

SALINITY TOLERANCE IN WHEAT: RESPONSES, MECHANISMS AND ADAPTATION APPROACHES

MAHBOOB, W.^{1,2} – RIZWAN, M.² – IRFAN, M.² – HAFEEZ, O. B. A.³ – SARWAR, N.^{4,5} – AKHTAR, M.⁵
– MUNIR, M.³ – RANI, R.⁶ – EL SABAGH, A.^{7,8} – SHIMELIS, H.^{9*}

¹*College of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, China*

²*Nuclear Institute of Agriculture (NIA), Tandojam 70060, Pakistan*

³*University of Agriculture Faisalabad, Sub-campus Burewala 61010, Pakistan*

⁴*Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Beijing, China*

⁵*Nuclear Institute for Agriculture and Biology (NIAB), Faisalabad 38000, Pakistan*

⁶*Agricultural Biotechnology Division, National Institute for Biotechnology and Genetic Engineering (NIBGE), Constituent College Pakistan Institute of Engineering and Applied Sciences (PIEAS), Faisalabad, Pakistan*

⁷*Department of Agronomy, Faculty of Agriculture, University of Kafrelsheikh, Egypt*

⁸*Department of Field Crops, Faculty of Agriculture, Siirt University, Turkey*

⁹*School of Agricultural, Earth and Environmental Sciences, African Centre for Crop Improvement, University of KwaZulu-Natal, Pietermaritzburg, South Africa*

**Corresponding author
e-mail: shimelish@ukzn.ac.za*

(Received 17th Apr 2023; accepted 1st Aug 2023)

Abstract. Soil salinity is one of the most devastating environmental stresses, causing a significant reduction in cultivable land worldwide. Salinity restricts the growth, development, and yield of plants. In response to salinity, plants alter their morpho-physiological, biochemical and molecular responses. Under salt stress, plants, including wheat, employ a variety of morpho-physiological, biochemical, and metabolic changes at the cellular, tissue, and whole-plant levels to survive. Although significant progress has been made in understanding the mechanism of salinity tolerance in wheat, there are still challenges in bridging the gap between yields in favorable environments and under salt stress conditions. Salt tolerance is a polygenic trait controlled by multiple genes making it difficult to comprehend. Therefore, a comprehensive understanding of different mechanisms of salinity tolerance, as well as the identification and isolation of novel genes using diverse wheat germplasm, is essential for developing robust salt-tolerant wheat varieties. Recently, advanced approaches have been reported for salinity mitigation in wheat to optimize production. This article summarizes the current understanding of salt stress response in wheat plants, different approaches to management (use of salinity tolerant lines/varieties, seed or seedling priming, application of exogenous protectants etc.), and strategies for developing climate-smart crops.

Keywords: *abiotic stress, gas exchange attributes, gene expression, morphological response, oxidative damages, physiological response, salinity stress, and wheat improvement*

Introduction

Soil salinity is one of the most devastating environmental stresses, causing a reduction in cultivated land area and limiting agricultural productivity and quality globally (Turki et al., 2012; Maqbool et al., 2016; Mahboob et al., 2017). In the world, nearly 7% of the total land area is affected by different degrees of salinity, including agricultural lands in semi-arid or arid regions primarily affected by salt stress. More than 20% of the irrigated arable land (about 45 million hectares) is compromised by salt stress (Gupta and Huang, 2014). Climatic modelling suggests that more than 50% of the arable land will be salinized by 2050 (Jamil et al., 2011). The problem will further be exacerbated by the coordinated effects of xerothermic factors, such as drought and heat (Huang et al., 2019). Soil salinity impacts plants in two ways: (i) elevated salt concentrations in the soil impede the extraction of soil water by the roots, resulting in water stress, and (ii) high salt concentrations within plant cells cause ionic stress. The salts surrounding plant roots have an abrupt effect on cell development and cellular metabolism. However, the ionic toxicity of salts requires time to build up within plants before affecting plant function (Munns and Tester, 2008). Wheat is one of the most critical cereal staples and is the primary source of protein for humans. In addition, it contains vitamins (B and E), magnesium, phosphorus, cellulose, and other human-beneficial components (Ma et al., 2016). However, rising soil salt concentration significantly reduces its yield and quality since plant susceptibility varies according to physiological and biochemical processes (Mahboob et al., 2016; Otu et al., 2018; Mahboob et al., 2019; Yassin et al., 2019). Wheat plants are often salt-sensitive and exceedingly susceptible to salinity during all developmental phases, particularly during the early growth stages (Hasanuzzaman et al., 2022). Understanding morpho-physiological, biochemical, and molecular responses of wheat to salt stress is essential for developing salt-tolerant cultivars. Therefore, this review will provide an overview of wheat plant responses to salt stress, tolerance mechanisms, and prospective techniques to increase salinity tolerance in wheat for sustainable production.

Wheat responses to salt stress

The growth and development of crops, including wheat, are severely inhibited by salt stress, leading to lower grain yield and quality (Guo et al., 2012; Turki et al., 2012; Desoky and Merwad, 2015). Soil salinity affects the growth, reproduction, and yield of wheat plants in various ways. In response to salt stress, changes in hormonal balances, photosynthesis, ion transport systems, anatomy, and water transport systems cause morphological, physiological, and biochemical changes in plants (Ashraf and Harris, 2013). Plant sensitivity to salt stress is determined by the growth stages, genetic and physiological factors, the toxicity level of salt in the soil, and the duration of the salt stress exposure (Bacu et al., 2020). This section discusses morphological, biochemical, structural, and molecular responses observed in wheat in response to salt stress.

Morphological responses

Salinity effects result from complex interactions among morphological, physiological and biochemical processes. Morphological changes include impaired germination, altered growth patterns and structural reforms to adapt to stressful conditions. Salt concentrations above a certain threshold causes various malfunctions in growth patterns

(root, stems, and leaves) and reduces the overall yield of wheat (*Fig. 1*). A high germination percentage with vigorous early growth and synchronized stand establishment is preferred for harvesting a better wheat yield, but seed germination and early seedlings growth are the developmental phases of wheat most sensitive to salinity (Kochak-Zadeh et al., 2013; Mahboob et al., 2018). Germination is a dynamic and critical phase in the plant lifecycle that begins with water imbibition (Kumari and Kaur, 2018). Thus, salinity-induced water scarcity influences the germination and crop stand establishment, which has significant importance and is the primary factor limiting crop production in saline regimes (Zafar et al., 2015). Excessive soluble salts in the soil reduces osmotic potential and delays the onset of seedling germination by preventing water uptake of the seeds or exosmosis and distributing the germination-related processes such as optimal functioning of enzymes required for metabolic activity and seed reserves utilization (Munns, 2005; El-Hendawy et al., 2019; Mahboob et al., 2019; El Sabagh et al., 2020, 2021; Seleiman et al., 2021). Poor germination on the salt-affected soils could result from embryo damage and disequilibrium of nutrients induced by Na^+ and Cl^- ions. In addition, salinity-induced oxidative stress causes lipid peroxidation and disrupts nucleic acids, which negatively impacts the subsequent metabolic processes related to seedling growth and development (Hussain et al., 2019). Thus, salinity negatively impacts wheat germination, which modulates the normal germination mechanism, resulting in reduced growth and development and, ultimately, a lower economic yield.

Like seed germination, soil salinity also detrimentally affects the various morphological and yield-related characteristics of wheat plants (*Fig. 1*). Generally, a 0.2% to 0.5% soil salinity affects plant growth (Singh, 2015). Salinity stress initially causes a significant reduction in seed germination and seedling establishment, and later it alters wheat growth and reproductive behaviour (Azeem et al., 2015). Recent studies revealed that salinity caused significant decrease in total leaf area, leaf and stem diameter, wall thickness, vascular bundles length and width (Nassar et al., 2020) and a considerable increase in leaf senescence (Kumar et al., 2017). Salt stress is responsible for the disturbance of plant metabolism due to the osmotic effect of salts around the roots, leading to dehydration, and ionic imbalance in transpiring leaves that reduces meristem activity and cell elongation, consequently inhibiting the growth and development of wheat (Zhu, 2001; Munns, 2005; Shafi et al., 2010). Salinity induces a change in the signal transduction originating from the root, which alters the hormonal balance of the plant and ultimately inhibits root and shoot growth (Lerner et al., 1994). Overall, salinity negatively affects wheat phenological developments such as plant height, leaf development (El-Hendawy et al., 2005; Kumar et al., 2017), biomass accumulation (Mahboob et al., 2018; Shirazi et al., 2018; Mahboob et al., 2019; Nassar et al., 2020; Zeeshan et al., 2020; El Sabagh et al., 2021) and grain yield formation (Guo et al., 2012; Abbas et al., 2013; Zou et al., 2016; Khan et al., 2017; Mahboob et al., 2017; Shirazi et al., 2018; Sadak et al., 2019; Sorour et al., 2019). Wheat yield losses have been reported as up to 45% in salt-stressed plants (Ali et al., 2009). Sathee et al. (2015) observed a 7.1% yield reduction in wheat with each unit of increase in salinity up to 6 dS m^{-1} . This reduced grain yield could result from hampered growth and poor tiller formation due to excessive salt-induced ionic toxicity and osmotic stress. However, the shortened duration of spikelet differentiation and grain filling caused a further decrease in grain yield under salinity (Francoise et al., 1994). These salinity effects are evident in salt-sensitive wheat and salt-tolerant cultivars under varying

degrees of salt stress. However, sensitive genotypes are more prone to salinity (Hasan et al., 2015; Mahboob et al., 2017; Shirazi et al., 2018). The inhibitory effects of excessive ions directly influence cell division and expansion (Zhu, 2001) and impaired plant growth and development, hence further growth retardation results from physiological water deficit under salinity (Munns, 2002; Cha-um et al., 2010; Mahboob et al., 2017). Moreover, the essential mineral imbalance occurs by antagonism among ions during their uptake under relatively high concentrations of Na^+ and Cl^- hinders the absorption of available water and essential nutrients such as K^+ , Ca^{2+} , and Mg^{2+} (Munns, 2002; Chen, 2006; Khan et al., 2010; Desoky and Merwad, 2015; Mahboob et al., 2016). Under these circumstances, the wheat plants tend to reinstate ionic homeostasis and alleviate hyperosmotic stress. It directs the leaves to close their stoma to curtail transpiration and carbon dioxide uptake (Aldesuquy et al., 2012). Still, these changes cause a decline in photosynthesis, a rapid increase in intracellular ROS and ultimately reduced plant growth and yield of wheat plants (Abid et al., 2018).

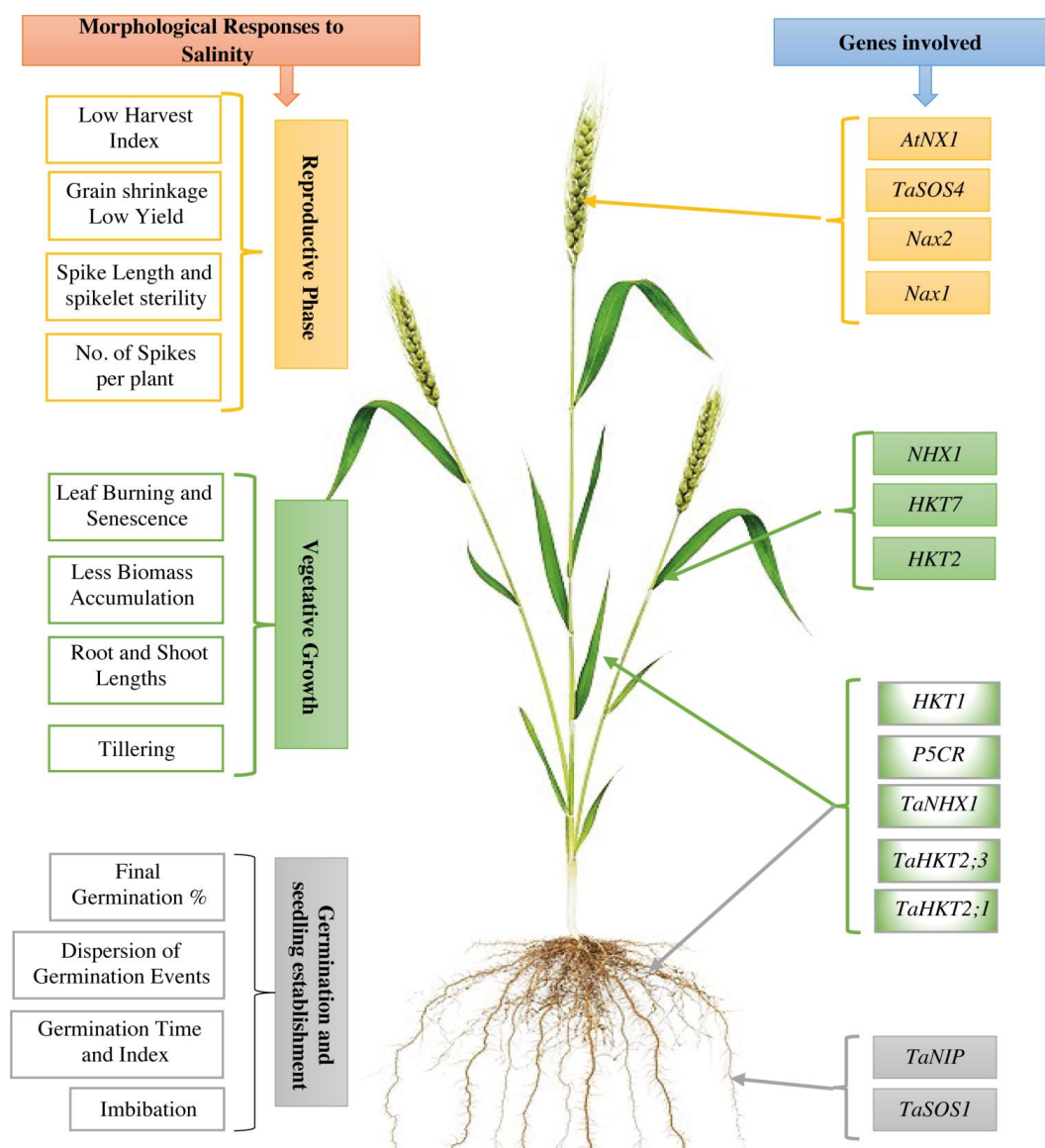


Figure 1. Morphological modifications and associated genes in wheat (*Triticum aestivum* L.) under salinity

In conclusion, at an initial stage, salinity causes a significant reduction or delay in seed germination by modulating seed metabolic processes and results in poor or uniform seedling establishment. At a later stage, salinity alters wheat's growth traits and reproductive behavior, seriously reducing the final economic yield.

