Scilight

Annals of Agri-bio Research
https://agribiop.com/



Article

Assessment of Morphological and Physiological Mechanisms for Salt Tolerance and Adaptation in Wheat and Oat Cultivars

Anna Harutyunyan [1], Abhishek Singh [1], Hrant Khachatryan [1], Rupesh Kumar Singh [2], Vishnu D. Rajput [3,*] and Karen Ghazaryan [1,*]

[1] Faculty of Biology, Yerevan State University, Yerevan 0025, Armenia
[2] Centre for the Research and Technology of Agroenvironmental and Biological Sciences, CITAB, Inov4Agro, Universidadede Trás-os-Montes e Alto Douro (UTAD), Quinta de Prados, 5000-801 Vila Real, Portugal
[3] Academy of Biology and Biotechnology, Southern Federal University, 344090 Rostov-On-Don, Russia
* Correspondence: rvishnu@sfedu.ru (V.D.R.); kghazaryan@ysu.am (K.G.)

How To Cite: Harutyunyan, A., Singh, A., Khachatryan, H., Singh, R. K., Rajput, V. D., & Ghazaryan, K. (2026). Assessment of Morphological and Physiological Mechanisms for Salt Tolerance and Adaptation in Wheat and Oat Cultivars. *Annals of Agri-bio Research*, *31*(2), 192–211. https://doi.org/10.53941/agrbio.2026.100021

Received: 16 June 2026
Revised: 1 November 2026
Accepted: 16 November 2026
Published: 24 November 2026

Abstract: Salinity stress is a major constraint on cereal crop productivity worldwide, necessitating a comprehensive understanding of plant adaptive mechanisms across salinity gradients. The present study evaluated the morphological and physiological responses of wheat and oat cultivars exposed to increasing soil salinity gradients, categorised as Non (EC_e = 0–2 dS m^{-1}), Slight (EC_e = 2–4 dS m^{-1}), Moderate (EC_e = 4–8 dS m^{-1}), High (EC_e = 8–16 dS m^{-1}), Extreme-1 (EC_e = 16–24 dS m^{-1}), and Extreme-2 (EC_e = 24–32 dS m^{-1}). We assessed morphological traits, including stem height and diameter, and physiological parameters such as biomass accumulation, root, stem, and leaf water contents, relative electrolytic leakage, leaf succulence index, and chlorophyll content index (CCI) to elucidate salinity-induced structural and functional alterations. In addition, gas exchange parameters, namely net photosynthetic rate (Pn), transpiration rate (E), and water use efficiency (WUE), were analyzed to evaluate photosynthetic performance and plant water relations under salinity stress. Increasing salinity progressively reduced growth, biomass, water content, chlorophyll concentration, and photosynthetic activity in both crops, accompanied by increased membrane injury, as indicated by elevated electrolyte leakage. However, wheat showed greater tolerance, maintaining higher biomass, water status, photosynthetic efficiency, and WUE under high and extreme salinity than oat. Leaf succulence responded sensitively to salinity gradients, reflecting adaptive adjustments in leaf structure and pigment composition, and was closely associated with physiological performance. Phytodesalination capacity was also analyzed in this study for both crops. Overall, the results demonstrate that integrated morpho-physiological and spectral traits effectively discriminate salinity tolerance levels between wheat and oat. These findings provide valuable insights for screening salt-tolerant cereal cultivars and developing salinity-resilient crop management strategies.

Keywords: wheat; oat; morphological and physiological traits; salinity stress

Copyright: © 2026 by the authors. This is an open access article under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).
Publisher's Note: Scilight stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.

1. Introduction

Soil is one of the major and essential resources on Earth, but its significance is somewhat underestimated, especially at the political and decision-making levels. Low-quality soil endangers the supply of cereals, vegetables, clean fresh water, biodiversity, and ecosystems. As soil is one of the most economically, ecologically and environmentally precious natural resources, in recent years, soils have been exposed to diverse kinds of degradation processes worldwide and among those, conventional farming practices are one of the major reasons (FAO, 2025). Salt stress, an important abiotic stress factor, has been a major limiting factor for worldwide agricultural production and food security (Fang et al., 2021; Sohrabizadeh et al., 2023). Therefore, the screening and breeding of salt-tolerant varieties, as well as emerging sustainable management tools and techniques, are significant practices for the improvement and utilization of salt-affected soils (Afzal et al., 2023). Salt stress threatens crop productivity by two main ways: osmotic stress from high salt levels, which inhibits seed hydration and germination, and ionic toxicity from sodium and chloride ions, which disrupt cell membranes and internal ion balance (Krishnamurthy et al., 2016; Park et al., 2016). Excess sodium limits photosynthesis and metabolic functions (Sodaeizadeh et al., 2025), while chloride ions decrease chlorophyll and cause stomatal closure, reducing photosynthesis and damaging cell structures (Hao et al., 2021). Salt stress also suppresses enzyme activity and leaf growth, lowering photosynthesis and plant vitality (Khamesi et al., 2020). Plants adapt by limiting salt in meristematic tissues and translocating excess salts to older leaves or specialized organs (Barberon, 2017). Roots absorb nutrients from soil, with the endodermis acting as a barrier against salt ions. In leaves, NaCl impacts water potential, prompting plants to close stomata and modify water channels to conserve water (Manuel et al., 2023). Wheat (*Triticum aestivum* L.) is the second most cultivated cereal after maize serving as a major staple food for over one-third of the global population and providing about 20% of the daily protein and caloric intake (Sharma & Sharma, 2025). Its production is vital for food security, but abiotic stresses, especially soil salinity, threaten yields (Igrejas & Branlard, 2020). Around 20% of irrigated land and 7% of the world's land are affected by salt, impairing wheat growth, causing osmotic stress, ion toxicity, oxidative damage, and nutrient imbalances, which lead to reduced germination, stunted growth, and lower grain quality (Mahboob et al., 2023). Oat ranks sixth in global cereal production and is a primary fodder crop for livestock (Chand et al., 2025). Some oat varieties can thrive in soil with a pH up to 9.0, aiding land use and environmental improvement. Recent research on oat salt tolerance focuses on germination, physiological responses, and molecular regulation. Germplasm diversity helps understand plant salt resistance mechanisms. ding the mechanism of plant salt resistance (Munns et al., 2020; Ponce et al., 2021). Therefore, wheat and oat cultivars were screened in this study for salt tolerance using a large set of morphological, physiological and spectral parameters, including stem diameter, biomass, root, stem, and leaf water contents, relative electrolyte leakage, leaf succulence index, chlorophyll content index (CCI), gas exchange parameters, and phytodesalination capacity. This combined morphological and physiological screening strategy has been utilized for the saline-related Ararat plain region of Armenia for the evaluation of the wheat and oat crops for salinity stress response. This research primarily aimed to establish a robust system for assessing the salt tolerance of wheat and oat crops. The focus was on the crucial adaptations of these crops, particularly the morphological and physiological strategies that allow them to adapt to saline environments. The study strongly emphasised evaluating these adaptations in the context of food security, specifically under the saline soil conditions found in Armenia.

2. Materials and Methods

2.1. Experimental Sites, Design, Plant Material, Growth Conditions and Salt Treatments

Experiments were carried out at the experimental field of Yerevan State University, Republic of Armenia (coordinates: 40°10′57.85″ N, 44°31′36.97″ E). The site is located at an altitude of approximately 1040 m above sea level and is characterized by a dry continental climate, with very dry and warm summers and mild to moderately cold winters, the average annual temperature is +10 °C to +11 °C, the amount of precipitation is 300–400 mm. Armenian genotypes of wheat (Nairi-68) and oat (indigenous variety) were selected for the study. Plant seeds were obtained from the seed reserve fund of the National Agrarian University of Armenia. Before sowing, the seeds were disinfected for 15 min in a 3% sodium hypochlorite solution, then for 5 min in distilled water.

The experiment was conducted under outdoor conditions, and the duration of the experiment was three months (March to May 2024). Clay loam soil was selected because it is representative of agricultural soils of the Ararat Plain, which are affected by salinity, and has moderate water retention and permeability,

allowing reliable simulation of salinity development and crop responses under controlled conditions. The humus content in the soil was 2.1%, the pH was 8.2, the degree of alkalinity of the soil was classified as moderately alkaline, and the soil was classified as "Fine" by texture. The soil was placed in 7 L plastic containers, each containing approximately 8 kg of dry soil. An experimental design, known as a Completely Randomized Design (CRD), was employed, where each treatment represented three replicate pots (Figure 1). The pots were sealed at the bottom without drainage holes to prevent leaching and ensure full accumulation of salts. Initially, the soil was non-saline, with a saturated paste electrical conductivity (EC_e) of about 1.70 dS m^{-1}. Wheat and oat were sown in non-saline soil, and 15 days after sowing, irrigation with saline (NaCl) water was initiated to induce soil salinity. The quality of the irrigation water was classified according to the classical Wilcox (Allison et al., 1954) method and its modified version (Ghazaryan & Chen, 2016), based on electrical conductivity (EC) (Table 1). After salt treatment, the salinity levels in the pot soils corresponded to the international classification of the electrical conductivity of the saturated soil extract (Table 2) (Allison et al., 1954). The resulting EC_e values were 1.7, 2.9, 6.2, 12.5, 21.6, and 29.5 dS m^{-1}, corresponding to non, slight, moderate, high, extreme-1, and extreme-2 salinity levels. To induce salt stress, irrigation waters of different qualities were prepared by adding NaCl to tap water. Specifically, during one month, the non-saline soil was irrigated with excellent quality water (tap water, 231 μS cm^{-1}), the slightly saline soil with good quality water (517 μS cm^{-1}), the moderate saline soil with permissible quality water (1897 μS cm^{-1}), the high saline soil with doubtful quality water (4311 μS cm^{-1}), and the extreme-1 and extreme-2 soils with unsuitable quality water (8846 μS cm^{-1} and 12,296 μS cm^{-1}, respectively). During this period, 10 L of water were added to each pot, corresponding to an addition of 3.0 g NaCl for the slightly saline soil, 11.1 g for the moderately saline, 29.0 g for the highly saline, 51.3 g for extreme-1, and 71.3 g for extreme-2. This irrigation approach was chosen to avoid osmotic stress in plants. Irrigation was carried out every three days. After achieving the desired salinity levels, all soils were subsequently irrigated with tap water.

Table 1. Classification of irrigation water quality assessment according to Electrical conductivity (EC, μS cm^{-1}).

Excellent	Good	Permissible	Doubtful	Unsuitable
<250	250–750	750–2250	2250–5000	>5000
Low salinity water	Medium salinity water	High-salinity water	Doubtful for irrigation	Unsuitable for irrigation

During the salinization period, soil electrical conductivity (EC) was regularly monitored to maintain controlled and stable salinity conditions. The established salinity gradients were used for the comparative evaluation of the physiological responses and phytodesalination potential of the studied cereal crops.

After 15 days, when the plants had already adapted to salt stress, measurements began. Measurements were carried out 3 times at 15-day intervals. After the final measurements, whole plants, including root systems, were harvested when the plants were at the maturation stage. Plants were initially washed with tap water, followed by rinsing with distilled water. Prior to fresh mass determination, plant tissues were gently blotted dry with towels. Before weighing and drying, the plant roots, stems, upper leaves, and lower leaves were separated. Fresh mass was recorded, after which the samples were placed in a constant-temperature drying oven ((BJPX-HDO138, BIOBASE Group, Jinan, China) at 70 °C for approximately 72 h until a constant dry mass was achieved. Ion concentrations were subsequently determined in the dry tissue (Pedrero & Alarcón, 2009).

Table 2. Classification of soil salinity degree according to EC_e (dS m^{-1}).

