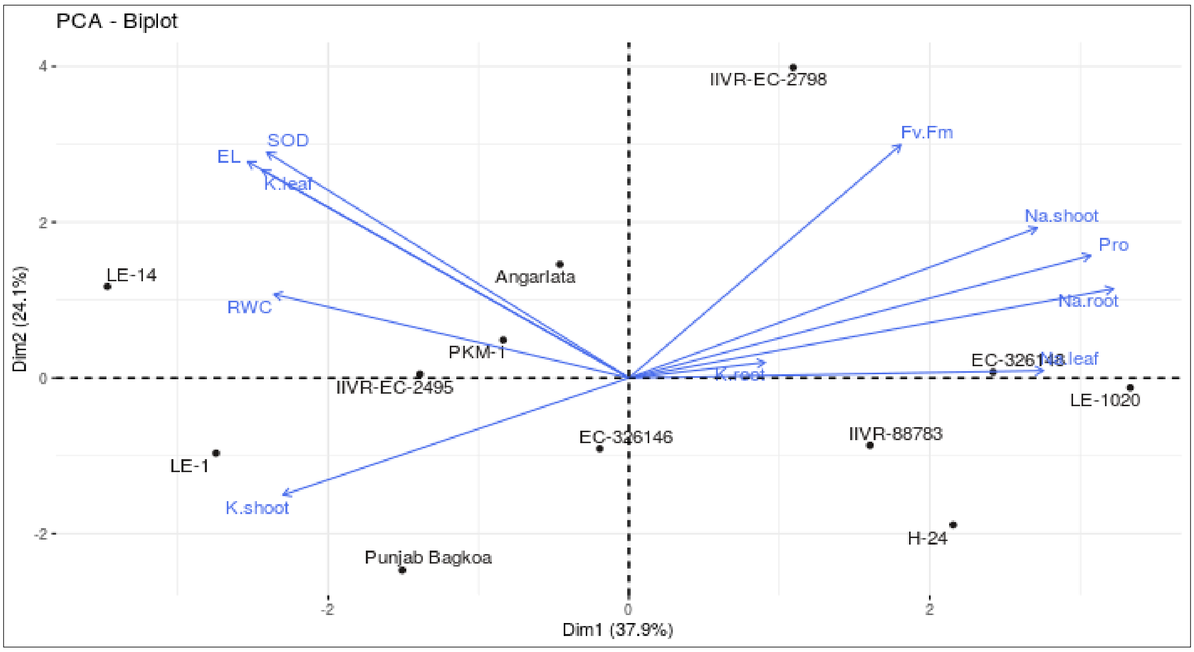

Fig. 4. Principal component analysis (PCA) of tomato genotypes under well water condition. SOD: Superoxide dismutase activity, RWC: Relative water content, Fv/Fm: Fluorescence parameter, Pro: Proline content, EL: Electrolyte leakage, Na leaf: Leaf sodium content, Na shoot: Shoot sodium content, Na root: Root sodium content, K leaf: Leaf potassium content, K shoot: Shoot potassium content, K root: Root potassium content.