Physiological and biochemical responses

Plants exhibit certain physiological and biochemical adaptations to maintain their growth under salinity stress (Fig. 2). Salt stress disturbs plants' whole physiology with osmotic and ionic imbalances at the cellular level (Muranaka et al., 2002; Mahboob et al., 2017; Ghonam et al., 2020). For example, salinity causes K^+ deficiency in plants by impairing the selectivity mechanism in root membranes (Ahanger and Agarwal, 2017). Increased ion toxicity, changes in mineral distribution, and membrane permeability also result in the replacement of Ca^{2+} by Na^+ (Marschner, 1986). Mahboob et al. (2017) reported that the root zone salinization resulted in a significant decrease in leaf osmotic potential of wheat genotypes, which might be due to the unrestricted flow of toxic ions like Na^+ inside the cells. This character is mainly observed in salt-sensitive genotypes, which showed higher leaf Na^+ content accompanied by lower content of K^+ in response to salinity. These physiological changes affect the overall growth of the wheat by affecting vital physiological processes such as photosynthesis (Mahboob et al., 2017; Cisse et al., 2019; Zeeshan et al., 2020). This indicates that salt stress is a major factor limiting wheat growth and overall productivity by impairing photosynthetic machinery and the biomass assimilation process (Munns, 2002; Sayed, 2003; Mahboob et al., 2016; Kumar et al., 2017; Bacu et al., 2020). The decreased chlorophyll content due to salinity is presumed as the stability of chlorophyll is associated with membrane strength, which under saline conditions, rarely remains intact (Mahboob et al., 2017).

Salinity-induced change in chloroplast structure and photocatalysis system was also reported to inhibit photosynthesis in wheat (Salama et al., 1994). High salt stress can significantly decrease chlorophyll, photosynthetic parameters, and antioxidants with disrupted ion transport, severely affected root and leaf ultrastructure and enhanced lipid peroxidation in wheat (Zeeshan et al., 2020). Accumulating toxic salt at higher levels in wheat leaves apoplast also causes dehydration and turgor loss, eventually leading to the death of cells and tissues of the whole plant (Flowers et al. 1986). This situation severely affects plants' metabolism and other enzymatic pathways (Yousfi et al., 2012). At a high transpiration rate, xylem tissues of almost all plants have low levels of Na^+ and Cl^- compared to the external saline medium. However, high salt concentrations cause the accumulation of Na^+ and Cl^- ions in the chloroplasts that leads to a decrease in growth rate due to disruption in photosynthetic activity and electron transport chain (ETC) owing to the accumulation of ROS and methylglyoxal (MG) (Salama et al., 1994; Li et al., 2017). Salt stress disrupts photosystem (II) in wheat plants (Hasanuzzaman et al., 2017).

Different wheat genotypes show differential responses in salt-affected soils. For instance, some wheat genotypes significantly reduce growth, development, and yield parameters, while others are less affected under salt stress (Turki et al., 2012; Atiq-ur-Rahman et al., 2014) could be due to differences in K^+ levels in leaves. Salt-sensitive genotypes showed lower K^+ content, while salt-tolerant genotypes showed higher K^+ content in leaves under salinity. Moreover, salt-tolerant wheat cultivars generally exhibit higher proline content than salt-sensitive (Hasan et al., 2015; Mahboob et al., 2016). Various investigations involving wheat have demonstrated that the increased

production of phenols, soluble sugars, glycine betaine, and proline results in enhanced tolerance against salinity stress (Khan et al., 2014; Desoky and Merwad, 2015; Li et al., 2017; Kumar et al., 2017; Mahboob et al., 2016, 2017, 2019). These compounds usually act as osmoprotectants and protect plants against stress injury and damage. High chlorophyll and proline contents with a high K^+/Na^+ ratio and low Na^+ and Cl^- contents result in salinity tolerance improvement of wheat cultivars (Hasan et al., 2015). Increased accumulation of carbohydrates, proline, total flavonoid, total phenols, and antioxidants and decreased chlorophyll, GSH content and photosynthetic capacity was observed in wheat under high salt concentrations (Datta et al., 2009; Bacu et al., 2020; Ghonaim et al., 2020; Zeeshan et al., 2020).

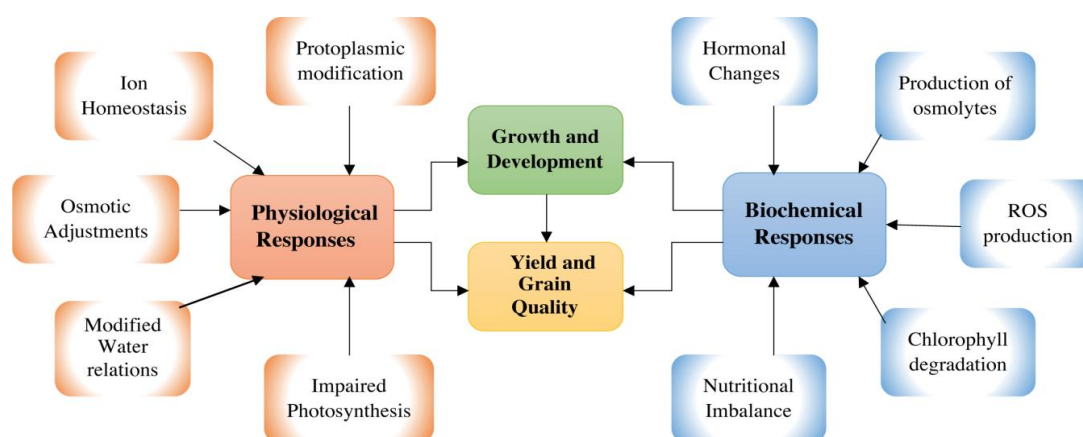


Figure 2. Effects of salt stress on morpho-physiological and biochemical responses of wheat

Molecular responses

Plants respond to salinity stress by modulating various gene activations and molecular mechanisms, which enable the plants to cope with stress conditions. These genes are involved in osmoprotection and activating different enzymes regulating physiological and biochemical functions. Functions of multiple enzymes involved in maintaining cell membrane potential depend on cellular ionic homeostasis, especially Na^+ and K^+ balance (Conde et al., 2011). Salinity-mediated changes in Na^+ and K^+ levels affect various enzymes and proteins and disturb the overall plant metabolism (Hasegawa et al., 2000; Conde et al., 2011), including the stability of many essential proteins, genes, RNA, metabolites, cytoskeleton structure, and membrane integrity (Shulaev et al., 2008). Plants adapt to salinity by changing the composition of various proteins, lipids, transcripts, and metabolites through differential gene regulation (Charkazi et al., 2010; Zhang et al., 2016; Sing et al., 2020; Wang et al., 2020; Fig. 3). Upregulated genes under normal conditions turn into down-regulated due to stress conditions, which affect the overall plant growth (Fig. 4). Oyiga et al. (2019) observed similar results in the case of two genes (*NRAMP2* and *OPAQUE1*) in wheat under salt stress, which are associated with osmoprotectants production. Similarly, hormones and antioxidants-related genes expression is also involved in the better performance of wheat under salt stress (Gao et al., 2010; Zhan et al., 2019). For instance, melatonin is an antioxidant and free radical scavenger in wheat that allows plants to adapt under highly saline conditions (Sadak, 2016). Various gene expression and regulation studies against salt stress in wheat are illustrated in Table 1.

Table 1. Gene expression in wheat crop under salt stress

Experimental conditions	Genes	Gene expression and regulation under stress	Reference
Glasshouse	<i>TaHKT1;4</i> , <i>TaHKT2;1</i> and <i>TaHKT2;3</i>	<i>TaHKT1;4</i> show shoot specific expression while <i>TaHKT2;1</i> and <i>TaHKT2;3</i> expresses both in shoots and roots. In some wheat genotypes these genes are down-regulated while in some others, upregulated	Kumar et al. (2017)
	<i>HKT1;4</i>	These genes undergo two deletions, six transitions, and 12 transversions. <i>TaHKT1;4.3</i> revealed point mutations which change the structure and function of amino acids sequence	
	<i>HKT1;4</i> and <i>HKT1;5</i>	NaCl decreased the leaf blade Na ⁺ concentration by 50%, Na ₂ decreased it by 30%, and both genes together decreased it by 60%	James et al. (2011)
Hydroponic	<i>TaNHX1</i> antiporter	Under stress, this gene is up-regulated in both roots and shoots of wheat genotypes (HD 3086 and KL)	Singh et al. (2020)
Greenhouse	<i>TaPUB1</i>	Overexpression of this gene leads to salt tolerance and better antioxidant activity in transgenic wheat. However, silencing of this gene by RNAi leads to salt sensitivity	Wang et al. (2020)
Hydroponic	Sugar transporter genes <i>SuT4</i> and <i>SuT5</i>	Transcripts level was higher in tolerant plants, however; under salt stress, transcript level was downregulated in sensitive plants	Charkazi et al. (2010)
Lab experiment	SOD, POD and CAT genes	Inoculation of wheat seedlings with <i>Trichoderma longibrachiatum</i> T6 upregulated SOD, POD and CAT genes in seedlings under salt stress. Without inoculation, these genes were downregulated	Zhang et al. (2016)
Greenhouse	<i>Hsp17.8</i> , <i>Hsp26.3</i> , <i>Hsp70</i> and <i>Hsp101</i>	Heat shock proteins were upregulated under salt stress in wheat seedlings while under normal conditions these genes were down-regulated	Al Khateeb et al. (2020)
Hydroponic	<i>GPX1</i> , <i>GPX2</i> , <i>DHAR</i> , <i>GR</i> , <i>GS</i> , <i>GST1</i> , <i>MDHAR</i> and <i>GST2</i>	These genes encode for glutathione and ascorbate which induce abiotic stress tolerance in plants. When salicylic acid (SA) was applied to seedlings these eight genes were up-regulated which make wheat crop plants more salt tolerant	Li et al. (2013)
Lab experiment	<i>TaGLYI</i>	A two-fold increase in <i>TaGlyI</i> expression was observed in response to 100 mM NaCl application. However, its expression decrease at higher concentration of salt stress which may suggest post transcription or translation regulation of <i>TaGly I</i> in response to salinity exposure	Lin et al. (2010)
Lab experiment	GABA (gamma-aminobutyric acid) shunt pathway	The abundance of GABA shunts metabolites	AL-Quraan et al. (2019)

Gene expression of a salt tolerant and susceptible cultivar of wheat when subjected to salt stress

Gene ID	Salt tolerant cultivar (JM22)	Salt susceptible cultivar (YM20)
1. TraesCS1A02G186600	1. Up regulated ↑	1. Down regulated ↓
2. TraesCS5D02G513000	2. Up regulated ↑	2. Down regulated ↓
3. TraesCS7B02G382000	3. Up regulated ↑	3. No change ●
4. TraesCS5A02G000200	4. No Change ●	4. Down regulated ↓
5. TraesCS5A02G291200	5. No change ●	5. Down regulated ↓
6. TraesCS7D02G142000	6. No change ●	6. Down regulated ↓
7. TraesCS7A02G145100	7. Up regulated ↑	7. No change ●
8. TraesCS3A02G037700	8. Up regulated ↑	8. No change ●
9. TraesCS5B02G565600	9. Up regulated ↑	9. No change ●
10. TraesCS7A02G392800	10. No change ●	10. Down regulated ↓