Non	Slight	Moderate	High	Extreme
Impacts of salinity are minimal	Extremely sensitive crops may have limited harvests	The harvests of numerous crops is limited	The yield of just resistant crops is sufficient	Only some extremely resistant crops can survive
0–2	2–4	4–8	8–16	>16

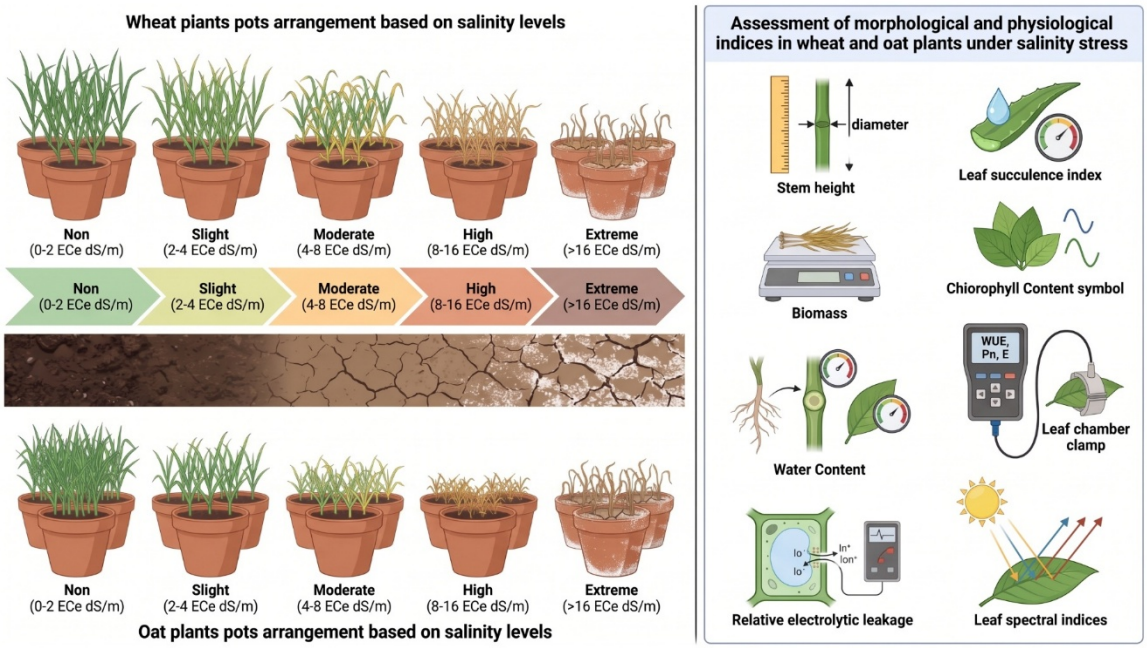


Figure 1. Pot experiment setup for wheat and oat plants to analyze morphological and physiological indices under salinity stress.

2.2. Determination of Morphological Indices

Wheat and oat genotypes were assessed using two primary morphological parameters: stem diameter and shoot height. The results are presented as mean values. Stem diameter was measured immediately after harvest using a Vernier caliper, at a point located approximately 2 cm above the root–shoot junction along the basal stem. Shoot height was determined from the soil surface to the apical point of the plant. (Ntawuguranayo et al., 2024).

2.3. Determination of Physiological Indices

2.3.1. Measurement of Biomass

Biomass was assessed for both control and salt-stressed plants. Roots and shoots were collected separately from each plant replication at harvest. We measured root fresh weight (FW_r), stem fresh weight (FW_s), and leaf fresh weight (FW_l). After drying the samples at 70 °C until they reached a constant weight, root dry weight (DW_r), stem dry weight (DW_s), and leaf dry weight (DW_l) were determined for each plant.

2.3.2. Measured Roots, Stems, and Leaves Water Contents

RWC%, SWC% and LWC% were calculated using the following formulas (Al Hassan et al., 2016; Garnier et al., 2001; Slama et al., 2008):

$$\mathrm{RWC\%} = \frac{\mathrm{FW_r} - \mathrm{DW_r}}{\mathrm{FW_r}} \times 100 \quad (1)$$

$$\mathrm{SWC\%} = \frac{\mathrm{FW_s} - \mathrm{DW_s}}{\mathrm{FW_s}} \times 100 \quad (2)$$

$$\mathrm{LWC\%} = \frac{\mathrm{FW_l} - \mathrm{DW_l}}{\mathrm{FW_l}} \times 100 \quad (3)$$

where FW_r, FW_s and FW_l are the fresh weights of root, stem and leaves, and DW_r, DW_s and DW_l are the dry weights of root, stem and leaves, respectively.

2.3.3. Relative Electrolytic Leakage (REL)

Membrane damage was assessed by determining the relative electrolyte leakage (REL), following the methods described by the previous method (Dionisio-Sese & Tobita, 1998; González & González-Vilar, 2001). Fresh leaf tissues (0.50 g) were placed in test tubes containing 50 mL of distilled water and incubated at room temperature (≈25 °C) for 24 h. After incubation, the initial electrical conductivity (EC_1) of the

bathing solution was measured using a conductivity meter. Subsequently, the samples were autoclaved for 15 min at 121 °C to release all electrolytes from the leaf tissues. After cooling the samples to room temperature, the final electrical conductivity (EC_2) was recorded. The relative electrolyte leakage (REL), expressed as a percentage, was calculated using the following formula:

$$\mathrm{REL} = \frac{\mathrm{EC}_1}{\mathrm{EC}_2} \times 100 \quad (4)$$

This parameter reflects the integrity of the cellular membranes, where higher REL values indicate greater membrane injury under salt stress conditions.

2.3.4. Leaf Succulence Index

Leaf succulence (LS) was determined following the procedures described in the previous method (Agarie et al., 2007; Jennings, 1976). For each plant, the leaf area (LA) and leaf fresh weight (LFW) of one fully expanded leaf were measured.

Leaf succulence was then calculated according to the following equation:

$$\mathrm{LS} = \frac{\mathrm{LFW}}{\mathrm{LA}} \quad (5)$$

where LFW is the leaf fresh weight (g), and LA is the leaf area (cm^2).

This parameter reflects the degree of water retention in leaf tissues and serves as an indicator of plant adaptation to saline conditions.

2.3.5. Estimation of Chlorophyll Content Index (CCI)

Chlorophyll content was measured as an indicator of the physiological response of plants growing under saline soil conditions. The measurements were conducted on fully expanded leaves from the upper part of the plants using a CCM-200 Plus Chlorophyll Content Meter (Opti-Sciences, Hudson, NH, USA). For each plant, ten readings were taken at different points on the leaf surface, and the mean chlorophyll content index (CCI) was automatically calculated by the device.

CCI is calculated using the following equation:

$$\mathrm{CCI} = \frac{\%\mathrm{T}_{931}}{\%\mathrm{T}_{653}} \quad (6)$$

where $\%T_{931}$ and $\%T_{653}$ represent the leaf spectral transmittance values measured at wavelengths of 931 nm and 653 nm, respectively. The wavelength of 653 nm corresponds to the major absorption peak of chlorophyll pigments in the red region of the visible spectrum. In comparison, 931 nm lies in the near-infrared region with minimal chlorophyll absorption. This ratio provides a rapid and non-destructive estimate of relative chlorophyll content in leaf tissues, where higher CCI values indicate greater chlorophyll concentration (Silla et al., 2010).

2.3.6. Gas Exchange Parameters

The net photosynthetic rate (Pn) and transpiration rate (E) were measured using a portable photosynthesis system CI-340 (CID Bio-Science, Inc., Camas, WA, USA) under the following environmental conditions: air pressure between 89.55 and 89.90 kPa, air temperature within 25–30 °C, and ambient CO_2 concentration ranging from 390 to 405 μmol mol^{-1}. Measurements were performed on one young, fully expanded leaf from each plant, with three replicates per leaf, between 8:00 a.m. and 11:00 a.m., after 30 days of salt treatment.

Water use efficiency (WUE) was expressed as the net carbon uptake per amount of water lost through transpiration and calculated according following (Rabhi et al., 2012):

$$\mathrm{WUE} = \frac{\mathrm{Pn}}{\mathrm{E}} \quad (7)$$

where Pn is the net photosynthetic rate (μmol CO_2 m^{-2} s^{-1}) and E is the transpiration rate (mmol H_2O m^{-2} s^{-1}).

2.4. Biochemical Indices

Dried shoots and roots of the plants were ground into a fine powder and digested in 0.5% HNO_3 solution for 30 min at 100 °C to extract the soluble ions, following the previously described procedures (Al Hassan et al., 2016; Zouhaier et al., 2015). The digestion was performed using 1.00 g of dry plant material

in 100 mL of acid solution. After digestion, the extracts were filtered through filter paper and immediately analyzed. The concentrations of sodium (Na^+) and potassium (K^+) ions were determined using a flame photometer (FP-I6431, Bioevopeak Co., Ltd., Jinan, China), while the concentration of chloride (Cl^-) ions was measured using a laboratory ionometer (I-160M, Antech LLC, Gomel, Belarus). Each determination was carried out with five replicates per sample to ensure analytical accuracy.

2.5. Statistical Analysis

A comprehensive analysis was performed to assess the statistical significance of differences in both morphological and physiological metrics among various cultivars under salt stress conditions. An ANOVA test was implemented, followed by a Dunnett's post hoc test to further evaluate significance levels between groups. The criterion for significance was set at a p value less than 0.05. All statistical procedures were carried out using GraphPad Prism software, version 8.0 (GraphPad Software, San Diego, CA, USA).

3. Results and Discussion

3.1. Effect of Salinity Stress on Plant Growth and Development

Salinity, depending on the degree, can exert both positive or negative influences on various plant growth parameters, including length, biomass, stem diameter, viability, and threshold responses (Dikobe et al., 2021). The impact is contingent upon the specific salinity level and the plant's tolerance. Growth and biomass of the studied crops changed significantly under treatments with different NaCl concentrations, indicating the crops' resistance and response to varying degrees of salt stress (Pandit et al., 2024; Wang et al., 2023).

The growth dynamics of crop shoot height under different salt treatment conditions is presented in Figure 2. In general, crop height decreased significantly with increasing salinity, but the response differed among crop species. 15 days after the end of salt addition, the shoot heights of wheat grown under Slight group compared to the Non group was increased 1.4%, but with further increase in salinity, a decrease in height was observed, in particular, 1% in the Moderate group, 1.6% in High, 5% in Extreme-1, and 5.6% in Extreme-2, and in the case of oats, a decrease in height was observed at all levels of salinity: Slight—8%, Moderate—12.8%, High—19.8%, Extreme-1—27.9%, and Extreme-2—29.1%. After 45 days, the effect of salinity on the change in wheat height became more noticeable: in the Slight and Moderate groups, the increase compared to Non was 5.8% and 5.3%, respectively, and in High, Extreme-1 and Extreme-2 it decreased by 5.5%, 6.8% and 15.3%, respectively. In oat, the dynamics of height change after 45 days was maintained and the decrease in growth from Slight to Extreme-2 was 6.9%, 10.9%, 19.9%, 24.5% and 28.5%, respectively. Our current finding support by previous findings of Wang et al. (2026) increasing the salinity level reduced the shoot length of the plant.

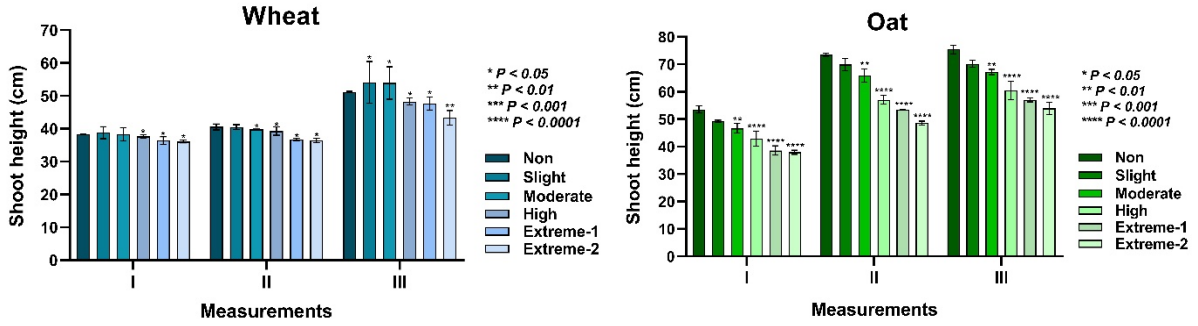


Figure 2. Effect of salt stress on growth of studied crops during salt treatment. The data in the figure represent means ± standard errors (n = 3).

The degree of salinity also affected the diameter of the crops stems (Figure 3). As shown in the graph, wheat stem diameter initially increased and then decreased as salinity increased. In particular, wheat grown in the Slight group increased by 5.85% compared to the Non group, then decreased in the Moderate group by 7.44%, in High by 11.73%, in Extreme-1 by 12.75%, and in Extreme-2 by 14.96%. In oats, stem diameter increased and then decreased as salinity increased. Oats grown in the Slight group increased by 11.85% compared to the Non group, and in the Moderate group by 3.31%, then decreased in the High by 7.44%, in Extreme-1 by 14.90%, and in Extreme-2 by 17.36%. Tomato stem diameter consistently decreased with increasing NaCl salinity, indicating that salinity stress adversely affected vegetative growth. However,

differences were observed among the varieties; compared to others, *'BARI Tomato-17'* maintained a better stem diameter even under saline conditions (Alam et al., 2023). This finding is consistent with our results, indicating that salt tolerance potential varies with both the variety and the salinity level.