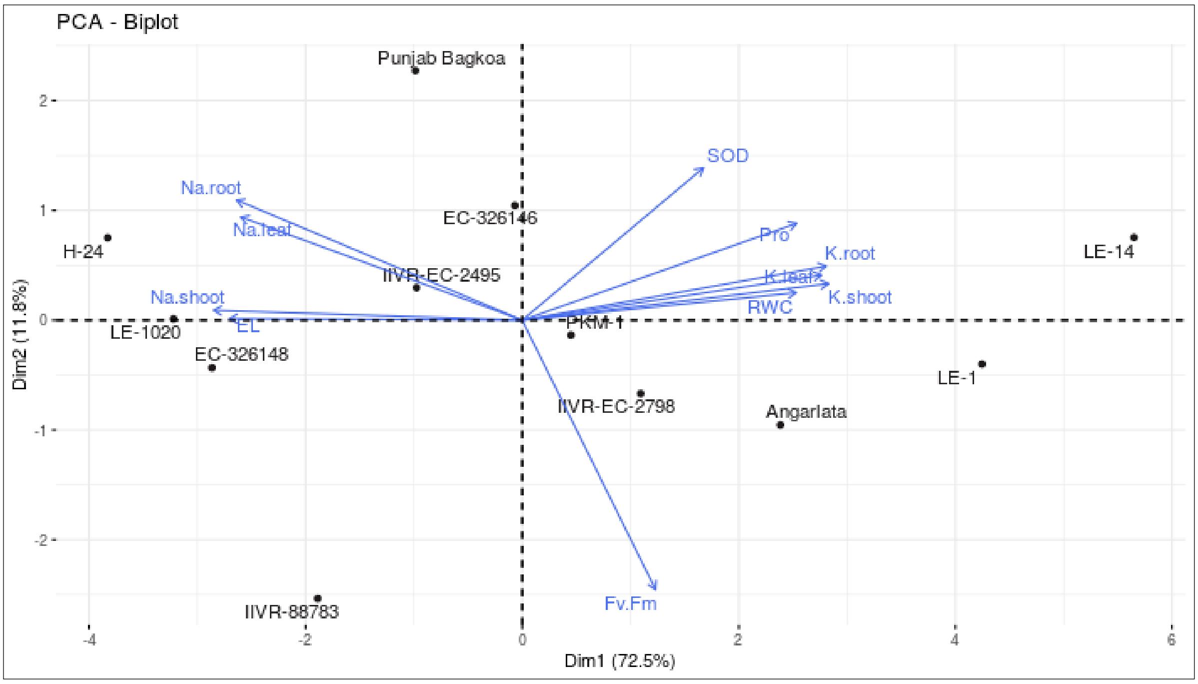

Fig. 5. Principal component analysis (PCA) of tomato genotypes under salt stress condition. SOD: Superoxide dismutase activity, RWC: Relative water content, Fv/Fm: Fluorescence parameter, Pro: Proline content, EL: Electrolyte leakage, Na leaf: Leaf sodium content, Na shoot: Shoot sodium content, Na root: Root sodium content, K leaf: Leaf potassium content, K shoot: Shoot potassium content, K root: Root potassium content.

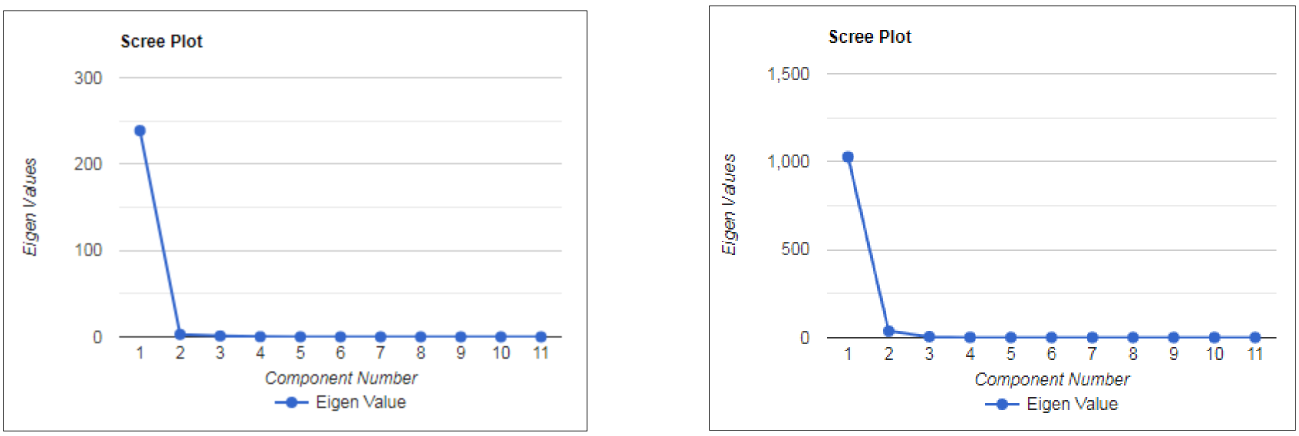

Fig. 6. Scree plots of eigen values for tomato genotypes.

show positive correlations with K content in roots, shoots and leaves, proline, RWC and SOD. Additionally, K content in roots, shoots and leaves, along with proline and RWC, are correlated with PKM1, while Na content in roots, leaves, shoots and EL are associated with IIVR-EC-295. Punjab Bagkoa, LE-14, IIVR-88783 and LE-1 fall outside the range and do not correlate with other parameters (Table 1, Fig. 4-6).

Correlation analysis

Under well-watered conditions, superoxide dismutase (SOD) activity shows a strong positive correlation with EL, RWC and K content in leaves, ranging from 0.5 to 0.88. Proline content is positively correlated with Na content in roots and shoots, as well as with Fv/Fm (range: 0.5 to 0.75). K content in shoots exhibits a strong negative correlation with Na content in roots and Fv/Fm (range: -0.29 to -0.65). Na content in leaves is positively correlated with Na content in shoots and roots (range: 0.58 to 0.65) (Fig. 7a).