Figure 3. Gene expression variation between a salt tolerant (JM22) and salt susceptible (YM20) wheat cultivar (based on the work published by Dugasa et al., 2021)

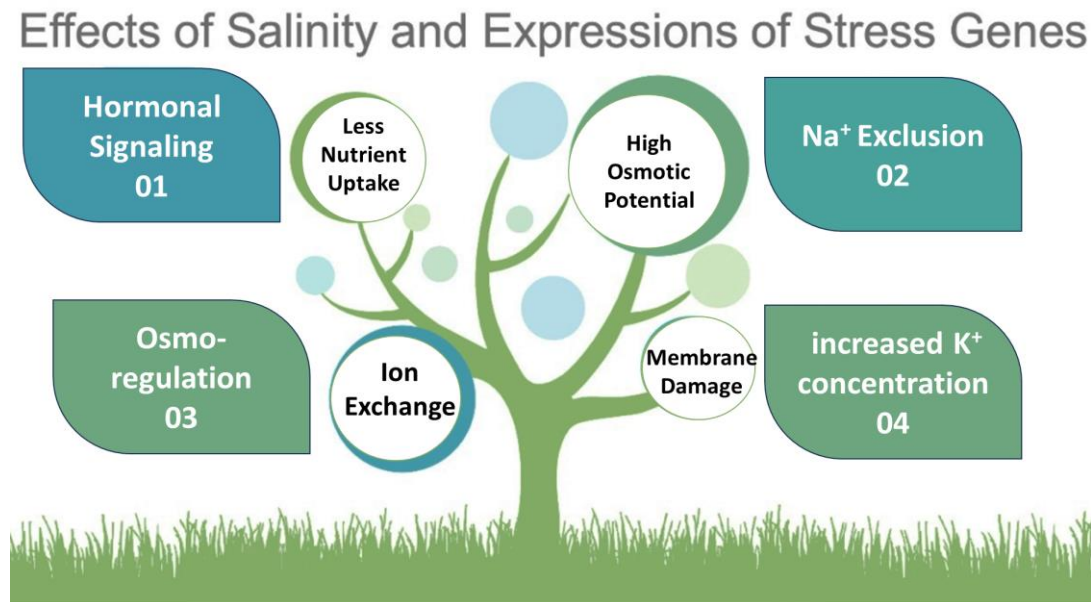


Figure 4. Plant responses to salt stress (modified from Miransari and Smith, 2019 with permission)

Mechanisms of salinity tolerance in wheat

Salt-tolerant crops have evolved adaptive mechanisms to withstand salinity stress (Gupta and Huang, 2014; Naeem et al., 2020; Sarwar et al., 2021). Wheat is moderately salt-tolerant, but there are considerable inter-and intra-specific genetic variations in crop plants for salt tolerance. For instance, bread wheat is more tolerant to salinity than durum wheat (Maas and Hoffman, 1977). Cultivating salt-tolerant wheat genotypes is considered one of the most viable strategies for achieving higher yields in saline environments (Oyiga et al., 2016). Therefore, a comprehensive understanding of various mechanisms for salinity tolerance in wheat is imperative to developing durable salt-tolerant varieties. Some crucial mechanisms of salinity tolerance in wheat are discussed in this section.

Growth adaptation

Salinity adversely affects seed germination, seedling growth, and biomass production in wheat (Mahboob et al., 2018; Fig. 1). The presence of excessive salt usually affects seed germination and slows down plant growth and development. The impaired growth rate is primarily attributed to the high salt concentration in the rooting medium exerting osmotic imbalances. Wheat plants exhibit considerable variations in salinity tolerance by reducing the growth rate (Hasan et al., 2020), which could vary with the developmental stages. For example, inhibition of lateral shoot development during the early growth phase becomes evident under moderate salinity stress (Robin et al., 2016). Similarly, salt stress affects shoot growth more than wheat root growth (Munns and Tester, 2008; Bacu et al., 2020). Salt accumulation in older leaves is more than in new leaves, which ultimately kills the cells of older leaves (Munns et al., 2006). The death rate of leaves is critical for the maintenance of plant growth. For example, if new emerging leaves are more than dying, plenty of photosynthates will be available for proper flowering and seed development (Munns, 2005). Increase in leaf weight and area

ratio in response to salinity indicates the high efficiency of transpiration for removal of salts through translocation to aerial parts which can later be shed. Some wheat genotypes, however, are unable to eliminate salts through transpiration. As a result, such genotypes may employ alternative mechanisms to remove salts from leaves (Hasan et al., 2020). Less leaf surface expansion under salinity impedes the photosynthesis, resulting in fewer carbohydrates required for proper cell growth (Hasegawa et al., 2000). Precise mechanisms underlying decreased shoot development and leaf growth in response to salinity are still unclear. However, salinity-induced changes in hormones or their precursors might be responsible for suppressing leaf growth (Jehan et al., 2012).

Changes in root architecture

Plants have developed strategies to synchronize hormonal signals to change root architecture under saline stress to maintain sufficient water and nutrient uptake (Zelm et al., 2020). Salt stress often affects the growth of the primary root, inhibits lateral root formation, and generally reduces root length and biomass (Julkowska et al., 2014; Fig. 1). Salinity affects the rate of root elongation and the initiation of adjacent roots through hormone-mediated cell division (Rubinigg et al., 2004). Lateral root growth is primarily altered by auxin, while abscisic acid (ABA) signaling is needed for salt-mediated lateral root growth quiescence (Jehan et al., 2012). Some wheat genotypes exhibit more significant lateral root numbers and a decrease in primary root elongation than lateral roots. These variations in root system architecture under salinity are associated with a differential shoot Na^+/K^+ ratio and ABA sensitivity (Jehan et al., 2012). The selection of such genotypes may help to avoid salinity-related yield loss in wheat crops.

Modulation of photosynthesis and stomatal conductance

Under salinity, reduced size of stomatal aperture is a readily measurable whole plant response due to perturbed water relations and local synthesis of ABA. Such changes in size of stomatal aperture is induced by the osmotic effect due to salts present outside the roots (Jehan et al., 2012). At high salinity, salts may continue building up in the apoplast that causes cytoplasmic dehydration and inhibit enzymes involved in carbohydrate metabolism in the chloroplast. This exerts a direct toxic effect on photosynthetic processes. The chloroplast is highly sensitive to salinity and plays a crucial role in modulating stress responses (Ashraf and Harris, 2013). The photosynthetic rate per unit leaf area often remains unchanged despite reduced stomatal conductance. Salinity stress often damages pigments, enzymes, and electron transport systems involved in photosynthesis (Fig. 2). Salt-tolerant wheat genotypes produce more pigments and glutathione (GSH) content than salt-sensitive genotypes (Bacu et al., 2020). However, a lower photosynthetic rate due to salinity is undoubtedly not the single factor of growth reduction since many other factors contribute to salt stress responses under salinity stress in wheat (Jehan et al., 2012).

Ion compartmentalization

Wheat plants are unable to tolerate a higher level of salts in their cytoplasm. As a result, extra salts, such as vacuoles, are transported inside the organelles to support critical cellular processes (Zhu, 2003). Higher salt concentration interferes with ion homeostasis within the plant cell, so ion uptake and compartmentalization have a crucial

role in plant survival and growth under salinity (Shafiq et al., 2020). During stress, plants accumulate low Na^+ concentrations than K^+ in the cytosol by regulating Na^+/K^+ ion carriers and H^+ ion pumps (Zelm et al., 2020). Salt tolerance in wheat can be enhanced by the over-expression of Na^+/H^+ EXCHANGER 1 (NHX1) transporters, an essential factor in ion compartmentalization. NHX transporters regulate a significant part of the Na^+/H^+ exchange activity in the tonoplast (Yamaguchi and Blumwald, 2005). Molecular characterization of Na^+/H^+ antiporters that regulate vacuolar Na^+ accumulation in vacuoles is essential for the salt tolerance of wheat crop. Higher Na^+ accumulation in salt-tolerant wheat cultivars preferentially occurs in the mature root zone (James et al., 2011; Wu et al., 2015). Moreover, a study of salt-tolerant and salt-sensitive bread wheat cultivars suggested that more Na^+ accumulation in roots is essential for salt tolerance. Salt-tolerant species efficiently maintain ion compartmentalization within vacuole through a tonoplast Na^+/H^+ antiporter (Munns et al., 2006; Brini et al., 2009). These reports suggest the importance of ion compartmentalization for salinity tolerance in wheat.

Regulation by phytohormones

Under salinity stress, wheat growth is reduced or temporarily arrested, usually regulated by hormone levels (Munns et al., 2006). For instance, stress hormone ABA concentration is correlated with the growth arrest period. Being an essential cellular signal, ABA regulates the expression of numerous salt-responsive genes. Salinity-mediated osmotic stress produced an elevated concentration of ABA in wheat roots and shoots (Jehan et al., 2012). ABA accumulation plays a vital role in retrieving the adverse effect of salinity on wheat growth, photosynthesis and assimilates translocation. The positive relationship between ABA-regulated salinity tolerance in wheat is partially attributed to the accumulation of compatible solutes (like sugars, Pro) and K^+ and Ca^{2+} ions roots vacuole, which reduce the uptake of Cl^- and Na^+ (Gurmani et al., 2013). ABA can inhibit leaf elongation by lowering the active GA contents. DELLA proteins expressions integrate signals from a range of hormones under salinity and mediate the growth-promoting effects of GA in wheat (Jusovic et al., 2018). The level of ABA declines during the recovery phase while concentrations of jasmonic acid (JA) and gibberellic acid (GA) increase. Primary root growth and plant cell elongation are also controlled by plant hormones such as JA biosynthesis and signaling under saline stress (Liu et al., 2016; Zhao et al., 2014). Therefore, plant hormones can effectively regulate salinity stress in wheat and need further exploration.

Biosynthesis of compatible solutes

Compatible solutes such as sugars, amino acids, glycine betaine (GB), and polyols are low molecular weight compounds whose accumulation in the cytoplasm is necessary for maintaining the osmotic stability of ions (Yancey, 2005; Hasegawa et al., 2000). Wheat plants growing under salinity stress usually accumulate carbohydrates like sugars (sucrose, glucose, fructose, fructans, etc.), which perform critical functions within the cell, including osmoprotection, carbon storage, and scavenging of free radicals (Sairam et al., 2002; Ahanger et al., 2019). Similarly, polyols have an essential role in osmotic adjustment. Functions of nitrogen under salinity include maintaining cell pH, cell detoxification, osmotic adjustment, free radicals scavenging, and protection of cellular macromolecules in wheat (Munns and Tester, 2008; Annunziata, 2017). The compatible

solutes also protect the enzymatic activities of several molecules in wheat under salinity stress. Generally, stress leads to the synthesis of osmolytes through modification/diversion of essential intermediary metabolites. For instance, GB is synthesized from choline by chemical reactions mediated by choline monooxygenase and betaine aldehyde dehydrogenase (Rhodes and Hanson, 1993).

Wheat growing under saline conditions generally face the problem of water loss because of reduced osmotic pressure. Under such a situation, wheat plants can compensate for changes in osmotic pressure by accumulating organic solutes to maintain cell volume and turgor (Datir et al., 2020). Osmolytes are low-molecular-weight compounds such as proline, alcohols, sugars, sorbitol, α -amino nitrogen, and quaternary ammonium compounds (Hossain et al., 2013). Osmotic adjustment via osmolytes accumulation is one of the prime salt tolerance mechanisms in wheat (Flowers et al., 2015). Reduced cell solute potential in salt-sensitive wheat genotypes leads to drastic effects under salinity. However, the osmolyte profiles may differ from between wheat genotypes depending on salinity level and exposure times. Tolerant genotypes adjust osmotically and resist alterations in cytoplasmic considerations under reduced cell solute potential. In many genotypes, osmotic adjustment maintains high water content in the cytoplasm (Munns and Tester, 2008).

Ion exclusion

Na^+ exclusion is an essential mechanism for increasing salinity tolerance. The genetic difference for Na^+ exclusion may contribute to better salinity tolerance under high salt stress that causes more accumulation of Na^+ in leaves (Munns and Tester, 2008). Under salinity, Na^+ exclusion from the cytosol needs thermodynamically active transport coupled with the activity of H^+ ATPases. Na^+ travels in the symplast across the endodermis and is released into the stelar apoplast (Steudle, 2000). Efflux of Na^+ from stelar cells into the xylem and retrieval of Na^+ from the xylem is controlled by plasma membrane Na^+/H^+ antiporter SOS1 (Shi et al., 2002; James et al., 2011). Nevertheless, such an electro-neutral exchange could only be possible with a significant difference in Na^+ activity due to the pH variations between apoplast and stelar cytosol. Some members of the *HKT* gene family are also involved in retrieving Na^+ from the xylem in wheat (Byrt et al., 2007). An *HKT1;5* gene *Kna1* is associated with a higher leaf K^+/Na^+ ratio and is attributed to providing bread wheat with better salinity tolerance over tetraploid wheat (Laurie et al., 2002). In some salt-tolerant wheat species, more Na^+ is detained in roots and stems from other tissues (Munns, 2005). Efficient exclusion of Na^+ from young tissue and leaves has been found in salt-tolerant wheat (Husain et al., 2004). This mechanism lowers the Na^+ load and sustains a favorable K^+/Na^+ ratio in plant tissue, reducing leaf death and higher grain yield under salinity. Bread wheat can efficiently regulate Na^+ transport in shoots as compared to durum wheat. Salt-tolerant wheat genotypes exhibit a lower rate of Na^+ transfer in the xylem (Munns et al., 2006).