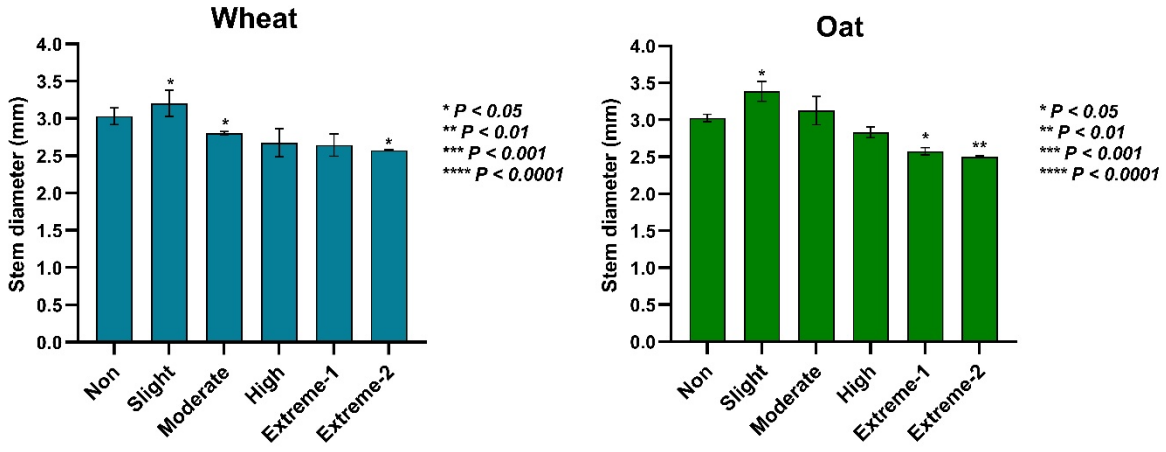


Figure 3. Effect of salt stress on the stem diameter of the studied crops. The data in the figure represent means ± standard errors (n = 3).

Biomass (FW and DW) is a key integrative parameter reflecting plant growth and overall viability. Maintaining biomass under salt stress indicates the plant's adaptability. The results of the study of FW and DW in root, stem and leaf of crops are presented in Table 3. The maximum fresh and dry masses of the root, stem and leaf of the studied crops were mainly observed in plants grown at a Slight group, then a decrease in FW and DW was observed with an increase in the degree of salinity. The analysis shows that the changes in plant biomass under different salinity levels do not follow a consistent or proportional trend. The reductions in both fresh and dry mass are irregular, with evident breakpoints, mild decreases, and even occasional increases (Slight group).

Table 3. Effect of salinity stress on biomass content of studied crops (n = 3, g).

Crops	Salinity Degree	FW_r	DW_r	FW_s	DW_s	FW_l	DW_l	FW_r/FW_{s+l}	DW_r/DW_{s+l}
Wheat	Non	1.38 ± 0.15	0.28 ± 0.03	3.39 ± 0.36	0.71 ± 0.07	2.21 ± 0.23	0.51 ± 0.06	0.25 ± 0.03	0.23 ± 0.02
	Slight	1.34 ± 0.14	0.25 ± 0.03	4.13 ± 0.43	0.75 ± 0.08	2.82 ± 0.30	0.60 ± 0.07	0.19 ± 0.02	0.19 ± 0.02
	Moderate	0.87 ± 0.08	0.19 ± 0.02	3.36 ± 0.34	0.72 ± 0.07	1.73 ± 0.18	0.43 ± 0.05	0.17 ± 0.02	0.17 ± 0.02
	High	0.81 ± 0.08	0.19 ± 0.02	2.70 ± 0.28	0.60 ± 0.06	1.53 ± 0.16	0.39 ± 0.04	0.19 ± 0.02	0.19 ± 0.02
	Extreme-1	0.79 ± 0.08	0.18 ± 0.02	2.61 ± 0.26	0.58 ± 0.06	1.35 ± 0.14	0.35 ± 0.03	0.20 ± 0.02	0.19 ± 0.02
	Extreme-2	0.74 ± 0.07	0.17 ± 0.02	2.10 ± 0.21	0.47 ± 0.05	1.26 ± 0.13	0.33 ± 0.03	0.22 ± 0.02	0.22 ± 0.02
Oat	Non	1.27 ± 0.14	0.24 ± 0.03	6.31 ± 0.70	1.26 ± 0.13	2.52 ± 0.27	0.40 ± 0.04	0.14 ± 0.01	0.14 ± 0.01
	Slight	1.36 ± 0.16	0.25 ± 0.03	7.09 ± 0.85	1.28 ± 0.14	3.33 ± 0.37	0.53 ± 0.05	0.13 ± 0.01	0.14 ± 0.01
	Moderate	1.24 ± 0.14	0.23 ± 0.02	6.13 ± 0.68	1.26 ± 0.13	2.56 ± 0.28	0.43 ± 0.04	0.14 ± 0.01	0.14 ± 0.01
	High	1.10 ± 0.11	0.21 ± 0.02	4.80 ± 0.53	1.05 ± 0.11	2.28 ± 0.24	0.41 ± 0.04	0.16 ± 0.02	0.14 ± 0.01
	Extreme-1	0.97 ± 0.09	0.19 ± 0.02	4.13 ± 0.45	0.96 ± 0.09	1.86 ± 0.19	0.35 ± 0.03	0.16 ± 0.02	0.14 ± 0.01
	Extreme-2	0.65 ± 0.06	0.13 ± 0.01	2.85 ± 0.31	0.70 ± 0.07	1.16 ± 0.14	0.27 ± 0.03	0.16 ± 0.02	0.13 ± 0.01

Note: The data in the table represent means ± standard errors ($p < 0.05$).

In wheat, a sharp decrease in root and leaf biomass was observed during the transition from Slight to Moderate. In oat, sharp decreases were distributed in several stages, mainly in the Extreme-1 to Extreme-2 section, except for the stem fresh mass, where a sharp decrease was also observed during the transition from Moderate to High, and in fresh leaves during the transition from Slight to Moderate. It should be noted that the fresh and dry leaf biomass of oat did not decrease during the initial salinity stages and were higher compared to the Non group, in particular, in the case of fresh mass, the increase in the Moderate group compared to the Non group was 1.3%, and in the case of dry mass, the increase in the Moderate and High groups was 8.6% and 2.0%, respectively. However, as salinity increases (Extreme-1), stress mechanisms are exhausted and a decrease in dry mass is observed. The change of FW_r/FW_{s+l} and DW_r/DW_{s+l} ratios under different salinity levels varied between crops (Table 3). In the case of wheat, both FW_r/FW_{s+l} and DW_r/DW_{s+l} ratios initially decreased with increasing salinity, reaching the lowest values at the moderate salinity level. However, at higher salinity levels (Extreme-1 and Extreme-2), the ratios showed a partial recovery, approaching the values observed under non-saline conditions. In general, the change was non-monotonic and inconsistent, but reflects a possible adaptive adjustment at extreme salt levels. In oat, FW_r/FW_{s+l} ratios

initially decreased with increasing salinity, reaching the lowest values at the slight salinity level, after which they began to increase and already in Extreme-2, this ratio exceeded the Non group by 13%, and the DW_r/DW_{s+l} ratio did not follow a clear trend. The values fluctuated slightly across salinity degrees, without significant or directional changes. This suggests that oat may maintain a relatively stable root-to-stem dry mass distribution, and that its biomass allocation pattern remains less affected by increasing salinity stress compared to wheat.

The salinity content of soil has negative effects on the different morphological parameters, e.g., seedling growth, plant height, shoot and root length, number of roots (Ehsanzadeh et al., 2025), leaves and leaf area, fresh and dry weight, root/shoot ratio of wheat and oat plants (Saddiq et al., 2021; Zhang et al., 2022). Salinity stress typically reduced the plant growth through reduced stem height, leaf area, and total biomass (fresh and dry weight) due to osmotic stress and ion toxicity effects, thus causing stunted growth, wilting and reduced photosynthesis, although some plants respond at a lower level of salinity before declining (Liu et al., 2025; Rehman et al., 2025; Saddiq et al., 2021; Zhang et al., 2022). Accumulation of salt inhibits water and nutrient uptake, which affects the chlorophyll content in plant leaves and directly reduces the dry weight content of shoots and roots with varying severity according to salt concentrations in wheat and oat plants (Figure 7 and Table 3) (EL Sabagh et al., 2021; Liu et al., 2025; Rehman et al., 2025). Generally, shoot heights of genotypes declined with increase in salinity and salt source. Furthermore, shoot height values were affected by salinity (NaCl) only at 200 mM (De Lima et al., 2016) and pinto bean (Plaut et al., 2013) and castor bean (Guo et al., 2019) emergence rate, shoot height and leaf area were decreased by increasing levels of salinity (NaCl) similarly these findings also observed that the decrement in emergence, plant height and leaf area were bigger for 50 to 100 mM NaCl than from 0 to 50 mM NaCl. Another finding also show that salinity in negative effect order; high (3 dS/m) > medium (2 dS/m) > low (1 dS/m) > control (0.05 dS/m) decreased the biomass of faba bean (Bimurzayev et al., 2021). These all finding support our result like increasing the salinity levels leads to decreasing into stem heights, diameters (Figures 2 and 3) and biomass content (Table 3) which also correlates with some previous studies related cereal crops (Cope et al., 2022; Hasanuzzaman et al., 2017). Moderate saline water irrigation could enhance crop growth and yield to certain extent, while the high concentration salt-alkaline environment beyond the optimal range does not benefit to the crop growth (Zhang, Wang et al., 2024). Water uptake and accumulation of dry matter can be enhanced by low salinity, but growth, water uptake, and ultimately yield are reduced by high salinity because of osmotic stress, ion toxicity and oxidative damage (Ahmed et al., 2024).

3.2. Influence of Osmotic Tolerance on Membrane Stability and Integrity

The water uptake and translocation to the leaf are pivotal for plants to survive under osmotic stress. The osmotic stress is typically caused by high salts especially Na^+ in the soil that suppress water absorption of plant roots (Sinthumule et al., 2022). Salinity usually induces the injury of cell membrane structure and function, modifications in membrane lipids, and enhancement of membrane permeability (Steinhorst & Kudla, 2019). Membrane damage degree was employed to assess the protoplasmic tolerance of abiotic stresses (Scotti-Campos et al., 2016). The preservation of membrane integrity, and thus compartmentalization and metabolism at the cellular level is essential for plants survival in stress conditions (Abdehpour et al., 2025). Plants subjected to salinity stress typically reduce RWC, SWC and LWC representing the loss of water and increasing REL indicates cell membrane damage (Figures 4 and 5 and Table 4) (Azimychetabi & Sabokdast Nodehi, 2021; Ghazaryan et al., 2023; Mou et al., 2021). In order to assess the osmotic resistance and water status of plants, RWC%, SWC%, and LWC% indices were determined. The data in Table 4 show that with increasing salinity, these indices decreased to varying degrees in both wheat and oats. In the case of wheat, under initial conditions of increased salinity (Slight group), a significant increase in water content is observed in all organs, then, as salt stress intensifies, a decrease in water content is observed and already under Extreme-2 salinity conditions, compared to non-saline conditions, RWC% decreased by 4.18%, SWC% by 1.97%, and LWC% by 3.78%. These data show that despite the effects of salt stress, the decrease in water retention indices in wheat is relatively mild and may indicate some adaptation. In the case of oats, a significant increase in water content under Slight was observed only in the stem, while in Extreme-2 the decreases in water content occurred differently in different organs, in particular RWC% remained almost stable, decreasing by only 1.27%, but the decreases in SWC% and especially LWC% were more pronounced, by 5.70% and 9.16%, respectively. This suggests that oat roots, compared to wheat, retain their total water content better, but the effects of salt stress are more pronounced in oat aboveground parts.

Table 4. Effect of treatment with different concentrations of NaCl on wheat and oat (n = 3).

Salinity Degree	Wheat			Oat		
	RWC%	SWC%	LWC%	RWC%	SWC%	LWC%
Non	79.86 ± 2.42	79.23 ± 2.25	76.93 ± 2.15	81.43 ± 2.36	79.95 ± 2.79	84.25 ± 2.28
Slight	81.03 ± 2.64	81.73 ± 2.81	78.71 ± 2.09	81.97 ± 2.67	81.95 ± 2.59	84.03 ± 2.17
Moderate	78.12 ± 2.84	78.64 ± 1.99	75.19 ± 2.79	81.50 ± 2.45	79.40 ± 2.66	83.14 ± 1.98
High	77.06 ± 2.35	77.93 ± 2.73	74.78 ± 2.66	81.35 ± 2.27	78.04 ± 2.43	82.23 ± 2.79
Extreme-1	76.96 ± 2.25	77.74 ± 2.62	74.03 ± 2.49	80.56 ± 2.02	76.81 ± 2.22	81.22 ± 2.18
Extreme-2	76.52 ± 2.02	77.66 ± 2.51	74.03 ± 2.40	80.40 ± 1.92	75.39 ± 1.92	76.53 ± 2.11

Note: The data in the table represent means ± standard errors ($p < 0.05$).