Under salt stress conditions, SOD content positively correlates with RWC, proline and K content in leaves, shoots and roots (range: 0.32 to 0.66). RWC also shows a strong positive correlation with K content in leaves, shoots and roots (range: 0.75 to 0.80). RWC and K content in leaves, shoots and roots showed a strong negative correlation with Na content in leaves, roots and shoots with correlation coefficients ranging from -0.71 to -0.86. K content in leaves exhibited a strong positive correlation with K content in shoots and roots, with correlation coefficients ranging from 0.95 to 0.98. Similarly, Na content in leaves was strongly positively correlated with Na content in shoots and roots, with correlation coefficients ranging from 0.83 to 0.91 (Fig. 7b).

Conclusion

This study demonstrated that tomato genotypes exhibit considerable variability in their responses to salt stress, with LE-14 and LE-1 displaying the highest tolerance. These genotypes maintained higher RWC, reduced electrolyte leakage, enhanced SOD activity, increased proline accumulation and favorable potassium-to-sodium ratios under saline conditions. The findings suggest that LE-14 and LE-1 possess effective mechanisms to counteract the harmful effects of salt stress, making them promising candidates for cultivation in salt-affected environments. Field trials are recommended to further validate these genotypes' performance under real-world conditions. These insights are valuable for plant breeders seeking to develop salt-tolerant tomato varieties, supporting sustainable agriculture in regions impacted by soil salinity.

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Authors' contributions

MK carried out the experiment. KV participated in the design of the study, performed the statistical analysis and wrote the original manuscript. AS edited the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare

Ethical issues: None

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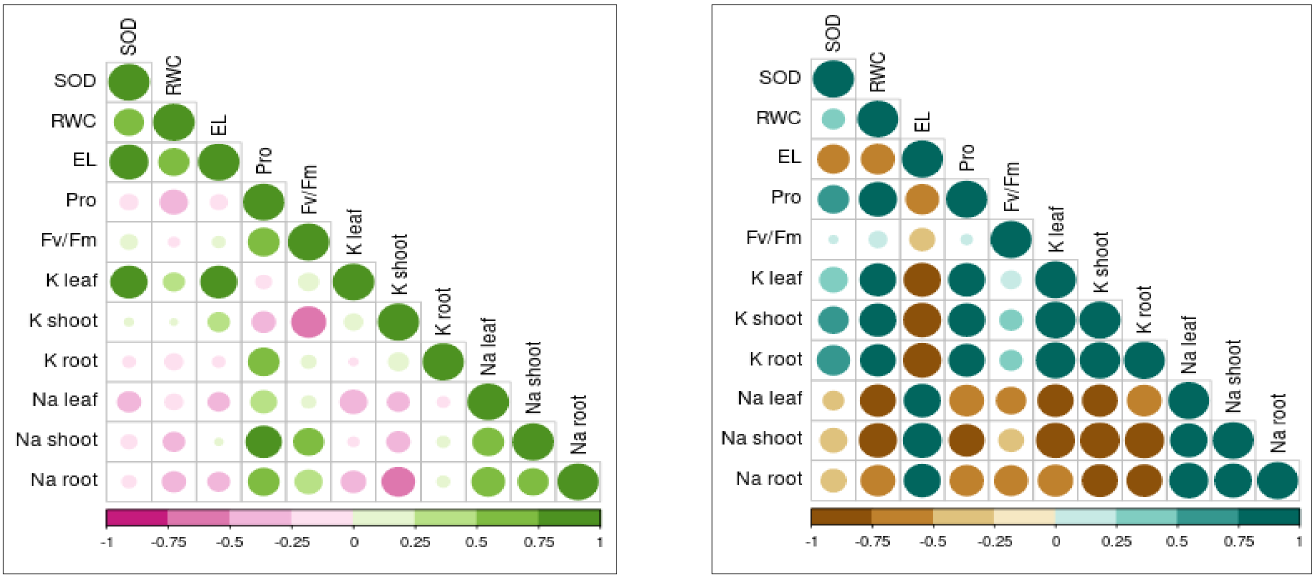

Fig. 7. Correlation analysis of tomato genotypes under well water condition. SOD: Superoxide dismutase activity, RWC: Relative water content, Fv/Fm: Fluorescence parameter, Pro: Proline content, EL: Electrolyte leakage, Na leaf: Leaf sodium content, Na shoot: Shoot sodium content, Na root: Root sodium content, K leaf: Leaf potassium content, K shoot: Shoot potassium content, K root: Root potassium contents.

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