Activation of the oxidative defense system

Oxidative stress in response to salt stress, results in the rapid production of various ROS in wheat (Esfandiari and Gohari, 2017). ROS signaling pathway has vital regulatory functions for salt tolerance through controlling ion homeostasis (Habib et al., 2021). Salinity tolerance depends upon the differential ability of plant species to detoxify ROS. Several studies have documented the differences in antioxidant enzyme activity in a more tolerant wheat genotype. ROS are generated in response to impaired

photosynthetic process in response to salinity, thereby increasing the activity of ROS detoxifying enzymes (Zheng et al., 2009). Salt-tolerant plants undergo specific leaf morphology, pigment composition, and biochemical processes that prevent oxidative damage to photosystems (Mahajan and Tuteja, 2005). Water deficit in plant cells under salinity stress also hampers multiple biochemical plant processes leading to the production of hydrogen peroxide (H_2O_2), superoxide radicals (O_2^-), hydroxyl radicals ($OH^\cdot$), and singlet oxygen (Mujeeb-Kazi et al., 2019). ROS damage lipids, proteins, nucleic acids, negatively affecting wheat's metabolic processes (García-Caparrós et al., 2019). Upregulation of ROS scavenging enzymes such as catalase, superoxide dismutase, glutathione reductase, glutathione peroxidase, glutathione S-transferase, ascorbate peroxidase, and peroxidase enable the plant to reduce cell damage caused by oxygen species under salinity (Zheng et al., 2009). Thus, plants with a high level of antioxidants are more resistant to oxidative damage by salt stress.

Molecular mechanism

Plants under salt stress respond by sensing and transducing the osmotic and ion signals to cell centers, followed by changes in cellular attributes. The Na^+ entry restriction into the cytosol is the most important mechanism underlying salinity tolerance which is due to selective regulation of Na^+ uptake and efflux systems (Zhu, 2003; Ji et al. 2013). Na^+ contests with K^+ and is taken up through K^+ uptake systems due to resemblances in ionic features (Plett and Moller, 2010). Salt stress leads to reduced plant growth, photosynthesis inhibition and enzyme activities due to the negative effect of Na^+ on K^+ nutrition (Zhu, 2003). Under stress conditions, plants sequester Na^+ into vacuoles by activating Na^+ efflux from roots in order to reduce cytosolic Na^+ levels (Plett and Moller, 2010). Bread wheat counter-balances the high Na^+ influx rate, resulting in a lower net Na^+ uptake. This is possibly due to the counter-balancing and efficient Na^+ efflux mechanism (Davenport et al., 2005). Sequestration of sodium ions into the vacuole depends on H^+ -ATPases, H^+ -pyrophosphatases, expression and activity of Na^+/H^+ antiporters (NHX). The NHX activity is dependent on proton motive force which is generated by proton pumps (Zeeshan et al., 2020).

So far, no particular receptor or sensor for Na^+ has been recognized in plants (Nongpiur et al., 2020). However, in *Arabidopsis*, the salt overly sensitive (SOS) signaling and calcineurin B-like (CBL)/CBL-interacting kinase (CIPK) pathways have been well characterized. Under salt stress conditions, cytosolic Ca^{2+} increases, activating the SOS2-SOS3 protein kinase complex. SOS2-SOS3 complex phosphorylates and stimulates the plasma membrane Na^+/H^+ antiporter - SOS1 (Qiu et al., 2014). The SOS1 is the first well-categorized Na^+ efflux protein in plants (Shi et al., 2000). The SOS1 regulates sodium ion transport from root to shoot by mediating Na^+ efflux at the root surface (Tester and Davenport, 2003) and maintaining the positive K^+/Na^+ ratio in leaves. The serine-threonine protein kinase - SOS2 belongs to the SnRK3-sucrose non-fermenting 1-related kinase 3 families. SOS3 belonging to the calcineurin B-like (CBL) protein family is recognized as Ca^{2+} sensor (Sun et al., 2015). Under salt stress conditions, SOS3, upon sensing the calcium oscillations, binds to FISL motif and activates SOS2. The expression of SOS1 gene is controlled by SOS3/SOS2 complex, which activates the Na^+/H^+ antiporter activity of SOS1 (Sathee et al., 2015; Feki et al., 2017). The mutant plants which are deficient in SOS2 and SOS3 show salt-sensitive phenotypes similar to SOS1 plants (Zhu, 2001).

Active efflux of Na^+ is one of the potent mechanisms of salinity tolerance. However, the role of SOS pathway genes is rarely studied in wheat. Cuin et al. (2011) identified the SOS1 homologue in bread wheat. Xu et al. (2008) identified the same in durum wheat. These identified homologues now have been functionally characterized; however, none of these studies examined the SOS2 and SOS3 genes in the whole SOS pathway. Ramezani et al. (2013) reported that all three alleles of SOS1 gene are active in their function while studying the expression of SOS1 and SOS4 genes in cultivated and wild wheat plants.

Sathee et al. (2015) examined bread wheat genotypes with contrasting salinity tolerance for the expression of all the genes of SOS pathway to analyze their association with salinity tolerance. A lesser amount of sodium ions was accumulated in root, stem and leaves of salinity tolerant genotypes. Under long-term salinity, transcript abundance of SOS genes was significantly higher in the tolerant genotypes. This also correlated with better sodium exclusion and a higher K^+/Na^+ ratio. Even under 200 mM NaCl stress, the expression levels of genes involved in vacuolar partitioning of sodium ions, vacuolar Na^+/H^+ antiporter (NHX1) and vacuolar pyrophosphatase (VP1) were higher in salt tolerant bread wheat genotypes. Partial coding sequences of SOS1, SOS2, SOS3, NHX1 and VP1 genes were cloned and sequenced from the studied genotypes (HD 2009, HD 2687 and Kharchia 65).

High-affinity potassium transporter (HKT) genes also play a major role in enhancing the salt tolerance of wheat. These transporters confer wheat salinity tolerance by stimulating Na^+ exclusion. Since the hexaploid wheat is able to maintain a higher ratio of K^+/Na^+ concentration in the leaves, therefore, it has long been known that durum wheat is less salt tolerant than the former (Francois et al., 1986). This trait was exhibited to be controlled by *Kna1* on chromosome 4D (Dubcovsky, 1996). Genetic analysis of a population derived from a cross between durum wheat and *Triticum monococcum* (line containing introgression from the A genome) revealed the involvement of two loci *Nax1* and *Nax2* in Na^+ exclusion ability (Munns et al., 2000; James et al., 2006). In higher plants, transport of sodium ions is regulated by class 1 *HKT* genes (Horie et al., 2009). *HKT1;1/2*-like, *HKT1;3*-like, *HKT1;4*-like, and *HKT1;5*-like genes have been identified and mapped to wheat homoeologous chromosome groups 2, 6, 2, and 4, respectively (Huang et al., 2008). *TmHKT1;5-A* was proposed to be the candidate of *Nax2* (Byrt et al., 2007) based on synteny and phylogeny analysis and the presence of this significantly reduces leaf Na^+ content. *HKT* genes mediated sodium exclusion in leaves is reported as a major mechanism in salt tolerance of wheat (James et al., 2011). However, some fundamental questions like how these genes respond to salt stress and how they are regulated need to be further addressed.

Strategies to improve tolerance in wheat against saline stress

Several strategies to mitigate the deleterious effects of salinity stress have been apparently discussed in number of comprehensive reviews (Munns et al., 2006; Ashraf and Foolad, 2007; Munns and Tester, 2008; Shahbaz et al., 2012; Hasanuzzaman et al., 2017; Kamlesh et al., 2020; El Sabagh et al., 2012). Among these are agronomic approaches such as seed priming, fertigation, and foliar application of various inorganic and organic compounds and plant growth regulators, as well as genetic strategies that use biotic approaches such as exploring available gene pools and producing highly salt-tolerant wheat genotypes. Because agronomic strategies are shotgun approaches to

salinity stress mitigation, the development of robust saline tolerant varieties is the only option for a long duration of saline stress. As a result, recent developments in this area are discussed in this section.

Agronomic approaches

Seed priming

Seed priming is well known for boosting seed germination and vigour. Several chemicals have been used for saline stress mitigation in wheat seedlings (Table 2). During the last decade, halopriming has been extensively used for seed invigoration and stress mitigation. Salts of Ca^{2+} and K^{+} (like chloride and sulphate) have been reported to mitigate saline stress in wheat seedlings (Iqbal et al., 2006; Afzal et al., 2008; Jaffar et al., 2012; Islam et al., 2015; Tabassum et al., 2017; Mahboob et al., 2019). Recently defence activation via stimulus is also found to be very active. Although higher Na^{+} concentration is dangerous for plant cells, thus the exogenous application of Na^{+} in minute quantities activates cell defence mechanisms, making them hardy for bearing any upcoming stress (Azeem et al., 2015; Ali et al., 2017).

Apart from using different salts, a direct approach uses plant growth regulators or hormones for seed priming. Their exogenous application activates several proteins, enzymes, and other defence mechanisms. Scientists have reported the utilization of auxins, cytokinin, GA, and melatonin to mitigate saline stress successfully. Although the mechanism of action is different for each hormonal class, all hormones directly or indirectly boost osmoprotectant synthesis, especially SA, reduce ABA concentration at the cellular level, and enhance the activities of antioxidant enzymes (Iqbal and Ashraf, 2013; Iqbal et al., 2006; Liang et al., 2009; Iqbal and Ashraf, 2016; Mahboob et al., 2019). Antioxidants and osmoprotectants have a direct and significant role in controlling stress. Therefore, using ascorbic acid (AsA), SA, and kinetin in seed priming enhances seedling stress tolerance (Hameed et al., 2010; Tabatabaei, 2013; Afzal et al., 2013; Mahboob et al., 2019).

Furthermore, microorganisms like PGPRs are also found effective in saline stress mitigation in wheat. *Trichoderma longibrachiatum* was highly effective in improving saline tolerance capabilities via boosting the antioxidant defense system and enhancing gene expression in the wheat plant (Zhang et al., 2016). Free-living nitrogen-fixing bacterial strains like *Azotobacter chroococcum* were also reported to improve wheat growth and yield under salinity (Silini et al., 2016).

Use of post-germination chemical application

Post-germination application methods to mitigate salinity stress in wheat, including foliar or root application, depend upon the chemical's nature and site of action (Table 3). The use of antioxidants like AsA and lipoic acid (LA) has been reported in salinity stress mitigation in wheat seedlings. SA being an antagonist of AsA slows down tissue degradation (Farouk et al., 2011). The exogenous application of antioxidants increases cellular concentration, thus protecting cells from oxidative damage from ROS accumulated under stress (Gorcek and Erdal, 2015). Osmoprotectants like proline are produced in cells under stress conditions; therefore, their exogenous application was also reported as equally effective in alleviating salinity stress in wheat (Mahboob et al., 2016). Excessive accumulation of proline in cells protects important cellular organelles and boosts the synthesis of the antioxidant defense system (Ahanger and Agarwal,

2017). Foliar application of hormones like brassinosteroids and JA is useful in wheat salinity stress mitigation in wheat (El Sabagh et al., 2021). These hormones trigger multiple biochemical processes in cells, boosting cellular phenolic contents, improving the K^+/Na^+ ratio in cells, and enhancing the synthesis of antioxidant enzymes (Ashraf et al., 2002; Eleiwa et al., 2011; Tofighi et al., 2017; Mansour et al., 2020).