The results of the study of leaves succulence are presented in Figure 4. In general, it can be said that the changes in LS indices in wheat were minimal and not significant, while in the case of oats the decrease was more pronounced, which may indicate a more sensitive structure to salinity conditions. However, the differences are not strongly expressed, and the data indicate that the succulence of the leaves in these crops did not change significantly under the influence of different degrees of salinity.

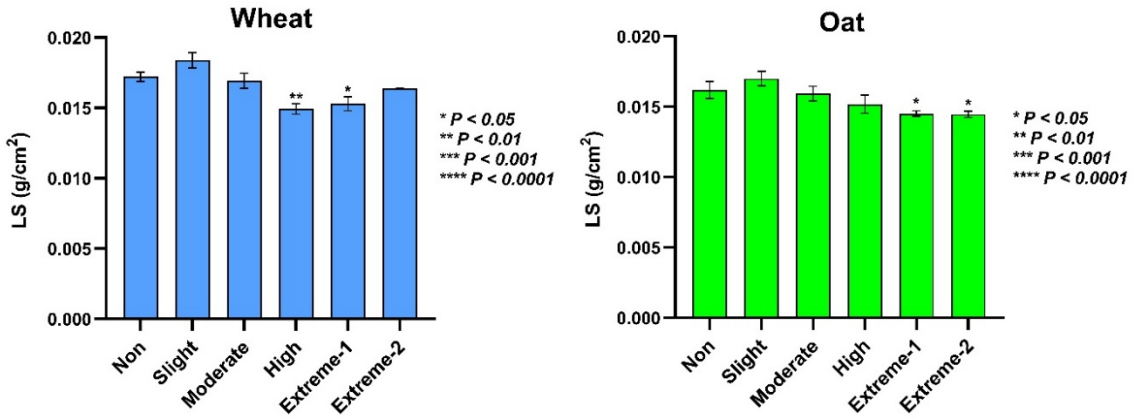


Figure 4. Effect of salt stress on the LS of the studied crops. The data in the figure represent means ± standard errors (n = 3).

The REL values are shown in Figure 5. In both crops, the change in REL values occurs at different rates with increasing salinity. In the case of wheat, the REL value increased by 3.44% in the Slight group, 9.17% in the Moderate group, 14.22% in the High group, 21.40% in the Extreme-1 group, and 27.34% in the Extreme-2 group compared to the Non group. In oat, the REL value increased from Slight to Extreme-2 groups by 1.24, 1.94, 1.99, 2.13, and 2.18 times, respectively. Although oat growth is higher, wheat REL was already high even without salt exposure and maintained a relatively stable increase with increasing salinity. These data may indicate that oat REL indices respond more sharply to salt exposure, while wheat's high REL and stable growth may indicate some salt tolerance.

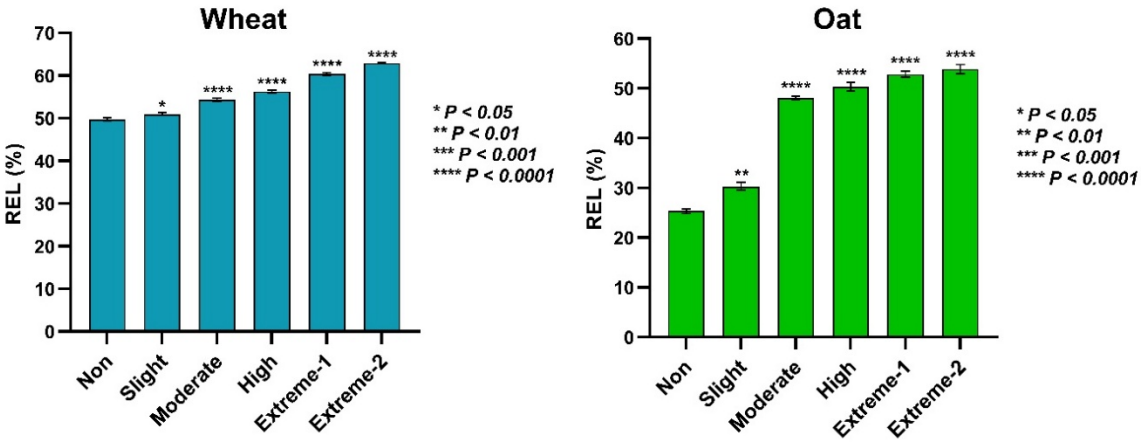


Figure 5. Effect of salt stress on leaves REL of studied crops. The data in the figure represent means ± standard errors (n = 3).

Salt tolerant plants tend to have a better overall water status. They will typically have a higher relative water status as measured by their RWC, SWC and LWC also they usually have less REL than salt sensitive plants (Nassar et al., 2020; Van Zelm et al., 2020; Zhang, Xia et al., 2024). This difference is an important parameter when considering stress responses of plants. Different (0.0, 50.0 and 100.0 mM) NaCl concentrations for three landraces of wheat (White Heteyeh, Black Heteyeh, and Norsi) were the tested that show the increased into salinity level caused decrease of RWC. According to the findings, *"Norsi"* landrace was the most tolerant because it has the lowest LRWC% under 50 and 100 mM NaCl (Shtaya et al., 2020). Another research also shows that common bean under three levels of NaCl (0, 100, and 200 mM) show reeducation in RWC by increasing the electrolyte leakage index (ELI) that also linked with K^+/Na^+ ratio (Azimychetabi & Sabokdast Nodehi, 2021). The difference in cell turgor pressure between inside and outside of the cells is developed because of water loss caused by this difference, in which should be related with the capacity of cells to take up water or stomata to hold water, and then results in lower LWC under NaCl stress (Xue et al., 2021). In another experiment, NaCl reduced LWC, plant height and stem diameter that are most effective indexes to evaluate plant growth under NaCl stress in magnoliaceae plant (Zhao et al., 2024). Another result show that salt-tolerant (three; S-24, LU-26S and Pasban-90) wheat genotypes showed a higher leaf water potential, osmotic potential (less negative) and leaf RWC compared with salt sensitive (four; MH-97, Kohistan-97, Inqilab-91 and Iqbal-2000) wheat genotypes which had more negative osmotic potential and lower RWC that is positively correlated with the higher accumulation of total free amino acids (Hussain et al., 2021). Similarly in oat plant RWC decreased and increased REL observed under higher level of salinity (Kappachery et al., 2024; Liu et al., 2023; Zhang et al., 2022). Furthermore, the increase in salt concentration had a negative impact on the water content in the roots, shoots, and leaves of wheat and oats (Table 4), as well as on their REL (Figure 5). However, studies on rice *(Oryza sativa* L.), sorghum (*Sorghum bicolor* L.) and buffaloberry (*Shepherdia argentea* L.) have investigated into the possibility that salinity stress treatment may reduce intercellular water status in plants which supports our finding (Gill et al., 2001; Pattanagul & Thitisaksakul, 2008; Qin et al., 2010)

3.3. Effect of Salinity Stress on Rates of Ionic Accumulation and Homeostasis

The analysis of Na^+, K^+, and Cl^- ion content in the roots, stems, and leaves of the studied crops under different degrees of soil salinity is presented in Table 5. In wheat, compared with the Non group, K^+ content decreased by 1.22 times in roots, 1.19 times in stems, 1.08 times in upper leaves,

The Na^+/K^+ ratio generally increased in all plant organs with increasing salinity, reflecting ionic imbalance and altered selectivity in ion transport. In wheat, as a result of the activation of anti-stress mechanisms, the Na^+/K^+ ratio decreased in the various organs of Slight group plants, except for the stem, after sharply increased. In the Extreme-2 group, compared to the Non group, the Na^+/K^+ ratio increased 5.23 times in the root, 17.87 times in the stem, 5.81 times in the upper leaves, and 13.85 times in the lower leaves. In the case of oats, the activation of regulatory mechanisms observed with increasing salinity was not sufficient to maintain a stable Na^+/K^+ ratio, and a certain increase was observed starting from the Slight group, but it was more rapid in the Moderate group. In Extreme-2 group compared to the Non group, it increased 14.05 times in the root, 13.37 times in the stem, 19.74 times in the upper leaf, and 27.63 times in the lower leaf.

The excessive Na^+ accumulation in the cytosol leads to ion toxicity, suppresses enzyme activity and inhibits K^+ and Ca^{2+} uptake (Tian et al., 2020; Wu et al., 2019; Zhang et al., 2020). The low cytosolic Na^+ and the intracellular ion homeostasis, mainly K^+ and Na^+ homeostasis is vital for many physiological and biochemical functions in a live cell including salt tolerance of plants (Ma et al., 2017). In order to prevent the accumulation of Na^+ and Cl^- in shoots at very high levels plants need to exclude almost all of the Na^+ and Cl^- taken up when they take up water from saline soil (Munns et al., 2020). Since mesophyll cells of shoot are more sensitive to salinity than that of roots, Na^+ exclusion from the shoot is highly valuable for salt tolerance in crops (James et al., 2011). Different crop species or different cultivars within the same crop developed different Na^+ exclusion mechanisms to maintain cytosolic Na^+ low in the shoot, including inhibition of Na^+ uptake into the root, restriction of xylem Na^+ loading, efflux of Na^+ from the root and sequestration of Na^+ into vacuoles (Munns et al., 2020). Na^+ uptake into the root system in response to salt stress induces plasma membrane depolarization, resulting in inhibition of inward K^+ channels and activation of K^+ efflux out of the cells, resulting cellular K^+ depletion also decreases in K^+/Na^+ ratio that disturbing ionic homeostasis (Table 5) (Khan et al., 2021). Therefore, controlling the cytosolic K^+/Na^+ ratio is considered to be a key adaptation that helps plants tolerate salinity stress (Su et al., 2019). This concept

is further support by the research finding of Yong et al. (2020) showed that increased K^+ levels in mesophyll cells contribute to salt tolerance in rice (Yong et al., 2020). Our results are correlated with these observations (Table 5). K^+ concentrations and K^+/Na^+ ratios in the roots, stems, and leaves of wheat and oat exhibited variable responses to increasing salinity. Although K^+ concentrations generally declined under higher salinity levels, slight salinity resulted in increased K^+ concentrations in certain plant tissues compared with the non-saline control, indicating a non-linear response. Overall, these findings suggest that elevated Na^+ accumulation under saline conditions may interfere with K^+ homeostasis and alter the ionic balance in plant tissues. (Table 5). In comparison to wheat, oat showed a greater decrease in K^+ content and K^+/Na^+ ratio this indicating weak ionic adjustment in oat plants compared to wheat (Table 5). On the other hand, wheat showed less reduction in K^+ content and a more favorable K^+/Na^+ ratio in shoot tissues compared to oat, indicating better maintenance of K^+ content as well as selective ion transport under saline conditions. These findings together support the idea that efficient K^+ retention and a high K^+/Na^+ ratio are key physiological traits for salt tolerance (Hussain et al., 2021).

The Figure 6 illustrates the variation of Na^+ and Cl^- ion accumulation in the aboveground parts of wheat and oat at different salinity levels. In wheat, Na^+ accumulation increased progressively and reached its maximum under extreme salinity, while Cl^- content per plant remained relatively stable, showing only minor fluctuations. It should be noted that with increasing salinity, an increase in the contents of Na^+ and Cl^- is observed, but at the same time a decrease in the aboveground mass is also observed. As a result, the total content of Cl^- in the aboveground mass of per plant almost does not change, while in the case of Na^+, the increase in the content is more than the decrease in biomass, due to which its amount in the aboveground part of per plant increases significantly. In oat, both Na^+ and Cl^- contents increased considerably across all salinity levels. In parallel with the increase in salinity the sharp increase in sodium in the plant, which depending on the group is 1.5–4.1 times greater than in wheat, indicates the strong phytodesalination potential of this crop. And despite the fact that the Cl^- content is on average 30% higher than wheat at all salinity levels, in this case, too, due to the decrease in aboveground mass, the amount of Cl^- per plant has hardly changed. Phytodesalination is an emerging technique that involves the utilization of plants desalination potential an essential aspect of phytoextraction for rehabilitating saline soils (Zorrig et al., 2012). This approach basically consisted of a process where 'salt' is taken up from soil by plants and moved to different parts including the roots, stem, leaves etc., thus lowering its concentration in the soil and making it possible for other non-salt-tolerant plant species to grow that further leading to ecosystems recovery (Manasathien & Khanema, 2024). The procedure is regarded as being more eco-friendly than mechanical and chemical methods of salt extraction. However, it should be noted that the choice of plants is usually not random, but based on certain characteristics (Manasathien & Khanema, 2024). The selected plants should have some unique characteristics such as salinity tolerance, high biomass production environmentally easy propagation and cultivation, and preferably multipurpose utilization for fodder or biofuel production and other value-added uses (Mushtaq et al., 2020).