Table 2. Seed priming/treatment for mitigation of salinity stress in wheat crop

Seed priming agent	Mechanism of action	Citation
Triacantanol, Auxin, AsA, proline	Alleviated the detrimental effects of salinity stress by improving germination standards. Enhanced wheat seedling growth by stabilizing leaf chlorophyll, improving osmotic adjustment and reducing Na accumulation in leaves	Mahboob et al. (2019)
Melatonin	Increased polyamine contents and reduced their degradation under salt stress	Ke et al. (2018)
Sodium nitroprusside	Increased activity of antioxidant enzymes, higher production of AsA, proline and total phenolics	Ali et al. (2017)
Calcium chloride (CC)	Seed harvested from drought-stressed crop were more tolerant to salt stress compared to those from normal plants. Seed priming with CC further enhanced salinity tolerance by increasing cellular proline and GB contents	Tabassum et al. (2017)
	In MH-97 CC pretreatment reduced the concentration of ABA and increased SA concentration in leaves. In Inqlab-19, CC increased IAA and IBA concentrations in plants	Iqbal et al. (2006)
Azotobacter	Increased cellular K^+ and chlorophyll (a and total) and reduced intracellular proline and amino acids	Silini et al. (2016)
PGPR: <i>Trichoderma longibrachiatum</i>	Successful colonization in a symbiotic relation, Improved plant nutrient and water uptake. Colonization also protected roots from stress-induced changes with enhanced proline and antioxidant enzyme activity, and reduced cellular MDA concentration	Zhang et al. (2016)
Sodium silicate	Silicon treatment reduced cellular Na^+ concentration	Azeem et al. (2015)
Kinetin, CC, AsA and salicylic acid (SA)	AsA, SA and kinetin improved K^+ concentration in cells and decreased the uptake of Na^+ and Cl^-	Afzal et al. (2013)
Auxin	Improved hormonal homeostasis and increases net CO_2 assimilation rate	Iqbal and Ashraf (2013a)
GA_3	Enhanced cellular SA concentration along with reduced putrescine and spermidine concentration due to seed priming with 100-150 ppm GA_3	Iqbal and Ashraf (2013b)
GB	Increased GB and glutathione concentration reduced proline and lipid peroxidation in cells after priming with 25 mM GB	Salama et al. (2015)
	Over accumulation of GB reduced cellular Na^+ and Cl^- and increased K^+ concentration. Moreover, GB enhanced the activity of antioxidant enzymes	Liang et al. (2009)
SA, GA_3	Increased production of catalase and ascorbate peroxidase with the priming of SA and Gibberellin	Tabatabaei (2013)
CC, ascorbate (ASC)	Priming with CC followed by ASC increased the total phenolic contents, total soluble proteins (TSP), α -amylase and protease activities	Jaffar et al. (2012)
CC, potassium chloride	Halopriming increased antioxidant enzyme activities (CAT, POD, APX)	Islam et al. (2015)
Choline	Significantly reduced in cellular Na^+ concentration and increased in K^+ concentration after priming with choline 5 mM	Salama et al. (2011)
	The choline priming retained sterol/phospholipid ratio even under saline stress. It also decreased the cellular concentration of phosphatidylserine and phosphatidylglycerol, which were very high under saline stress	Salma and Mansour (2015)
AsA, SA, CC	Salinity induced 29 kDa protein was completely suppressed by priming treatments	Hameed et al. (2010)
CC, calcium sulfate (CS)	The high concentration of potassium ions in cells observed after priming with CC and $CaSO_4$	Afzal et al. (2008)
Sodium nitroprusside (SN)	Increased production of SOD and CAT and higher K^+ concentration. Reduced cellular MDA and superoxide anions along with Na^+ concentration	Zheng et al. (2009)
	Increased $\square$ -amylase activity resulting in higher cellular K^+ concentration even at very small (0.06 mM) concentration	Duan et al. (2007)
Cytokinin (CK)	Increased cellular IBA concentration and reduces ABA concentration along with improved hormone homeostasis	Iqbal et al. (2006)
	Enhanced cellular SA synthesis and also increased polyamines (spermidine and spermine) under salt stress	Iqbal and Ashraf (2006)

Table 3. Post-germination chemical application for mitigation of salinity stress in wheat

Chemical name	Methods of application	Mechanisms	Citation
AsA	Foliar	Delayed flag leaf senescence was mainly attributed due to enhanced production of antioxidant enzymes involved in scavenging ROS produced during stress	Farouk (2011)
LA	Foliar	Prevented excessive accumulation of Na ⁺ , and, improved K:Na ratio and Ca contents in cells. Significantly reduced the ROS production	Gorcek and Erdal (2015)
Brassinosteroid: BRs 28-homoBL	Foliar	The maintained activity of photosynthetic pigments under saline stress	Eleiwa et al. (2011)
Pro	Foliar	Enhanced chlorophyll contents, osmoprotectants and antioxidant phenolics	Talat et al. (2013)
Pro	Foliar	Increased cellular K ⁺ concentration and K:Na ratio along with the enhanced accumulation of proline, GB and total phenolic contents	Mahboob et al. (2016)
Paclobutrazol	Foliar	Accumulated more water-soluble carbohydrates and reducing sugars, improved N, P and K ions concentration in cells thus improving Na-K balance	Hajihashemi et al. (2009)
JA	Foliar	Decreased the concentration of MDA and H ₂ O ₂ and enhanced the activities of SOD, POD, CAT, APX, and the GSH, Chl b, and Car contents	Qiu et al. (2014)
5-aminolevulinic acid	Foliar	Markedly reduced the concentration of ROS by a significant increase in the synthesis of antioxidants	Genişel and Erdal (2016)
P	Foliar	Improved cellular potassium ion contents and reduced-sodium ion uptake	Khan et al. (2013)
P and N	Foliar	Increased cellular K contents and reduced Na ⁺ uptake improved salt tolerance	Khan et al. (2016)
Spermine	Root	Decreased cellular Na contents and increased K contents along with enhanced production of glutathione reductase	Saeidnejad et al. (2016)
AsA	Root: Fertigation	Significantly mitigated saline stress via enhanced proline accumulation and reduced H ₂ O ₂	Azzedine et al. 2011
Nitric oxide, calcium nitrate	Root: Hoagland	Boosted salinity tolerance by enhancing the synthesis of antioxidant enzymes. Calcium application facilitated in the maintenance of ion homeostasis	Tian et al. (2015)
Sulfated chitoooligo-saccharide	Root: Hoagland	Maintained chlorophyll integrity via boosting the activity of SOD, CAT, peroxidase, ascorbate peroxidase, glutathione reductase, and dehydroascorbate reductase	Zou et al. (2016)
Hydrogen peroxide	Root: Hoagland	Enhanced plant salt tolerance capabilities via a significant reduction in MDA and overproduction of antioxidant enzymes (CAT, POD, SOD, APX)	Li et al. (2011)
Silicate and abscisic acid	Root: Hoagland	Increased K ⁺ concentration and reduced Na ⁺ uptake along with the enhanced accumulation of antioxidant enzyme systems	Gurmani et al. (2013)
Potassium sulfate	Root: Hoagland	Increased nutrient uptake like K, Ca, N and P with fertigation of K ₂ SO ₄	Kausar and Gull (2014)
Pro	Root: MS Media	Restored the synthesis of 98 KDa polypeptide and enhanced the synthesis of 112 and 48KDa polypeptide in protecting protein turnover machinery	Ismail (2014)

Interestingly, growth retardants like paclobutrazol (PBZ) also boost saline stress mitigation. However, the mechanism of action was utterly different from phytohormones. PBZ retards the growth of shoots compared to roots and thus improves the root-to-shoot ratio. However, these short-statured plants were more tolerant against saline stress and contained more N, P, and K⁺ in cells (Hajihashemi et al., 2009). Foliar application of P and N has also been reported to improve wheat plant capabilities to bear saline stress. These elements enhanced cellular K⁺ concentration and significantly declined the Na⁺ uptake from the root (Khan et al., 2016). Root cells are the first and most affected by saline stress. Therefore, applying osmoprotectants and antioxidants in the root zone is beneficial to lowering and halting the salinity impact on the plant. Applications of spermine and AsA, nitric oxide, and proline have been found helpful in saline stress mitigation in the wheat plant. Potassium sulfate is a carrier of K⁺ and was

also reported to boost the immunity of root cells when applied in Hoagland solution to the plant. Oxidizers like H_2O_2 in small quantities were also found effective in activating plant defense mechanisms, thus making it ready for upcoming stress.

Plant genetics approaches

Use of tolerant wheat varieties

Several salt-tolerant wheat varieties have been identified in different regions using either conventional methods or marker-assisted selection. The mechanism of saline stress tolerance depends on the genetic makeup of varieties; however, the primary mechanism of saline tolerance can broadly be expressed via two mechanisms. i) significant reduction of Na^+ uptake from the roots or enhanced accumulation of K^+ in cells for improved K^+/Na^+ ratio in cells, ii) marked increase in the synthesis of antioxidants, osmoprotectants, and hormones. Improved K^+/Na^+ ratio was observed in almost all tolerant varieties. Enhanced antioxidant enzymes such as SOD, POD, CAT, and APX activities and proline synthesis in tolerant varieties were also reported by several research groups (Khatkhar and Kuhad, 2000; Latef et al., 2010; Ashraf et al., 2012; Siddiqui et al., 2017).

The mechanism of salt tolerance in a tolerant variety is complex and multidimensional and cannot be explained entirely by one mechanism alone. However, since all mechanisms (genetic, biochemical, and even morpho-physiological) are interconnected, salinity tolerance can be partially defined with numerous approaches. These approaches include screening based on activation of genes responsible for salinity tolerance in plant, K^+/Na^+ ratio in cells, antioxidant levels in roots and shoots, sugar and osmoprotectant concentration in cells, morphological traits (root and shoot length, fresh and dry weight, etc.), and physiological traits (chlorophyll concentration, stomatal conductance, etc.). Interestingly, the discrepancy in rooting behavior was also found due to differences in tolerant and sensitive cultivars of wheat. A tolerant wheat cultivar showed longer axial roots, more branching, and higher distal branch root number than susceptible wheat cultivars (Roshan and Tabbasi, 2019). These approaches have been utilized to develop several varieties reported in the past two decades for different countries (Table 4). Sometimes tolerant varieties have faced problems like these are time-based and lead to losing their vigor after successive cultivation over the years owing to inbreeding depression. Additionally, these varieties are also area-specific, which means the behavior of a tolerant variety in a particular location could be diverse due to climatic conditions compared to other places.

Table 4. Resistant cultivars of wheat from different countries

Varieties	Country	Reported mechanisms of tolerance	Reference
BARI Gom 27, BARI Gom 28	Bangladesh	Increased concentration of cellular K^+ , biosynthesis of Pro, and reduced Na^+ uptake in tolerant cultivars	Siddiqui et al. (2017)
DK961	China	Increased K:Na ion ratio, protein concentration and antioxidant enzyme activities	Zheng (2020)
Jing-411	China	Up-regulated proteins like guanine nucleotide-binding protein subunit beta-like protein, Rubisco large subunit-binding protein, subunit alpha and pathogenesis-related proteins	Guo et al. (2012)
Ningchun	China	Increased H_2O_2 accumulation in root cells which was responsible to enhance tolerance	Zhang et al. (2014)
Gimeza 9	Egypt	Increased spermidine, spermine, proline and ethylene accumulation and decreased lipid peroxidation	El-Bassiouny and Bekheta (2005)
Banysoif 1	Egypt	Higher Pro contents and K:Na ratio and increased activities of SOD, POD and CAT	Abdel Latef (2010)

Sakha 93 and Sahel	Egypt	Higher K:Na ratio	Maha et al. (2017)
HD2689	India	Higher sugar and proline contents	Datta et al. (2009)
KRL 210, KRL 19	India	Higher K:Na ion concentration in resistant varieties	Rao et al. (2016)
HD-2160, K-7634, WL-711, WL-1531, HD-2260, UP-115	India	Better antioxidant enzyme activation, K:Na ratio and better gene expressions	Sharma (2017)
HD-2160	India	Increased antioxidant activity along with better K ⁺ accumulation compared to Na ⁺	Sharma (2015)
Roshan	Iran	Higher K:Na ion concentration was major difference between tolerant (Roshan) and sensitive cultivars	Poustini and Siosemardeh (2004)
Kavir, Niknejad, Chamran & Falat	Iran	Lower Na ⁺ uptake and better K:Na ion ratio was observed in tolerant varieties compared to sensitive	Goudarzi and Pakniyat (2008)
Kavir, Niknejad & Marvdasht	Iran	Significant increased proline concentration and POD activity	Goudarzi and Pakniyat (2009)
Hamoon, Sorkhtokhm and Bolani	Iran	Improved K:Na ratio in these varieties made them more salinity tolerant compared to Hirmand, Chamran and Kavir	Akbarimoghaddam et al. (2011)
Bam	Iran	Increased SOD activity, higher proline contents were observed in tolerant Bam variety compared to Tajan	Borzouei et al. (2012)
Roshan & Tabbasi	Iran	Longer seminal axial roots, shorter distance from the tip, higher distal branch root numbers, higher branch root length, lower Na ⁺ uptake and improved K:Na ratio	Rahnama et a. (2019)
Sham 1, Haurani 27, Acsad 65	Jordan	Resistant varieties showed increased proline synthesis when subjected to salt stress	Abel-Ghani et al. (2009)
LU26	Pakistan	Significantly lower Na ion uptake and very high cellular K ion concentration	Ahmad et al. (2005)
S-24	Pakistan	Significantly higher activities of antioxidants (CAT, SOD, POD, APX), increased accumulation of proline, and lower levels of H ₂ O ₂	Ashraf et al. (2012)
Sehar-06, NARC-09 and Millat-2011	Pakistan	Increased activity of APX and GPX, and higher K:Na ratio in salt-tolerant varieties	Rao et al. (2013); Hussain et al. (2013)
LU26S	Pakistan	Enhanced activities of CAT, POD, APX, higher K/Na contents compared to salt-sensitive Lasani-06 cultivar	Islam et al. (2015)
Al-Moiaya	Saudi Arabia	Improved K:Na ratio	Abbas and Mobin (2015)
Hidhab	Tunisia	Lower Na transfer rate from root to shoot and higher exclusion rate from leaf sheath. Improved cellular K:Na ratio	Benderradji et al. (2011)
Gerek-79	Turkey	Increased activity of POX, CAT and SOD	Mutlu et al. (2009)
Selçuklu 97	Turkey	Improved cells K contents and reduced Na in cells	Borlu et al. (2018)