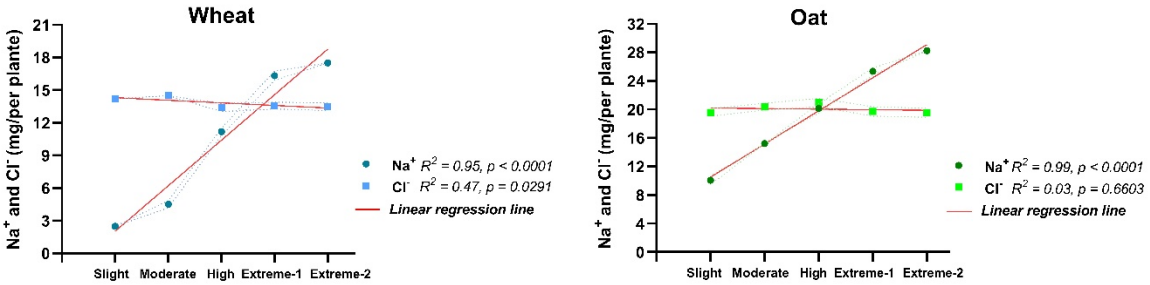


Figure 6. The mass of Na^+ and Cl^- (mg) accumulated in the aboveground parts of the studied crops per plant. The data in the figure represent means ± standard errors (n = 3).

In phytodesalination process specific halophytes are employed to extract a large amount of Na^+ out of contaminated sites, accumulate these ions in their plant bodies, and subsequently translocate them from unharvestable parts (Al-Nasir, 2009). Phytodesalination potential is species-specific and is also influenced by soil characteristics (salinity, sodicity and porosity) and climatic factors (primarily rainfall) (Rabhi et al., 2015). In our finding also saw that oat exhibits higher Na^+ and Cl^- accumulation and greater phytodesalination potential, while wheat maintains more stable ionic regulation and better physiological salt tolerance (Figure 6).

Table 5. Effect of salt stress on the ionic content of roots, stems, and leaves of the studied crops (n = 3, mg g^{-1}).

Crops	Salinity Degree	K^+				Na^+				Cl^-			
		Root	Stem	Upper Leaf	Lower Leaf	Root	Stem	Upper Leaf	Lower Leaf	Root	Stem	Upper Leaf	Lower Leaf
Wheat	Non	16.10 ± 1.69	32.75 ± 3.80	34.50 ± 4.01	27.30 ± 3.01	3.51 ± 0.36	0.40 ± 0.04	0.61 ± 0.06	0.99 ± 0.11	0.34 ± 0.03	8.56 ± 1.01	8.83 ± 1.06	9.71 ± 1.17
	Slight	24.17 ± 2.71	39.98 ± 4.80	40.50 ± 4.86	34.80 ± 4.05	4.72 ± 0.51	0.52 ± 0.06	0.67 ± 0.07	1.14 ± 0.13	0.43 ± 0.04	9.67 ± 1.16	11.44 ± 1.42	12.50 ± 1.55
	Moderate	19.15 ± 2.09	28.60 ± 3.22	35.20 ± 4.11	26.00 ± 2.82	7.24 ± 0.82	1.08 ± 0.12	1.02 ± 0.11	2.64 ± 0.31	0.63 ± 0.06	10.53 ± 1.30	14.80 ± 1.89	16.60 ± 2.15
	High	16.40 ± 1.74	27.80 ± 3.10	32.90 ± 3.81	23.40 ± 2.50	10.28 ± 1.20	2.68 ± 0.31	2.56 ± 0.30	5.70 ± 0.67	0.68 ± 0.07	12.09 ± 1.50	15.70 ± 2.02	17.90 ± 2.35
	Extreme-1	14.00 ± 1.46	27.50 ± 3.03	32.70 ± 3.78	18.60 ± 1.99	13.55 ± 1.60	5.52 ± 0.65	2.91 ± 0.34	8.19 ± 0.98	0.79 ± 0.08	13.13 ± 1.66	16.87 ± 2.19	18.52 ± 2.45
	Extreme-2	12.60 ± 1.30	26.60 ± 2.89	31.60 ± 3.61	17.20 ± 1.82	14.37 ± 1.71	5.79 ± 0.68	3.24 ± 0.39	8.61 ± 1.01	0.96 ± 0.11	15.19 ± 1.97	19.91 ± 2.68	20.65 ± 2.78
Oat	Non	16.25 ± 1.55	34.30 ± 3.98	47.20 ± 5.61	39.00 ± 4.55	5.02 ± 0.55	4.58 ± 0.47	2.97 ± 0.27	3.14 ± 0.35	0.82 ± 0.07	7.12 ± 0.69	13.00 ± 1.53	12.60 ± 1.51
	Slight	20.10 ± 2.02	40.27 ± 4.81	46.90 ± 5.43	36.30 ± 4.27	6.47 ± 0.60	5.84 ± 0.54	3.49 ± 0.33	5.05 ± 0.49	0.83 ± 0.07	8.29 ± 0.84	15.40 ± 1.81	17.50 ± 1.94
	Moderate	13.70 ± 1.29	31.20 ± 3.83	35.40 ± 4.60	20.65 ± 2.40	9.33 ± 0.89	8.58 ± 0.84	10.10 ± 1.11	11.50 ± 1.26	1.04 ± 0.10	9.42 ± 1.00	18.80 ± 2.10	19.10 ± 2.05
	High	9.26 ± 0.89	24.50 ± 2.86	29.10 ± 3.64	15.40 ± 1.75	12.90 ± 1.30	12.60 ± 1.35	14.70 ± 1.75	17.50 ± 1.84	1.50 ± 0.16	11.67 ± 1.22	19.90 ± 2.32	21.10 ± 2.51
	Extreme-1	8.53 ± 0.81	22.50 ± 2.59	21.90 ± 2.62	11.00 ± 1.21	21.40 ± 2.60	19.90 ± 2.40	19.20 ± 2.15	18.80 ± 2.21	1.97 ± 0.19	12.60 ± 1.47	23.00 ± 3.24	23.70 ± 3.02
	Extreme-2	7.14 ± 0.73	17.20 ± 1.89	19.40 ± 2.23	10.70 ± 1.16	31.00 ± 3.34	30.70 ± 4.29	24.10 ± 2.81	23.80 ± 2.74	2.52 ± 0.29	16.40 ± 2.10	26.70 ± 3.68	29.00 ± 3.99

Note: The data in the table represent means ± standard errors ($p < 0.05$).

3.4. Effect of Salinity Stress on Chlorophyll Content and Gas Exchange

Plant productivity is governed by photosynthesis, regulated by both stomata for CO_2 water exchange and photosynthetic activity in mesophyll cells. The photosynthesis rate is reduced by the high salinity level, as it disturbs the photosynthetic process and apparatus. Osmotic stress due to the rise of NaCl concentration in the soil inhibited cell expansion, reduced stomatal aperture and restricted photosynthesis activity of cotton (Maryum et al., 2022). The initial visible sign of salt stress is the decrease in leaf area. Early on the lessened leaf area imposed by restriction in cell extensibility is more important than the photosynthetic rate occurring on a unit surface (Shabala & Lew, 2002). Reduced photosynthetic rate is also attributable to reduced RuBP carboxylase activity at sub-optimal RuBP supply, PSII sensitivity and regenerative capacity of RuBP (Seemann & Sharkey, 1986). Salt stress also disrupts photosynthetic biochemistry by depolarizing the chloroplast lamellar system and leading to loss of chloroplast integrity, which reduces activity of the photosystem in cotton. The possible indirect impact of salt stress on the photosynthetic enzymes might be due to reduction in CO_2 pressure concentration in the leaves owing to stomatal closure (Maryum et al., 2022). Changes in the chlorophyll content index (CCI) of wheat and oat under salt stress are presented in Figure 7. CCI values changed depending on both the change in NaCl content in the root medium and the growth stages of the crops. In other words, along with plant growth, depending on the change in the vegetation stages (budding, flowering, earing, etc.), an increase or decrease in the CCI value was observed in different crops. In conditions of non-saline and slight salinity, high indicators were recorded in both crops, and in some cases an increase in the indicator was observed in the second measurement, which is associated with the stages of active vegetative growth. According to the results of the first measurement conducted 15 days after salt treatment, in the case of wheat, compared to the Non group, the percentage decrease in the CCI value from the Slight to Extreme-2 groups was 0.9%, 22.35%, 28.67%, 46.95%, and 53.05%, respectively. During the next measurements, on the 30th (second measurement) and 45th (third measurement) days, an increase in the CCI value was observed at Slight groups, and then a decrease. In particular, during the second measurement, in Slight it increased by 4.16%, then starting from Moderate it decreased to 22.38%, in High it was 36.63%, in Extreme-1 it was 52.87%, and in Extreme-2 it was 56.04%. During the third measurement, the CCI value in Slight increased by 2.31%, and then a decrease in the value was observed from the Moderate to Extreme-2 groups, amounting to 19.92%, 27.88%, 37.53%, and 51.57%, respectively.

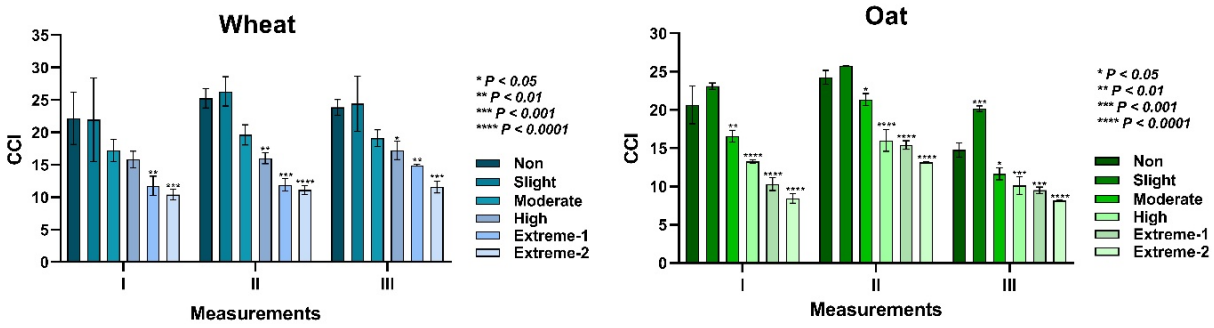


Figure 7. Effect of salt stress on CCI of studied crops. The data in the figure represent means ± standard errors (n = 3).

In oats, the results of the first measurements already indicated a change in the CCI value starting from the Slight group compared to the Non group, which was expressed as an overall increase followed by a gradual decrease under increasing salinity conditions. In particular, the percentage increase in the value in the Slight group was 11.86%, followed by decrease in the Moderate group amounting to 19.85%, in the High group to 35.84%, in the Extreme-1 group to 50.12%, and in the Extreme-2 group to 59.08%. During the second measurement, the pattern remained similar. In the Slight group, the CCI increased by 6.19%, indicating the formation of certain adaptive responses under low-salinity conditions. However, starting with the Moderate group, the value decreased continuously, amounting to 11.96% (Moderate), 34.02% (High), 36.49% (Extreme-1), and 45.57% (Extreme-2), respectively. The results of the third measurement confirmed the previously established pattern, where a relatively higher increase in CCI values was maintained in the Slight group, amounting to 36.61%, while from the Moderate to Extreme-2 groups a decrease was again observed, amounting to 21.02%, 31.53%, 35.59%, and 44.75%, respectively. Na^+ influx under salinity causes a disturbance in ionic balance, plasma membrane structure that decrease K^+ uptake and increase K^+ efflux that reduces cytosol K^+/Na^+ ratio along with unbalanced cellular metabolism (Assaha et al., 2017). Besides, that ionic imbalance are the stomatal movement, photosynthetic machinery and water

relations which directly limits gaseous exchange performance under salinity (Assaha et al., 2017). Previous studies in C_3 plants showed that leaf osmotic was tightly linked with stomatal conductance and photosynthesis (Chen et al., 2015). It has been reported that osmotic adjustment is the dominating control factor of stomatal conductance in C_3 plants under salinity (Munns, 2002). A decreased biomass, strong disturbance in photosynthesis parameters and decrease in chlorophyll contents due to the salinity stress were shown for both of wheat and barley cultivars (Zeeshan et al., 2020). These effects may be attributed to single or conjunctive effects of decreased stomatal conductance, metabolic inhibition and enhanced ROS formation enhancing the oxygen-driven cellular damage (Mahboob et al., 2023).