Genes responsible for salinity tolerance in plants

Identifying the genes responsible for improved salt tolerance opens up new possibilities for variety improvement. To make a variety tolerant, we can incorporate such genes from wild relatives of the same species, or even different species within the same family, into existing germplasm. The defense mechanism of a plant is linked with genes in one way or another. Significant genes have been identified in wheat for salt tolerance in the last decade and are summarized in *Table 5*. Genes responsible for osmoprotectants synthesis can be incorporated in plants to enhance cellular organelles under stress conditions. Genes like *BADH* and *P5CR* accountable for the synthesis of GB and proline, are reported intolerant varieties of wheat (Liang et al., 2009; Rana et al., 2016). The balance of ions, especially K⁺ to Na⁺ ion concentration, is essential (as already discussed above). Genes responsible for enhanced potassium uptake (*AKT1* gene), reduced uptake of sodium ions (*TaNIP* gene), and even exclusion of excessively deposited salt from cells (*HKT1*) have been successfully reported in intolerant varieties of wheat. Regardless of wheat variety (resistant and sensitive), increased sodium ion accumulation in the cell takes place under saline conditions. However, the tolerant

varieties exclude that sodium from their cells (especially from root cells) via transporter proteins. Transporter protein genes like *HKT1*, *HKT2*, *HKT7*, *NHX1*, and *TaSOS1* are reported in the wheat plant for excessive sodium ion exclusion from cells (Benderradji et al., 2011; Rana et al., 2016; Zeeshan et al., 2020). Interestingly, a NIP gene in *Triticum aestivum* was identified for the regulation of aquaporins. These unique structures enable plant cells to absorb water molecules selectively without letting ionic exchange, thus conserve cellular K⁺ reserves and reduces Na⁺ uptake under salt stress conditions (Gao et al., 2010). Few genes identified in resistant cultivars of wheat have a more complex mechanism of action that is not yet fully understood. An example of such gene is *TaMYBsdu1*, which activates/boosts as well as regulates several metabolic pathways leading to salinity tolerance (Rahaie et al., 2010); WRKY52 is another example of a gene that boosts salinity tolerance in wheat via complex pathways/processes (Yoruk et al., 2018). Similarly, the Salt overly sensitive (SOS) 1 gene produces SOS proteins mainly involved in the salinity stress signal transduction pathway. This protein senses excessive salt concentration and activates other defense mechanisms to remove excessive ion accumulation. Identification of more such genes will enable plant biologists to develop future generation wheat crops for salinity tolerance.

Table 5. Genes identified for enhanced salinity-tolerance in wheat

Gene complete name	Gene common name	Mode of action	Details	Citation
HKT: high-affinity potassium transporter gene	HKT1, HKT2 gene	Sodium/cation transporter	Excludes excessive sodium from cells	Zeeshan et al. (2020)
SOS: salt overly sensitive gene	SOS 1	SOS proteins	Initiates the SOS pathway to maintain ion homeostasis	
AKT1: serine/threonine kinase one gene	AKT1	K ⁺ channeling	Improves potassium ion permeability of the plasma membrane	
NHX1: sodium/hydrogen exchanger one gene	NHX1	Na ⁺ /H ⁺ antiporter	Exchanges sodium ions for hydrogen ions across membranes	
TaMYBsdu1	MYB gene	Transcription factor	Significant improvement in the short term as well as long term salinity tolerance in wheat	Rahaie et al. (2010)
WRKY transcription factor 52	WRKY52 gene	Transcription factor	Significant boost in resistance in the tolerant plant	Yörük et al. (2018)
Betaine-aldehyde dehydrogenase	BADH gene	GB synthesis	Protects important organelles of the cell under stress conditions	Liang et al. (2009)
pyrroline-5-carboxylate reductase	P5CR gene	Responsible for Pro biosynthesis	High expression of P5CR and glutamate synthase was observed in the leaves and roots of Kharchia 65 under saline stress	Rana et al. (2016)
<i>Triticum aestivum</i> nodulin 26-like intrinsic protein	TaNIP	Aquaporin gene	Reduced Na ⁺ uptake along with water via selective permeability	Gao et al. (2010)
High-affinity potassium transporter gene	HKT	Na ⁺ permeable membrane protein	Removed excessive Na from cells	Huang et al. (2008)
High-affinity potassium transporter gene	HKT7	Sodium transporter protein	Removed excessive Na from cells	Huang et al. (2006)
Salt overly sensitive-1 gene	TaSOS1 gene	A transmembrane Na ⁽⁺⁾ /H ⁽⁺⁾ antiporter	TaSOS1 gene is responsible for Na ion exclusion was highly expressed in the roots of salt-tolerant variety Kharchia 65	Rana et al. (2016)
Salt overly sensitive-1 gene	TaSOS1 gene	A transmembrane Na ⁺ /H ⁺ antiporter	TaSOS1 gene is responsible for Na and H ions antiporter was higher in the Hidhab cultivar	Benderradji et al. (2011)

Conclusion and future perspective

Salinity stress in wheat resulted in poor growth and development, leading to diminished yield. Strategies involving bridging the yield gap and increasing yield stability and adaptability to salinity stress are essential in assuring food security and sustainability. Hence, there is an urgent need to improve our understanding of complex mechanisms regulating salinity stress tolerance for developing modern wheat varieties that are more resilient to salt stress. A comprehensive understanding of various mechanisms for salinity tolerance in wheat could speed up developing salt-tolerant wheat varieties. The foliar application of exogenous protective compounds (proline, GB, AsA, GSH, etc.) and hormones like brassinosteroids, and jasmonic acid was found useful to alleviate short-term saline stress in wheat. Identification of genes responsible for enhanced salt tolerance and their integration in cultivated species will open up new avenues for varietal improvement in the future. Although few resistant genes from wild relatives have already been identified, they are difficult to transfer because of the phenomenon known as linkage-drag. Since in conventional breeding, positive loci are known to often co-segregate with negative loci, it is pretty impossible to separate them even by recurrent backcrossing. Additionally, few genes identified in resistant wheat cultivars have a more complex mechanism of action, which is not yet fully understood. Molecular breeding strategies should be undertaken for pyramiding multiple genes involved in salt stress tolerance to develop robust salinity tolerant wheat varieties to ensure food security. However, owing to the polygenic nature of salt tolerance, current progress has been limited, and potential targets portrayed here. Many others factors needs to be identified and used to develop salt-tolerant wheat genotypes and improve food security. Genome editing is another robust tool with great promise for precision genome editing towards targeted trait improvement in the crop plants. We can also utilize this genome engineering platform for the development of genome-edited salt-tolerant wheat to mitigate associated yield penalty.

REFERENCES

- [1] Abbas, Z. K., Mobin, M. (2016): Comparative growth and physiological responses of two wheat (*Triticum aestivum* L.) cultivars differing in salt tolerance to salinity and cyclic drought stress. – Arch. Agron. Soil Sci. 62(6): 745-758.
- [2] Abdel Latef, A. (2010): Changes of antioxidative enzymes in salinity tolerance among different wheat cultivars. – Cereal Res. Commun. 38(1): 43-55.
- [3] Abdel-Ghani, A. H. (2009): Response of wheat varieties from semi-arid regions of Jordan to salt stress. – J. Agron. Crop Sci. 195(1): 55-65.
- [4] Abid, M., Ali, S., Qi, L. K., Zahoor, R., Tian, Z., Jiang, D., Snider, J. L., Dai, T. (2018): Physiological and biochemical changes during drought and recovery periods at tillering and jointing stages in wheat (*Triticum aestivum* L.). – Sci. Rep. 8: 1-15.
- [5] Afzal, I., Rauf, S., Basra, S. M. A., Murtaza, G. (2008): Halopriming improves vigor, metabolism of reserves and ionic contents in wheat seedlings under salt stress. – Plant Soil Environ. 54(9): 382-388.
- [6] Afzal, I., Basra, S. M. A., Cheema, M. A., Farooq, M., Jafar, M. Z., Shahid, M., Yasmeen, A. (2013): Seed priming: a shotgun approach for alleviation of salt stress in wheat. – Int. J. Agric. Biol. 15(6).
- [7] Ahanger, M. A., Agarwal, R. M. (2017): Salinity stress induced alterations in antioxidant metabolism and nitrogen assimilation in wheat (*Triticum aestivum* L.) as influenced by potassium supplementation. – Plant Physiol. Biochem. 115: 449-460.

- [8] Ahanger, M. A., Qin, C., Begum, N., Maodong, Q., Dong, X. X., El-Esawi, M., El-Sheikh, M. A., Alatar, A. A., Zhang, L. (2019): Nitrogen availability prevents oxidative effects of salinity on wheat growth and photosynthesis by up-regulating the antioxidants and osmolytes metabolism, and secondary metabolite accumulation. – BMC Plant Biol. 19: 1-12.
- [9] Ahmad, M., Niazi, B. H., Zaman, B., Athar, M. (2005): Varietals differences in agronomic performance of six wheat varieties grown under saline field environment. – Int. J. Environ. Sci. Technol. 2(1): 49-57.
- [10] Akbarimoghaddam, H., Galavi, M., Ghanbari, A., Panjehkeh, N. (2011): Salinity effects on seed germination and seedling growth of bread wheat cultivars. – Trakia J. Sci. 9(1): 43-50.
- [11] Al Khateeb, W., Muhaidat, R., Alahmed, S., Al Zoubi, M. S., Al-Batayneh, K. M., El-Oqlah, A., Alkaraki, A. K. (2020): Heat shock proteins gene expression and physiological responses in durum wheat (*Triticum durum*) under salt stress. – Physiol. Mol. Biol. Plants 1-10.
- [12] Aldesuquy, H. S., Baka, Z. A., El-Shehaby, O. A., Ghanem, H. E. (2012): Varietal differences in growth vigor, water relations, protein and nucleic acids content of two wheat varieties grown under seawater stress. – J. Stress Physiol. Biochem. 8: 24-47.
- [13] Ali, Q., Daud, M. K., Haider, M. Z., Ali, S., Rizwan, M., Aslam, N., Noman, A., Iqbal, N., Shahzad, F., Deeba, F., Ali, I. (2017): Seed priming by sodium nitroprusside improves salt tolerance in wheat (*Triticum aestivum* L.) by enhancing physiological and biochemical parameters. – Plant Physiol. Biochem. 119: 50-58.
- [14] AL-Quraan, N. A., AL-Ajlouni, Z. I., Obedat, D. I. (2019): The GABA shunt pathway in germinating seeds of wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) under salt stress. – Seed Sci. Res. 29(4): 250-260.
- [15] Annunziata, M. G., Ciarmiello, L. F., Woodrow, P., Maximova, E., Fuggi, A., Carillo, P. (2017): Durum wheat roots adapt to salinity remodeling the cellular content of nitrogen metabolites and sucrose. – Front. Plant Sci. 7(2035): 1-16.
- [16] Ashraf, M., Harris, P. J. C. (2013): Photosynthesis under stressful environments: an overview. – Photosynthetica 51: 163-190.
- [17] Ashraf, M., Karim, F., Rasul, E. (2002): Interactive effects of gibberellic acid (GA3) and salt stress on growth, ion accumulation and photosynthetic capacity of two spring wheat (*Triticum aestivum* L.) cultivars differing in salt tolerance. – Plant Grow. Regul. 36: 49-59.
- [18] Ashraf, M. A., Ashraf, M., Shahbaz, M. (2012): Growth stage-based modulation in antioxidant defense system and proline accumulation in two hexaploid wheat (*Triticum aestivum* L.) cultivars differing in salinity tolerance. – Flora-Morphol. Distri. Func. Ecol. Plants 207(5): 388-397.
- [19] Atiq-ur-Rahman, M., Saqib, M., Akhtar, J., Ahmad, R. (2014): Physiological characterization of wheat (*Triticum aestivum* L.) genotypes under salinity. – Pakistan J. Agril. Sci. 51(4).
- [20] Azeem, M., Iqbal, N., Kausar, S., Javed, M. T., Akram, M. S., Sajid, M. A. (2015): Efficacy of silicon priming and fertigation to modulate seedling's vigor and ion homeostasis of wheat (*Triticum aestivum* L.) under saline environment. – Environ. Sci. Pollu. Res. 22: 14367-14371.
- [21] Azzedine, F., Gherroucha, H., Baka, M. (2011): Improvement of salt tolerance in durum wheat by ascorbic acid application. – J. Stress Physiol. Biochem. 7: 27-37.
- [22] Bacu, A., Ibro, V., Nushi, M. (2020): Compared salt tolerance of five local wheat (*Triticum aestivum* L.) cultivars of Albania based on morphology, pigment synthesis and glutathione content. – The Euro. Biotech. J. 4(1): 42-52.
- [23] Benderradji, L., Brini, F., Amar, S. B., Kellou, K., Azaza, J., Masmoudi, K., Bouzerzour, H., Hanin, M. (2011): Sodium transport in the seedlings of two bread wheat (*Triticum*

- aestivum* L.) genotypes showing contrasting salt stress tolerance. – Aust. J. Crop Sci. 5(3): 233.
- [24] Borlu, H. O., Celiktaş, V., Düzenli, S., Hossain, A., El Sabagh, A. (2018): Germination and early seedling growth of five durum wheat cultivars (*Triticum durum* Desf.) is affected by different levels of salinity. – Fres. Environ. Bull. 27(11): 7746-7757.
- [25] Borzouei, A., Kafi, M., Akbari-Ghogdi, E., Mousavi-Shalmani, M. (2012): Long term salinity stress in relation to lipid peroxidation, super oxide dismutase activity and proline content of salt-sensitive and salt-tolerant wheat cultivars. – Chilean J. Agril. Res. 72(4): 476.
- [26] Brini, F., Amara, I., Feki, K., Hanin, M., Khoudi, H., Masmoudi, K. (2009): Physiological and molecular analyses of seedlings of two Tunisian durum wheat (*Triticum turgidum* L. subsp. Durum [Desf.]) varieties showing contrasting tolerance to salt stress. – Acta Physiol. Planta. 31(1): 145-154.
- [27] Byrt, C. S., Platten, J. D., Spielmeyer, W., James, R. A., Lagudah, E. S., et al. (2007): HKT1;5-like cation transporters linked to Na⁺ exclusion loci in wheat, Nax2 and Kna1. – Plant Physiol. 143: 1918-1928.
- [28] Charkazi, F., Ramezani, S., Soltanloo, H. (2010): Expression pattern of two sugar transporter genes (SuT4 and SuT5) under salt stress in wheat. – Plant Omics 3(6): 194.
- [29] Conde, A., Silva, P., Agasse, A., Conde, C., Gerós, H. (2011): Mannitol transport and mannitol dehydrogenase activities are coordinated in *Olea europaea* under salt and osmotic stresses. – Plant Cell Physiol. 52(10): 1766-1775.
- [30] Cuin, T. A., Bose, J., Stefano, G., Jha, D., Tester, M., Mancuso, S., Shabala, S. (2011): Assessing the role of root plasma membrane and tonoplast Na⁺/H⁺ exchangers in salinity tolerance in wheat: in planta quantification methods. – Plant Cell Environ. 34: 947-996.
- [31] Datir, S., Singh, N., Joshi, I. (2020): Effect of NaCl-induced salinity stress on growth, osmolytes and enzyme activities in wheat genotypes. – Bull. Environ. Contam. Toxicol. 104: 351-357.
- [32] Datta, J., Nag, S., Banerjee, A., Mondai, N. (2009): Impact of salt stress on five varieties of wheat (*Triticum aestivum* L.) cultivars under laboratory condition. – J. Appl. Sci. Environ. Manag. 13(3).
- [33] Davenport, R., James, R. A., Zakrisson-Plogander, A., Tester, M., Munns, R. (2005) Control of sodium transport in durum wheat. – Plant Physiol. 137: 807-818.
- [34] Desoky, E. S. M., Merwad, A. R. M. (2015): Improving the salinity tolerance in wheat plants using salicylic and ascorbic acids. – J. Agril. Sci. 7(10): 203.
- [35] Dubcovsky, J., María, G. S., Epstein, E., Luo, M. C., Dvořák, J. (1996): Mapping of the K⁺/Na⁺ discrimination locus Kna1 in wheat. – Theoret. Appl. Genet. 92(3): 448-454.
- [36] Dugasa, M. T., Xue, F., Nian-Hong, W., Junmei, W., Feibo, W. (2021): Comparative transcriptome and tolerance mechanism analysis in the two contrasting wheat (*Triticum aestivum* L.) cultivars in response to drought and salinity stresses. – Plant Growth Regulation 94: 101-114.
- [37] El Sabagh, A., Hossain, A., Barutçular, C., Iqbal, M. A., Islam, M. S., Fahad, S. et al. (2020): Consequences of Salinity Stress on the Quality of Crops and Its Mitigation Strategies for Sustainable Crop Production: An Outlook of Arid and Semi-Arid Regions. – In: Fahad, A., Hasanuzzaman, M., Alam, M., Ullah, H., Saeed, M., Khan, I. A., Adnan, M. (eds.) Environment, Climate, Plant and Vegetation Growth. Springer, Cham, pp. 503-533. DOI: 10.1007/978-3-030-49732-3_20.
- [38] 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., Ullah, N., Arshad, A. (2021): Salinity stress in wheat (*Triticum aestivum* L.) in the changing climate: adaptation and management strategies. – Front. Agron. 3: 661932. DOI: 10.3389/fagro.2021.661932.

- [39] El-Bassiouny, H. M., Bekheta, M. A. (2005): Effect of salt stress on relative water content, lipid peroxidation, polyamines, amino acids and ethylene of two wheat cultivars. – Int. J. Agric. Biol. 7(3): 363-368.
- [40] Eleiwa, M. E., Bafeel, S. O., Ibrahim, S. O. (2011): Influence of Brassinosteroids on wheat plant (*Triticum aestivum* L.) production under salinity stress conditions I-growth parameters and photosynthetic pigments. – Aust. J. Basic Appl. Sci. 5: 58-65.
- [41] El-Hendawy, S., Elshafei, A., Al-Suhaibani, N., Alotabi, M., Hassan, W., Dewir, Y. H., et al. (2019): Assessment of the salt tolerance of wheat genotypes during the germination stage based on germination ability parameters and associated SSR markers. – J. Plant Interact. 14: 151-163. DOI: 10.1080/17429145.2019.1603406.
- [42] Esfandiari, E., Gohari, G. (2017): Response of ROS-scavenging systems to salinity stress in two different wheat (*Triticum aestivum* L.) cultivars. – Notulae Botanicae Horti Agrobotanici Cluj-Napoca 45: 287-291.
- [43] Farouk, S. (2011): Ascorbic acid and α -tocopherol minimize salt-induced wheat leaf senescence. – J. Stress Physiol. Biochem. 7: 58-79.
- [44] Feki, K., Tounsi, S., Masmoudi, K., Brini, F. (2017): The durum wheat plasma membrane Na⁺/H⁺ antiporter SOS1 is involved in oxidative stress response. – Protoplasma 254(4): 1725-1734.
- [45] Flowers, T. J., Yeo, A. R. (1986): Ion relations of plants under drought and salinity. – Funct. Plant Biol. 13: 75-91.
- [46] Flowers, T. J., Munns, R., Colmer, T. D. (2015): Sodium chloride toxicity and the cellular basis of salt tolerance in halophytes. – Ann. Bot. 115: 419-431.
- [47] Francois, L. E., Maas, E. V., Donovan, T. J., Youngs, V. L. (1986): Effect of salinity on grain yield and quality, vegetative growth, and germination of semi-dwarf and durum wheat. – Agron. J. 78(6): 1053-1058.
- [48] Gao, Z., He, X., Zhao, B., Zhou, C., Liang, Y., Ge, R., Shen, Y., Huang, Z. (2010): Overexpressing a putative aquaporin gene from wheat, *TaNIP*, enhances salt tolerance in transgenic Arabidopsis. – Plant Cell Physiol. 51(5): 767-775.
- [49] García-Caparrós, P., Hasanuzzaman, M., Lao, M. T. (2019): Oxidative Stress and Antioxidant Defense in Plants under Salinity. – In: Reactive Oxygen, Nitrogen and Sulfur Species in Plants: Production, Metabolism, Signaling and Defense Mechanisms. Wiley, Hoboken, NJ, pp.291-309.
- [50] Gençel, M., Erdal, S. (2016): Alleviation of salt-induced oxidative damage by 5-aminolevulinic acid in wheat seedlings. – AIP Conference Proceedings 1726: 020025. DOI: 10.1063/1.4945851.
- [51] Ghonaim, M. M., Mohamed, H. I., Omran, A. A. (2020): Evaluation of wheat (*Triticum aestivum* L.) salt stress tolerance using physiological parameters and retrotransposon-based markers. – Gen. Resour. Crop Evol. 1-16.
- [52] Gorcek, Z., Erdal, S. (2015): Lipoic acid mitigates oxidative stress and recovers metabolic distortions in salt-stressed wheat seedlings by modulating ion homeostasis, the osmo-regulator level and antioxidant system. – J. Sci. Food Agric. 95: 2811-2817.
- [53] Goudarzi, M., Pakniyat, H. (2008): Evaluation of wheat cultivars under salinity stress based on some agronomic and physiological traits. – J. Agric. Soc. Sci. 4: 35-38.
- [54] Goudarzi, M., Pakniyat, H. (2009): Peroxidase activity in wheat cultivars. – J. Appl. Sci. 9(2): 348-353.
- [55] Guo, G., Ge, P., Ma, C., Li, X., Lv, D., Wang, S., Ma, W., Yan, Y. (2012): Comparative proteomic analysis of salt response proteins in seedling roots of two wheat varieties. – J. Proteom. 75(6): 1867-1885.
- [56] Gupta, B., Huang, B. (2014): Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. – Int. J. Genom. 701596. DOI: 10.1155/2014/701596.
- [57] Gurmani, A. R., Bano, A., Najeeb, U., Zhang, J., Khan, S. U., Flowers, T. J. (2013): Exogenously applied silicate and abscisic acid ameliorates the growth of salinity stressed

- wheat (*Triticum aestivum* L.) seedlings through Na⁺ exclusion. – Aust. J. Crop Sci. 7: 1123-1130.
- [58] Gurmani, A. R., Khan, S. U., Mabood, F., Ahmed, Z., Butt, S. J., Din, J., Mujeeb-Kazi, A., Smith, D. (2014): Screening and selection of synthetic hexaploid wheat germplasm for salinity tolerance based on physiological and biochemical characters. – Int. J. Agric. Biol. 16: 681-690.
- [59] Habib, N., Ali, Q., Ali, S., Haider, M. Z., Javed, M. T., Khalid, M., Perveen, R., Alsahli, A. A., Alyemeni, M. N. (2021): Seed priming with sodium nitroprusside and H₂O₂ confers better yield in wheat under salinity: water relations, antioxidative defense mechanism and ion homeostasis. – J. Plant Grow. Regul. 40: 2433-2453.
- [60] Hajihashemi, S., Kiarostami, K., Enteshari, S., Saboori, A. (2009): Effect of paclobutrazol on wheat salt tolerance at pollination stage. – Russian J. Plant Physiol. 56: 251-257.
- [61] Hameed, A., Afzal, I., Iqbal, N. (2010): Seed priming and salinity induced variations in wheat (*Triticum aestivum* L.) leaf protein profile. – Seed Sci. Technol. 38(1): 236-241.
- [62] Hasan, A., Hafiz, H. R., Siddiqui, N., Khatun, M., Islam, R., Mamun, A. A. (2015): Evaluation of wheat genotypes for salt tolerance based on some physiological traits. – J. Crop Sci. Biotechnol. 18(5): 333-340.
- [63] Hasan, H., Ali, M., Javaid, A., Liaqat, A., Hussain, S., Siddique, R., Fayaz, T., Gul, A. (2020): Cellular Mechanism of Salinity Tolerance in Wheat. Chapter 4. – In: Ozturk, M., Gul, A. (eds.) Climate Change and Food Security with Emphasis on Wheat. Academic Press, London, pp. 55-76. DOI: 10.1016/B978-0-12-819527-7.00004-2.
- [64] Hasanuzzaman, M., Nahar, K., Rahman, A., Anee, T. I., Alam, M. U., Bhuiyan, T. F., Oku, H., Fujita, M. (2017): Approaches to Enhance Salt Stress Tolerance in Wheat. – In: Wanyera, R., Owuochi, J. (eds.) Wheat Improvement, Management and Utilization. IntechOpen, London, pp.151-187. DOI: 10.5772/67247.
- [65] Hasanuzzaman, M., Saha, N. R., Farabi, S., Tahjib-Ul-Arif, M., Yasmin, S., Haque, M. S. (2022): Screening of salt-tolerant wheat (*Triticum aestivum* L.) through morphological and molecular markers. – Cereal Research Commun. 17: 1-4.
- [66] Hasegawa, P. M., Bressan, R. A., Zhu, J. K., Bohnert, H. J. (2000): Plant cellular and molecular responses to high salinity. – Ann. Rev. Plant Biol. 51(1): 463-499.
- [67] Horie, T., Hauser, F., Schroeder, J. I. (2009): HKT transporter-mediated salinity resistance mechanisms in Arabidopsis and monocot crop plants. – Trends in Plant Science 14(12): 660-668.
- [68] Hossain, M. A., Hoque, M. A., Burritt, D. J., Fujita, M. (2013): Proline Protects Plants Against Abiotic Oxidative Stress: Biochemical and Molecular Mechanisms. – In: Ahmad, P. (ed.) Oxidative Damage to Plants. Elsevier, Amsterdam, pp. 477-522.
- [69] Huang, S., Spielmeyer, W., Lagudah, E. S., James, R. A., Platten, J. D., Dennis, E. S., Munns, R. (2006): A sodium transporter (HKT7) is a candidate for Nax1, a gene for salt tolerance in durum wheat. – Plant Physiol. 142(4): 1718-1727.
- [70] Huang, S., Spielmeyer, W., Lagudah, E. S., Munns, R. (2008): Comparative mapping of HKT genes in wheat, barley, and rice, key determinants of Na⁺ transport, and salt tolerance. – J. Exp. Bot. 59(4): 927-937.
- [71] Husain, S., von Caemmerer, S., Munns, R. (2004): Control of salt transport from roots to shoots of wheat in saline soil. – Func. Plant Biol. 31: 1115-1126.
- [72] Hussain, S., Khaliq, A., Matloob, A., Wahid, M. A., Afzal, I. (2013): Germination and growth response of three wheat cultivars to NaCl salinity. – Soil Environ. 32: 36-43.
- [73] Hussain, S., Shaukat, M., Ashraf, M., Zhu, C., Jin, Q., Zhang, J. (2019): Salinity stress in arid and semi-arid climates: effects and management in field crops. – Clim. Change Agric 123-145. DOI: 10.5772/intechopen.87982.
- [74] Imlay, J. A., Linn, S. (1988): DNA damage and oxygen radical toxicity. – Sci. 240: 1302-1309.