The results of the study of photosynthetic rate (Pn), transpiration rate (E) and water use efficiency (WUE) under different conditions of salt treatment are presented in Table 6. A consistent decline in photosynthetic activity was observed in both crops with increasing salinity. The reduction in Pn reached 45.4% in wheat and 67.6% in oat, indicating a stronger inhibitory effect of salt stress on oat photosynthesis. Transpiration rate also decreased in both species, by 51.1% in wheat and 44.3% in oat. The smaller decrease in transpiration rate in oat, together with a stronger decline in photosynthetic rate, suggests the involvement of non-stomatal limitations such as damage to the photosynthetic apparatus or reduction in enzyme activity. With increasing salinity, the change in WUE showed opposite trends for the two crops. In wheat, WUE showed a Slight overall increase, while in oat it decreased, implying that oat maintained a more effective water-use strategy under stress despite reduced photosynthetic activity. In summary, wheat maintained higher physiological stability under saline stress, whereas oat demonstrated enhanced water-use efficiency, reflecting distinct adaptive responses to the same stress conditions.

Table 6. Effect of salt stress on gas exchange of studied crops (n = 3).

Salinity Degree	Wheat			Oat		
	Pn (μmol CO_2 m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})	WUE (μmol CO_2 $mmol^{-1}$ H_2O)	Pn (μmol CO_2 m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})	WUE (μmol CO_2 $mmol^{-1}$ H_2O)
Non	7.37 ± 1.62	1.67 ± 0.31	4.42 ± 0.87	8.45 ± 1.91	1.10 ± 0.19	7.72 ± 1.67
Slight	5.27 ± 1.15	1.17 ± 0.22	4.52 ± 0.90	5.86 ± 1.23	0.69 ± 0.12	8.45 ± 1.92
Moderate	5.18 ± 1.12	1.13 ± 0.20	4.59 ± 0.93	5.22 ± 1.14	0.65 ± 0.11	8.02 ± 1.76
High	4.12 ± 0.80	0.86 ± 0.15	4.78 ± 0.98	4.59 ± 0.92	0.64 ± 0.11	7.13 ± 1.51
Extreme-1	4.06 ± 0.78	0.83 ± 0.14	4.89 ± 1.02	2.77 ± 0.53	0.62 ± 0.10	4.49 ± 0.89
Extreme-2	4.02 ± 0.76	0.82 ± 0.14	4.93 ± 1.05	2.74 ± 0.51	0.61 ± 0.10	4.48 ± 0.89

Note: The data in the table represent means ± standard errors ($p < 0.05$).

Our finding also shows that increasing the salinity level can decrease the chlorophyll contents which corelated with biomass of wheat and oat plants (Figure 7). Another finding show that there is a trade-off between safety and efficiency that limits stomatal function such that species with higher stomatal conductance in well-watered conditions (*g*max) are more sensitive to closure during leaf dehydration, as evidenced by their higher leaf water potential at which stomatal conductance is reduced by 50%(Ψgs50) (Henry et al., 2019). The *g*max—Ψgs50 trade-off and its mechanism is evidenced by experiments on leaves of California wood species. Connecting the two core roles of stomata: facilitation of gas exchange and the initial level of protection against drought, this trade-off limits water use rates and the susceptibility of leaves to drying which may have consequences at ecosystem levels (Henry et al., 2019). In another experiment show that under higher level of salinity stress can decreases in stomatal conductance (Gs), photosynthesis rate (Pn) and leaf chlorophyll content in sensitive (Sunmate) then in salt-tolerant (cv. Suntop) wheat cultivars and salt-tolerant barley cv. CM72 (Zeeshan et al., 2020). Similarly, another research carried out on sorghum [*Sorghum bicolor* (L.) Moench] that observed the variation in stomatal conductance (Gs) and intercellular CO_2 concentration (Ci) were significantly associated under salt stress which suggested that the stomata control was the major limitation factor that inhibiting net photosynthetic rates (Pn) of leaves under saline environments (Netondo et al., 2004). Normally, under stress condition, plants close their stomata when first exposed to stressful conditions in order to conserve water and this leads to lower stomatal conductance (Gs) and photosynthesis. The impact of salinity could be an indirect effect, mediated through the lower partial pressure of CO_2 in those green parts of the plant as a result of stomata closure on enzyme activities associated with photosynthesis (Shahid et al., 2020). In low level NaCl (171 mM) concentration not change gas exchange parameters *Pn, E* and *gs* (stomatal conductance) for willow (*Salix alba* L.) plant but with the increase of salt concentration, these each index (Ran et al., 2021). Our experiment also supports all these current findings (Table 6).

4. Conclusions and Future Prospective

This study explored the morphological and physiological factors contributing to salt tolerance and adaptation in wheat and oat. Salinity stress affected various aspects including plant growth, biomass, water relations, membrane stability, ionic balance, photosynthesis, and leaf reflectance in both species, with clear differences observed. Wheat showed better salt tolerance, maintaining stable growth, higher K^+ content, and lower Na^+/K^+ ratios, which suggests more effective ionic regulation and osmotic adjustment. Meanwhile, oat accumulated more Na^+ and Cl^- in its aboveground parts, demonstrating its phytodesalination capacity despite experiencing reduced photosynthesis under high salinity levels. Future research should investigate the biochemical pathways involved in ion homeostasis and osmotic regulation for both species. Moreover, advanced techniques like nanoparticles and nanofertilizers could be utilized in crop management to improve adaptation and promote sustainable salinity stress mitigation.

Author Contributions

A.H., A.S., H.K., R.K.S., V.D.R. and K.G. were responsible for conceptualization, methodology, software, writing-original draft, and writing—reviewing and editing; A.H., A.S., H.K. and K.G. assisted with conceptualization, supervision, resources, and writing—reviewing and editing. All authors have read and agreed to the published version of the manuscript.

Funding

K.G. is supported by Higher Education and Science Committee of the Republic of Armenia: grant number 21AG-4C075. VDR is supported by Priority 2030 programe implemented at Southern Federal University.

Institutional Review Board Statement

Not applicable.

Informed Consent Statement

Not applicable.

Data Availability Statement

The datasets generated during analyzed during the current study are available from the corresponding author on reasonable request.

Conflicts of Interest

The authors declare no conflict of interest. Given the role as Associate Editor-in-Chief in *Annals of Agri-bio Research*, Vishnu D Rajput had no involvement in the peer review of this paper and had no access to information regarding its peer-review process. Full responsibility for the editorial process of this paper was delegated to another editor of the journal.

Use of AI and AI-Assisted Technologies

No AI tools were utilized for this paper.

References

Abdehpour, Z., Ehsanzadeh, P., & Ghanati, F. (2025). Expression level of NHX1 and SOS1 genes is key to high salt tolerance of ancient emmer wheat: Implications to tackling salt stress penalties of wheat yield. *Functional Plant Biology*, *52*(8), FP25034. https://doi.org/10.1071/FP25034.

Afzal, M., Hindawi, S. E. S., Alghamdi, S. S., Migdadi, H. H., Khan, M. A., Hasnain, M. U., Arslan, M., Habib ur Rahman, M., & Sohaib, M. (2023). Potential Breeding Strategies for Improving Salt Tolerance in Crop Plants. *Journal of Plant Growth Regulation*, *42*(6), 3365–3387. https://doi.org/10.1007/S00344-022-10797-W.

Agarie, S., Shimoda, T., Shimizu, Y., Baumann, K., Sunagawa, H., Kondo, A., Ueno, O., Nakahara, T., Nose, A., & Cushman, J. C. (2007). Salt tolerance, salt accumulation, and ionic homeostasis in an epidermal bladder-cell-less mutant of the common ice plant *Mesembryanthemum crystallinum*. *Journal of Experimental Botany*, *58*(8), 1957–1967. https://doi.org/10.1093/JXB/ERM057.

Ahmed, M., Tóth, Z., & Decsi, K. (2024). The Impact of Salinity on Crop Yields and the Confrontational Behavior of Transcriptional Regulators, Nanoparticles, and Antioxidant Defensive Mechanisms under Stressful Conditions: A Review. *International Journal of Molecular Sciences*, *25*(5), 2654. https://doi.org/10.3390/IJMS25052654.

Al Hassan, M., López-Gresa, M. D. P., Boscaiu, M., & Vicente, O. (2016). Stress tolerance mechanisms in Juncus: Responses to salinity and drought in three Juncus species adapted to different natural environments. *Functional Plant Biology*, *43*(10), 949–960. https://doi.org/10.1071/FP16007.

Alam, M. M., Hossain, M. M., Rabbani, M. G., Tasmim, M. T., & Rahman, L. (2023). Effect of Salinity (NaCl) Stress on Root-shoot Traits of Tomato in Hydroponic Culture. *Agricultural Science Digest*, *43*(6), 751–757. https://doi.org/10.18805/AG.DF-442.

Allison, L., Bernstein, L., Bower, C. A., Brown, J. W., Fireman, J. T., Hatcher, J. T., Hayward, H. E., Pearson, R. C., Reeve, L. E., Richards, L. A., & Wilcox, L. (1954). Diagnosis and Improvement of Saline and Alkali Soils. In L. A. Richards, (Ed.), *Agriculture Handbook No. 60*. U.S. Department of Agriculture.

Al-Nasir, F. (2009). Bioreclamation of a saline sodic soil in a semi arid region/Jordan. *American-Eurasian Journal of Agricultural and Environmental Science*, *5*(5), 701–706.

Assaha, D. V. M., Ueda, A., Saneoka, H., Al-Yahyai, R., & Yaish, M. W. (2017). The Role of Na^+ and K^+ Transporters in Salt Stress Adaptation in Glycophytes. *Frontiers in Physiology*, *8*, 509. https://doi.org/10.3389/FPHYS.2017.00509.

Azimychetabi, Z., & Sabokdast Nodehi, M. (2021). Physiological and biochemical responses of four genotypes of common bean (*Phaseolus vulgaris* L.) under salt stress. *Journal of Agricultural Science and Technology*, *23*(5), 1091–1103. https://jast.modares.ac.ir/article_16589.html.

Barberon, M. (2017). The endodermis as a checkpoint for nutrients. *New Phytologist*, *213*(4), 1604–1610. https://doi.org/10.1111/NPH.14140.

Bimurzayev, N., Sari, H., Kurunc, A., Doganay, K. H., & Asmamaw, M. (2021). Effects of different salt sources and salinity levels on emergence and seedling growth of faba bean genotypes. *Scientific Reports*, *11*(1), 18198. https://doi.org/10.1038/s41598-021-97810-6.

Chand, S., Kumar, S., Roy, A. K., Vijay, D., Choudhary, B. B., Indu, Kumar, P., Agrawal, R. K., Yadav, V. K., Kaushal, P., Yadava, D. K., Kumar, R. V., Singh, A. K., Ahmed, S., Malaviya, D. R., Singhal, R. K., Prasad, B., Kapoor, R., Jha, A. K., & Panchta, R. (2025). Analyzing trends and future projections in fodder oats (*Avena sativa* L.) for quality seed production in India. *Frontiers in Plant Science*, *16*, 1525422. https://doi.org/10.3389/FPLS.2025.1525422.

Chen, T. W., Kahlen, K., & Stützel, H. (2015). Disentangling the contributions of osmotic and ionic effects of salinity on stomatal, mesophyll, biochemical and light limitations to photosynthesis. *Plant, Cell & Environment*, *38*(8), 1528–1542. https://doi.org/10.1111/PCE.12504.

Cope, J. E., Norton, G. J., George, T. S., & Newton, A. C. (2022). Evaluating Variation in Germination and Growth of Landraces of Barley (*Hordeum vulgare* L.) Under Salinity Stress. *Frontiers in Plant Science*, *13*, 863069. https://doi.org/10.3389/FPLS.2022.863069.

De Lima, G. S., Gheyi, H. R., Nobre, R. G., Xavier, D. A., Dos Anjos Soares, L. A., Cavalcante, L. F., & Dos Santos, J. B. (2016). Emergence, growth, and flowering of castor beans as a function of the cationic composition of irrigation water. *Semina: Ciências Agrárias*, *37*(2), 651–664. https://doi.org/10.5433/1679-0359.2016v37n2P651.

Dikobe, T. B., Mashile, B., Sinthumule, R. R., & Ruzvidzo, O. (2021). Distinct Morpho-Physiological Responses of Maize to Salinity Stress. *American Journal of Plant Sciences*, *12*(6), 946–959. https://doi.org/10.4236/AJPS.2021.126064.

Dionisio-Sese, M. L., & Tobita, S. (1998). Antioxidant responses of rice seedlings to salinity stress. *Plant Science*, *135*(1), 1–9. https://doi.org/10.1016/S0168-9452(98)00025-9.

Ehsanzadeh, P., Feizabadi, S., & Razmjoo, J. (2025). Enhanced grain yield of mycorrhizae-inoculated modern and ancient wheats across different salinities: The gains stem from physiological, photosynthetic, and root attributes. *BMC Plant Biology*, *25*(1), 1597. https://doi.org/10.1186/S12870-025-07619-Y.

EL Sabagh, A., Islam, M. S., Skalicky, M., Ali Raza, M., Singh, K., Anwar Hossain, M., Hossain, A., Mahboob, W., Iqbal, M. A., Ratnasekera, D., Singhal, R. K., Ahmed, S., Kumari, A., Wasaya, A., Sytar, O., Brestic, M., ÇIG, F., Erman, M., Habib Ur Rahman, M., … Arshad, A. (2021). Salinity Stress in Wheat (*Triticum aestivum* L.) in the Changing Climate: Adaptation and Management Strategies. *Frontiers in Agronomy*, *3*, 661932. https://doi.org/10.3389/FAGRO.2021.661932.

Fang, S., Hou, X., & Liang, X. (2021). Response Mechanisms of Plants Under Saline-Alkali Stress. *Frontiers in Plant Science*, *12*, 667458. https://doi.org/10.3389/FPLS.2021.667458.

FAO. (2025). *The State of the World's Land and Water Resources for Food and Agriculture 2025*. Food and Agriculture Organization. https://doi.org/10.4060/CD7488EN.

Garnier, E., Shipley, B., Roumet, C., & Laurent, G. (2001). A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology*, *15*(5), 688–695. https://doi.org/10.1046/J.0269-8463.2001.00563.X.

Ghazaryan, K. A., Harutyunyan, A. S., Khachatryan, H. E., Singh, A., Minkina, T. M., Rajput, V. D., & Movsesyan, H. S. (2023). Study of tolerance and phytodesalination potential of wheat, oat, emmer, and barley for sustainable saline agriculture. *Applied Ecology and Environmental Research*, *21*(5), 4853–4882. https://doi.org/10.15666/AEER/2105_48534882.

Ghazaryan, K., & Chen, Y. (2016). Hydrochemical assessment of surface water for irrigation purposes and its influence on soil salinity in Tikanlik oasis, China. *Environmental Earth Sciences*, *75*(5), 383. https://doi.org/10.1007/S12665-016-5287-0.

Gill, P. K., Dev Sharma, A., Singh, P., & Singh Bhullar, S. (2001). Effect of various abiotic stresses on the growth, soluble sugars and water relations of sorghum seedlings grown in light and darkness. *The Bulgarian Journal of Plant Physiology*, *27*(2), 72–84.

González, L., & González-Vilar, M. (2001). Determination of Relative Water Content. In *Handbook of Plant Ecophysiology Techniques* (pp. 207–212). Springer Dordrecht. https://doi.org/10.1007/0-306-48057-3_14.

Guo, X., Zhou, G., Zhu, G., & Jiao, X. (2019). Effects of calcium on emergence and seedling growth of castor bean under salinity stress. *Current Science*, *116*(12), 2028–2035. https://doi.org/10.18520/CS/V116/I12/2028-2035.

Hao, S., Wang, Y., Yan, Y., Liu, Y., Wang, J., & Chen, S. (2021). A Review on Plant Responses to Salt Stress and Their Mechanisms of Salt Resistance. *Horticulturae*, *7*(6), 132. https://doi.org/10.3390/HORTICULTURAE7060132.

Hasanuzzaman, M., Davies, N. W., Shabala, L., Zhou, M., Brodribb, T. J., & Shabala, S. (2017). Residual transpiration as a component of salinity stress tolerance mechanism: A case study for barley. *BMC Plant Biology*, *17*(1), 107. https://doi.org/10.1186/S12870-017-1054-Y.

Henry, C., John, G. P., Pan, R., Bartlett, M. K., Fletcher, L. R., Scoffoni, C., & Sack, L. (2019). A stomatal safety-efficiency trade-off constrains responses to leaf dehydration. *Nature Communications*, *10*(1), 3398. https://doi.org/10.1038/S41467-019-11006-1.

Hussain, N., Ghaffar, A., Zafar, Z. U., Javed, M., Shah, K. H., Noreen, S., Manzoor, H., Iqbal, M., Hassan, I. F. Z., Bano, H., Gul, H. S., Aamir, M., Khalid, A., Sohail, Y., Ashraf, M., & Athar, H. u. R. (2021). Identification of novel source of salt tolerance in local bread wheat germplasm using morpho-physiological and biochemical attributes. *Scientific Reports*, *11*(1), 10854. https://doi.org/10.1038/s41598-021-90280-w.

Igrejas, G., & Branlard, G. (2020). The Importance of Wheat. In *Wheat Quality for Improving Processing and Human Health* (pp. 1–7). Springer International Publishing. https://doi.org/10.1007/978-3-030-34163-3_1.

James, R. A., Blake, C., Byrt, C. S., & Munns, R. (2011). Major genes for Na+ exclusion, Nax1 and Nax2 (wheat HKT1;4 and HKT1;5), decrease Na^+ accumulation in bread wheat leaves under saline and waterlogged conditions. *Journal of Experimental Botany*, *62*(8), 2939–2947. https://doi.org/10.1093/JXB/ERR003.

Jennings, B. D. H. (1976). The effects of sodium chloride on higher plants. *Biological Reviews*, *51*(4), 453–486. https://doi.org/10.1111/J.1469-185X.1976.TB01064.X.

Kappachery, S., AlHosani, M., Khan, T. A., AlKharoossi, S. N., AlMansoori, N., AlShehhi, S. A. S., AlMansoori, H., AlKarbi, M., Sasi, S., Karumannil, S., Elangovan, S. K., Shah, I., & Gururani, M. A. (2024). Modulation of antioxidant defense and PSII components by exogenously applied acetate mitigates salinity stress in *Avena sativa*. *Scientific Reports*, *14*(1), 620. https://doi.org/10.1038/s41598-024-51302-5.

Khamesi, F., Amini, A., & Ehsanzadeh, P. (2020). Chickpea response to saline water: Concurrence of ion homeostasis sustainment and antioxidative defense measures. *South African Journal of Botany*, *133*, 245–252. https://doi.org/10.1016/J.SAJB.2020.08.001.

Khan, M. N., Siddiqui, M. H., Mukherjee, S., Alamri, S., Al-Amri, A. A., Alsubaie, Q. D., Al-Munqedhi, B. M. A., & Ali, H. M. (2021). Calcium-hydrogen sulfide crosstalk during K^+-deficient NaCl stress operates through regulation of Na^+/H^+ antiport and antioxidative defense system in mung bean roots. *Plant Physiology and Biochemistry*, *159*, 211–225. https://doi.org/10.1016/J.PLAPHY.2020.11.055.

Krishnamurthy, S. L., Gautam, R. K., Sharma, P. C., & Sharma, D. K. (2016). Effect of different salt stresses on agro-morphological traits and utilisation of salt stress indices for reproductive stage salt tolerance in rice. *Field Crops Research*, *190*, 26–33. https://doi.org/10.1016/J.FCR.2016.02.018.

Liu, L., Assaha, D. V. M., Islam, M. S., Rajendran, K., Theivasigamani, P., Soufan, W., Ayman, E. S., & Ueda, A. (2023). Effect of NaCl on physiological, biochemical, and ionic parameters of naked oat (*Avena nuda* L.) line Bayou1. *Frontiers in Sustainable Food Systems*, *7*, 1336350. https://doi.org/10.3389/FSUFS.2023.1336350.

Liu, T., Xia, L., Dong, X., Wang, J., Liu, X., Sun, H., & Fang, Y. (2025). Saline water concentration determines the reduction pathway for oat phosphorus absorption. *Agricultural Water Management*, *307*, 109236. https://doi.org/10.1016/J.AGWAT.2024.109236.

Ma, Q., Hu, J., Zhou, X. R., Yuan, H. J., Kumar, T., Luan, S., & Wang, S. M. (2017). ZxAKT1 is essential for K^+ uptake and K^+/Na^+ homeostasis in the succulent xerophyte *Zygophyllum xanthoxylum*. *Plant Journal*, *90*(1), 48–60. https://doi.org/10.1111/TPJ.13465.

Mahboob, W., Rizwan, M., Irfan, M., Hafeez, O. B. A., Sarwar, N., Akhtar, M., Munir, M., Rani, R., El Sabagh, A., & Shimelis, H. (2023). Salinity tolerance in wheat: Responses, mechanisms and adaptation approaches. *Applied Ecology and Environmental Research*, *21*(6), 5299–5328. https://doi.org/10.15666/AEER/2106_52995328.

Manasathien, J., & Khanema, P. (2024). Assessment of salt tolerance in phytodesalination candidates: Two varieties of Fimbristylis—*F. ferruginea* and *F. tenuicula*. *Journal of Environmental Quality*, *53*(2), 274–286. https://doi.org/10.1002/JEQ2.20544.

Manuel, J., Lozano, R., Lu, Y., & Fricke, W. (2023). Salt Stress—Regulation of Root Water Uptake in a Whole-Plant and Diurnal Context. *International Journal of Molecular Sciences*, *24*(9), 8070. https://doi.org/10.3390/IJMS24098070.

Maryum, Z., Luqman, T., Nadeem, S., Khan, S. M. U. D., Wang, B., Ditta, A., & Khan, M. K. R. (2022). An overview of salinity stress, mechanism of salinity tolerance and strategies for its management in cotton. *Frontiers in Plant Science*, *13*, 907937. https://doi.org/10.3389/FPLS.2022.907937.

Mou, M., Wang, Q., Chen, Y., Yu, D., & Chen, L. (2021). Functional characterization of the Arabidopsis SERRATE under salt stress. *Plant Diversity*, *43*(1), 71–77. https://doi.org/10.1016/J.PLD.2020.06.010.

Munns, R. (2002). Comparative physiology of salt and water stress. *Plant, Cell & Environment*, *25*(2), 239–250. https://doi.org/10.1046/J.0016-8025.2001.00808.X.

Munns, R., Passioura, J. B., Colmer, T. D., & Byrt, C. S. (2020). Osmotic adjustment and energy limitations to plant growth in saline soil. *New Phytologist*, *225*(3), 1091–1096. https://doi.org/10.1111/NPH.15862.

Mushtaq, W., Bedair, H., & Shakeel, A. (2020). Halophytes. In *Handbook of Halophytes* (pp. 1–16). Springer. https://doi.org/10.1007/978-3-030-17854-3_95-1.

Nassar, R. M. A., Kamel, H. A., Ghoniem, A. E., Alarcón, J. J., Sekara, A., Ulrichs, C., & Abdelhamid, M. T. (2020). Physiological and Anatomical Mechanisms in Wheat to Cope with Salt Stress Induced by Seawater. *Plants*, *9*(2), 237. https://doi.org/10.3390/PLANTS9020237.

Netondo, G. W., Onyango, J. C., & Beck, E. (2004). Sorghum and salinity: II. Gas exchange and chlorophyll fluorescence of sorghum under salt stress. *Crop Science*, *44*(3), 806–811. https://doi.org/10.2135/CROPSCI2004.8060.

Ntawuguranayo, S., Zilberberg, M., Nashef, K., Bonfil, D. J., Bainsla, N. K., Piñera-Chavez, F. J., Reynolds, M. P., Peleg, Z., & Ben-David, R. (2024). Stem traits promote wheat climate-resilience. *Frontiers in Plant Science*, *15*, 1388881. https://doi.org/10.3389/FPLS.2024.1388881.

Pandit, K., Chandni, Kaur, S., Kumar, M., Bhardwaj, R., & Kaur, S. (2024). Salinity stress: Impact on plant growth. *Advances in Food Security and Sustainability*, *9*, 145–160. https://doi.org/10.1016/BS.AF2S.2024.07.002.

Park, H. J., Kim, W. Y., & Yun, D. J. (2016). A New Insight of Salt Stress Signalingin Plant. *Molecules and Cells*, *39*(6), 447–459. https://doi.org/10.14348/MOLCELLS.2016.0083.

Pattanagul, W., & Thitisaksakul, M. (2008). Effect of salinity stress on growth and carbohydrate metabolism in three rice (*Oryza sativa* L.) cultivars differing in salinity tolerance. *Indian Journal of Experimental Biology*, *46*(10), 736–742.

Pedrero, F., & Alarcón, J. J. (2009). Effects of treated wastewater irrigation on lemon trees. *Desalination*, *246*(1–3), 631–639. https://doi.org/10.1016/J.DESAL.2008.07.017.

Plaut, Z., Edelstein, M., & Ben-Hur, M. (2013). Overcoming Salinity Barriers to Crop Production Using Traditional Methods. *Critical Reviews in Plant Sciences*, *32*(4), 250–291. https://doi.org/10.1080/07352689.2012.752236.

Ponce, K. S., Meng, L., Guo, L., Leng, Y., & Ye, G. (2021). Advances in Sensing, Response and Regulation Mechanism of Salt Tolerance in Rice. *International Journal of Molecular Sciences*, *22*(5), 2254. https://doi.org/10.3390/IJMS22052254.

Qin, J., Dong, W. Y., He, K. N., Yu, Y., Tan, G. D., Han, L., Dong, M., Zhang, Y. Y., Zhang, D., Li, A. Z., & Wang, Z. L. (2010). NaCl salinity-induced changes in water status, ion contents and photosynthetic properties of *Shepherdia argentea* (Pursh) Nutt. seedlings. *Plant, Soil and Environment*, *56*(7), 325–332. https://doi.org/10.17221/209/2009-PSE.

Rabhi, M., Atia, A., Abdelly, C., & Smaoui, A. (2015). New parameters for a better evaluation of vegetative bioremediation, leaching, and phytodesalination. *Journal of Theoretical Biology*, *383*, 7–11. https://doi.org/10.1016/J.JTBI.2015.07.027.

Rabhi, M., Castagna, A., Remorini, D., Scattino, C., Smaoui, A., Ranieri, A., & Abdelly, C. (2012). Photosynthetic responses to salinity in two obligate halophytes: *Sesuvium portulacastrum* and *Tecticornia indica*. *South African Journal of Botany*, *79*, 39–47. https://doi.org/10.1016/J.SAJB.2011.11.007.

Ran, X., Wang, X., Gao, X., Liang, H., Liu, B., & Huang, X. (2021). Effects of salt stress on the photosynthetic physiology and mineral ion absorption and distribution in white willow (*Salix alba* L.). *PLoS ONE*, *16*(11), e0260086. https://doi.org/10.1371/JOURNAL.PONE.0260086.

Rehman, S. u., Yang, J., Zhang, J., Zhang, L., Hao, X., Song, R., Chen, S., Wang, G., & Hua, L. (2025). Salt stress in wheat: A physiological and genetic perspective. *Plant Stress*, *16*, 100832. https://doi.org/10.1016/J.STRESS.2025.100832.

Saddiq, M. S., Iqbal, S., Hafeez, M. B., Ibrahim, A. M. H., Raza, A., Fatima, E. M., Baloch, H., Jahanzaib, Woodrow, P., & Ciarmiello, L. F. (2021). Effect of Salinity Stress on Physiological Changes in Winter and Spring Wheat. *Agronomy*, *11*(6), 1193. https://doi.org/10.3390/AGRONOMY11061193.

Scotti-Campos, P., Duro, N., Costa, M. da, Pais, I. P., Rodrigues, A. P., Batista-Santos, P., Semedo, J. N., Leitão, A. E., Lidon, F. C., Pawlowski, K., Ramalho, J. C., & Ribeiro-Barros, A. I. (2016). Antioxidative ability and membrane integrity in salt-induced responses of *Casuarina glauca* Sieber ex Spreng. in symbiosis with N2-fixing *Frankia* Thr or supplemented with mineral nitrogen. *Journal of Plant Physiology*, *196–197*, 60–69. https://doi.org/10.1016/J.JPLPH.2016.03.012.

Seemann, J. R., & Sharkey, T. D. (1986). Salinity and Nitrogen Effects on Photosynthesis, Ribulose-1,5-Bisphosphate Carboxylase and Metabolite Pool Sizes in *Phaseolus vulgaris* L. *Plant Physiology*, *82*(2), 555–560. https://doi.org/10.1104/PP.82.2.555.

Shabala, S. N., & Lew, R. R. (2002). Turgor regulation in osmotically stressed Arabidopsis epidermal root cells. Direct support for the role of inorganic ion uptake as revealed by concurrent flux and cell turgor measurements. *Plant Physiology*, *129*(1), 290–299. https://doi.org/10.1104/PP.020005.

Shahid, M. A., Sarkhosh, A., Khan, N., Balal, R. M., Ali, S., Rossi, L., Gómez, C., Mattson, N., Nasim, W., & Garcia-Sanchez, F. (2020). Insights into the Physiological and Biochemical Impacts of Salt Stress on Plant Growth and Development. *Agronomy*, *10*(7), 938. https://doi.org/10.3390/AGRONOMY10070938.

Sharma, K., & Sharma, P. K. (2025). Wheat as a Nutritional Powerhouse: Shaping Global Food Security. In *Triticum—The Pillar of Global Food Security*. IntechOpen. https://doi.org/10.5772/INTECHOPEN.1009499.

Shtaya, M., Yasin, A., Fatoom, J., & Jebreen, M. (2020). The effect of salinity on leaf relative water content and chlorophyll content of three wheat (*Triticum aestivum* L.) landraces from Palestine. *Hebron University Research Journal-A (Natural Sciences)*, *8*(1), 57–65. https://digitalcommons.aaru.edu.jo/hujr_a/vol8/iss1/4.

Silla, F., González-Gil, A., González-Molina, M. E., Mediavilla, S., & Escudero, A. (2010). Estimation of chlorophyll in *Quercus* leaves using a portable chlorophyll meter: Effects of species and leaf age. *Annals of Forest Science*, *67*(1), 108. https://doi.org/10.1051/FOREST/2009093.

Sinthumule, R. R., Ruzvidzo, O., & Dikobe, T. B. (2022). Elucidation of the morpho-physiological traits of maize (*Zea mays* L.) under salt stress. *Journal of Experimental Biology and Agricultural Sciences*, *10*(6), 1441–1452. https://doi.org/10.18006/2022.10(6).1441.1452.

Slama, I., Ghnaya, T., Savouré, A., & Abdelly, C. (2008). Combined effects of long-term salinity and soil drying on growth, water relations, nutrient status and proline accumulation of *Sesuvium portulacastrum*. *Comptes Rendus Biologies*, *331*(6), 442–451. https://doi.org/10.1016/J.CRVI.2008.03.006.

Sodaeizadeh, H., Hokmollahi, F., Ghasemi, S., Sadeghian, M., & Tarrah, S. (2025). Cyanobacteria inoculation mitigates salinity stress by regulating plant growth, photosynthetic performance, elemental concentrations and yield in wheat. *South African Journal of Botany*, *180*, 857–869. https://doi.org/10.1016/J.SAJB.2025.04.006.

Sohrabizadeh, Z., Sodaeizadeh, H., & Mosleh Arani, A. (2023). Role of mucilage in improving seedling emergence of *Ocimum basilicum* L. exposed to salinity stress. *Rhizosphere*, *26*, 100684. https://doi.org/10.1016/J.RHISPH.2023.100684.

Steinhorst, L., & Kudla, J. (2019). How plants perceive salt. *Nature*, *572*(7769), 318–320. https://doi.org/10.1038/d41586-019-02289-x.

Su, N., Wu, Q., Chen, J., Shabala, L., Mithöfer, A., Wang, H., Qu, M., Yu, M., Cui, J., & Shabala, S. (2019). GABA operates upstream of H^+-ATPase and improves salinity tolerance in Arabidopsis by enabling cytosolic K^+ retention and Na^+ exclusion. *Journal of Experimental Botany*, *70*(21), 6349–6361. https://doi.org/10.1093/JXB/ERZ367.

Tian, W., Wang, C., Gao, Q., Li, L., & Luan, S. (2020). Calcium spikes, waves and oscillations in plant development and biotic interactions. *Nature Plants*, *6*(7), 750–759. https://doi.org/10.1038/s41477-020-0667-6.

Van Zelm, E., Zhang, Y., & Testerink, C. (2020). Salt Tolerance Mechanisms of Plants. *Annual Review of Plant Biology*, *71*(1), 403–433. https://doi.org/10.1146/ANNUREV-ARPLANT-050718-100005.

Wang, J., Du, X., Wang, Y., Zhao, X., Gu, Y., Zhao, M., Zheng, J., Yu, X., Yang, H., Yin, Y., Zhang, L., Hao, X., Yu, T., & Sun, X. (2026). Differential Effects of Six Salt Types on Wheat (*Triticum aestivum* L.) Germination and Seedling Growth. *Agriculture*, *16*(1), 92. https://doi.org/10.3390/AGRICULTURE16010092.

Wang, Y., Ma, W., Fu, H., Li, L., Ruan, X., & Zhang, X. (2023). Effects of Salinity Stress on Growth and Physiological Parameters and Related Gene Expression in Different Ecotypes of *Sesuvium portulacastrum* on Hainan Island. *Genes*, *14*(7), 1336. https://doi.org/10.3390/GENES14071336.

Wu, H., Shabala, L., Zhou, M., Su, N., Wu, Q., Ul-Haq, T., Zhu, J., Mancuso, S., Azzarello, E., & Shabala, S. (2019). Root vacuolar Na^+ sequestration but not exclusion from uptake correlates with barley salt tolerance. *Plant Journal*, *100*(1), 55–67. https://doi.org/10.1111/TPJ.14424.

Xue, F., Liu, W., Cao, H., Song, L., Ji, S., Tong, L., & Ding, R. (2021). Stomatal conductance of tomato leaves is regulated by both abscisic acid and leaf water potential under combined water and salt stress. *Physiologia Plantarum*, *172*(4), 2070–2078. https://doi.org/10.1111/PPL.13441.

Yong, M. T., Solis, C. A., Rabbi, B., Huda, S., Liu, R., Zhou, M., Shabala, L., Venkataraman, G., Shabala, S., & Chen, Z. H. (2020). Leaf mesophyll K^+ and Cl^- fluxes and reactive oxygen species production predict rice salt tolerance at reproductive

stage in greenhouse and field conditions. *Plant Growth Regulation*, *92*(1), 53–64. https://doi.org/10.1007/S10725-020-00619-Y.

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*(1), 127. https://doi.org/10.3390/AGRONOMY10010127.

Zhang, H., Feng, H., Zhang, J., Ge, R., Zhang, L., Wang, Y., Li, L., Wei, J., & Li, R. (2020). Emerging crosstalk between two signaling pathways coordinates K^+ and Na^+ homeostasis in the halophyte *Hordeum brevisubulatum*. *Journal of Experimental Botany*, *71*(14), 4345–4358. https://doi.org/10.1093/JXB/ERAA191.

Zhang, J., Wang, H., Feng, D., Cao, C., Zheng, C., Dang, H., Li, K., Gao, Y., & Sun, C. (2024). Evaluating the impacts of long-term saline water irrigation on soil salinity and cotton yield under plastic film mulching: A 15-year field study. *Agricultural Water Management*, *293*, 108703. https://doi.org/10.1016/J.AGWAT.2024.108703.

Zhang, M. X., Bai, R., Nan, M., Ren, W., Wang, C. M., Shabala, S., & Zhang, J. L. (2022). Evaluation of salt tolerance of oat cultivars and the mechanism of adaptation to salinity. *Journal of Plant Physiology*, *273*, 153708. https://doi.org/10.1016/J.JPLPH.2022.153708.

Zhang, Z., Xia, Z., Zhou, C., Wang, G., Meng, X., & Yin, P. (2024). Insights into Salinity Tolerance in Wheat. *Genes*, *15*(5), 573. https://doi.org/10.3390/GENES15050573.

Zhao, X., Tian, L., Zhu, Z., Sang, Z., Ma, L., & Jia, Z. (2024). Growth and Physiological Responses of Magnoliaceae to NaCl Stress. *Plants*, *13*(2), 170. https://doi.org/10.3390/PLANTS13020170.

Zorrig, W., Rabhi, M., Ferchichi, S., Smaoui, A., & Abdelly, C. (2012). Phytodesalination: A solution for salt-affected soils in arid and semi-arid regions. *Journal of Arid Land Studies*, *22*(1), 299–302.

Zouhaier, B., Najla, T., Abdallah, A., Wahbi, D., Wided, C., Chedly, A., & Abderrazak, S. (2015). Salt stress response in the halophyte *Limoniastrum guyonianum* Boiss. *Flora—Morphology, Distribution, Functional Ecology of Plants*, *217*, 1–9. https://doi.org/10.1016/J.FLORA.2015.09.003.