- [75] Iqbal, M., Ashraf, M. (2006): Wheat seed priming in relation to salt tolerance: growth, yield and levels of free salicylic acid and polyamines. – *Annales Botanici Fennici* 43(4): 250-259.
- [76] Iqbal, M., Ashraf, M. (2013a): Gibberellic acid mediated induction of salt tolerance in wheat plants: growth, ionic partitioning, photosynthesis, yield and hormonal homeostasis. – *Environ. Exp. Bot.* 86: 76-85.
- [77] Iqbal, M., Ashraf, M. (2013b): Salt tolerance and regulation of gas exchange and hormonal homeostasis by auxin-priming in wheat. – *Pesquisa Agropecuária Brasileira* 48: 1210-1219.
- [78] Iqbal, M., Ashraf, M., Jamil, A. (2006a): Seed enhancement with cytokinins: changes in growth and grain yield in salt stressed wheat plants. – *Plant Growth Regul.* 50(1): 29-39.
- [79] Iqbal, M., Ashraf, M., Jamil, A., Ur-Rehman, S. (2006b): Does seed priming induce changes in the levels of some endogenous plant hormones in hexaploid wheat plants under salt stress? – *J. Integra. Plant Biol.* 48(2): 181-189.
- [80] Islam, F., Yasmeen, T., Ali, S., Ali, B., Farooq, M. A., Gill, R. A. (2015): Priming-induced antioxidative responses in two wheat cultivars under saline stress. – *Acta Physiol. Planta.* 37(8): 153.
- [81] Ismail, M. A. (2014): Exogenous proline induced changes in SDS-PAGE protein profile for salt tolerance in wheat (*Triticum aestivum* L.) seedlings. – *Res. J. Pharma. Biol. Chem. Sci.* 5: 749-755.
- [82] Jafar, M. Z., Farooq, M., Cheema, M. A., Afzal, I., Basra, S. M. A., Wahid, M. A., Aziz, T., Shahid, M. (2012): Improving the performance of wheat by seed priming under saline conditions. – *J. Agron. Crop Sci.* 198(1): 38-45.
- [83] James, R. A., Davenport, R. J., Munns, R. (2006): Physiological characterization of two genes for Na⁺ exclusion in durum wheat, Nax1 and Nax2. – *Plant Physiology* 142(4): 1537-1547.
- [84] 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.
- [85] Jamil, A., Riaz, S., Ashraf, M., Foolad, M. R. (2011): Gene expression profiling of plants under salt stress. – *Crit. Rev. Plant Sci.* 30: 435-458.
- [86] Jehan, B., Khan, M. J., Mohammad, S., Khan, M. A., Mohammad, S. (2012): Effect of salinity and ABA application on proline production and yield in wheat genotypes. – *Pak. J. Bot.* 44: 873-878.
- [87] Jusovic, M., Velitchkova, M. Y., Misheva, S. P., Börner, A., Apostolova, E. L., Dobrikova, A. G. (2018): Photosynthetic responses of a wheat mutant (Rht-B1c) with altered DELLA proteins to salt stress. – *J. Plant Grow. Regul.* 37: 645-656.
- [88] Kausar, A., Gull, M. (2014): Effect of potassium sulphate on the growth and uptake of nutrients in wheat (*Triticum aestivum* L.) under salt stressed conditions. – *J. Agril. Sci.* 6: 1-12.
- [89] Ke, Q., Ye, J., Wang, B., Ren, J., Yin, L., Deng, X., Wang, S. (2018): Melatonin mitigates salt stress in wheat seedlings by modulating polyamine metabolism. – *Fron Plant Sci.* 9: 914.
- [90] Khan, A., Ahmad, I., Shah, A., Ahmad, F., Ghani, A., Nawaz, M. (2013): Amelioration of salinity stress in wheat (*Triticum aestivum* L.) by foliar application of phosphorus. – *Phyton, Int. J. Exp. Bot.* 82: 281-287.
- [91] Khan, A., Shaheen, Z., Nawaz, M. (2016): Amelioration of salt stress in wheat (*Triticum aestivum* L.) by foliar application of nitrogen and potassium. – *Sci. Technol. Develop.* 32(2): 85-98.
- [92] Khan, M., Shirazi, M., Shereen, A., Mujtaba, S., Khan, M. A., Mumtaz, S., Mahboob, W. (2017): Identification of some wheat (*Triticum aestivum* L.) lines for salt tolerance on the basis of growth and physiological characters. – *Pak. J. Bot.* 49(2): 397-403.

- [93] Khan, M. A., Shirazi, M., Mahboob, W., Mujtaba, S., Khan, M. A., Mumtaz, S., Shereen, A. (2014): Morpho-physiological adaptations of wheat genotypes to salinity stress. – Pak. J. Bot. 46(6): 1981-1985.
- [94] Khatkar, D., Kuhad, M. S. (2000): Short-term salinity induced changes in two wheat cultivars at different growth stages. – Biol. Plant. 43(4): 629-632.
- [95] Kochak-Zadeh, A., Mousavi, S. H., Eshraghi-Nejad, M. (2013): The effect of salinity stress on germination and seedling growth of native and breded varieties of wheat. – J. Nov. Appl. Sci. 12: 703–709.
- [96] Kumar, S., Beena, A., Awana, M., Singh, A. (2017): Physiological, biochemical, epigenetic and molecular analyses of wheat (*Triticum aestivum*) genotypes with contrasting salt tolerance. – Fron. Plant Sci. 8: 1151.
- [97] Laurie, S., Feeney, K. A., Maathuis, F. J. M., Heard, P. J., Brown, S. J., Leigh, R. A. (2002): A role for HKT1 in sodium uptake by wheat roots. – Plant J. 32: 139-149.
- [98] Li, G., Peng, X., Wei, L., Kang, G. (2013): Salicylic acid increases the contents of glutathione and ascorbate and temporally regulates the related gene expression in salt-stressed wheat seedlings. – Gene. 529(2): 321-325.
- [99] Li, J., Qiu, Z., Zhang, X., Wang, L. (2011): Exogenous hydrogen peroxide can enhance tolerance of wheat seedlings to salt stress. – Acta Physiol. Plant. 33: 835-842.
- [100] Li, Z. G., Duan, X. Q., Min, X., Zhou, Z. X. (2017): Methylglyoxal as a novel signal molecule induces the salt tolerance of wheat by regulating the glyoxalase system, the antioxidant system, and osmolytes. – Protoplasma 254(5): 1995-2006.
- [101] Liang, C., Zhan, X. Y., Wang, G. P., Zou, Q., Wang, W. (2009): Overaccumulation of glycine betaine alleviates the negative effects of salt stress in wheat. – Russian J. Plant Physiol. 56: 370-376.
- [102] Lin, F., Xu, J., Shi, J., Li, H., Li, B. (2010): Molecular cloning and characterization of a novel glyoxalase I gene *TaGly I* in wheat (*Triticum aestivum* L.). – Mol. Biol. Reports 37: 729-735.
- [103] Liu, H., Carvalhais, L. C., Kazan, K., Schenk, P. M. (2016): Development of marker genes for jasmonic acid signaling in shoots and roots of wheat. – Plant Signal. Beh. 11: e1176654.
- [104] Ma, X., Liang, W., Gu, P., Huang, Z. (2016): Salt tolerance function of the novel C2H2-type zinc finger protein TaZNF in wheat. – Plant Physiology and Biochemistry. 106: 129-140.
- [105] Maas, E. V., Hoffman, G. J. (1977): Crop salt tolerance current assessment. – J. Irrig. Drain. Div. 103: 115-134.
- [106] Maha, A., Sanaa, I., Mabrook, Y. M., Amira, Y., Gouda, M. A. (2017): Evaluation of some Egyptian bread wheat (*Triticum aestivum*) cultivars under salinity stress. – Alex. Sci. Exch. J. 38(260): 2.
- [107] Mahajan, S., Tuteja, N. (2005): Cold, salinity and drought stresses: an overview. – Arch. Biochem. Biophys. 444: 139-158.
- [108] Mahboob, W., Khan, M. A., Shirazi, M. U. (2016): Induction of salt tolerance in wheat (*Triticum aestivum* L.) seedlings through exogenous application of proline. – Pak. J. Bot. 48: 861-867.
- [109] Mahboob, W., Khan, M. A., Shirazi, M. U. (2017): Characterization of salt tolerant wheat (*Triticum aestivum*) genotypes on the basis of physiological attributes. – Int. J. Agric. Biol. 19: 726-734.
- [110] Mahboob, W., Khan, M. A., Shirazi, M. U., Mumtaz, S., Shereen, A. (2018): Using growth and ionic contents of wheat seedlings as rapid screening tool for salt tolerance. – J. Crop Sci. Biotechnol. 21: 173-181.
- [111] Mahboob, W., Khan, M. A., Ubaidullah Shirazi, M., Faisal, S., Asma (2019): Seed priming modulates germination potential, osmoprotectants accumulation and ionic uptake in wheat seedlings under salt stress. – Intl. J. Agric. Biol. 22: 594-600.

- [112] Mansour, E., Moustafa, E. S., Desoky, E. S. M., Ali, M. M., Yasin, M. A., Attia, A., Alsuhaibani, N., Tahir, M. U., El-Hendawy, S. (2020): Multidimensional evaluation for detecting salt tolerance of bread wheat genotypes under actual saline field growing conditions. – *Plants* 9: 1324.
- [113] Maqbool, N., Wahid, A., Basra, S. M. A. (2016): Varied patterns of sprouting and nutrient status of sugarcane sprouts in simulated and natural saline/sodic soils across two growing seasons. – *Int. J. Agric. Biol.* 18: 873-880.
- [114] Marschner, H. (1986): *Mineral Nutrition of Higher Plants*. – Acad. Press. Inc., London.
- [115] Miransari, M., Smith, D. (2019): Sustainable wheat (*Triticum aestivum* L.) production in saline fields: a review. – *Crit. Rev. Biotechnol.* 39(8): 999-1014.
- [116] Mujeeb-Kazi, A., Munns, R., Rasheed, A., Ogbonnaya, F. C., Ali, N., Hollington, P., Dundas, I., Saeed, N., Wang, R., Rengasamy, P., Saddiq, M. S. (2019): Breeding strategies for structuring salinity tolerance in wheat. – *Adv. Agron.* 155: 121-187.
- [117] Munns, R. (2002): Comparative physiology of salt and water stress. – *Plant, Cell Environ.* 25(2): 239-250.
- [118] Munns, R. (2005): Genes and salt tolerance: bringing them together. – *New Phytol.* 167: 645-663.
- [119] Munns, R., Tester, M. (2008): Mechanisms of salinity tolerance. – *Annu. Rev. Plant Biol.* 59: 651-681.
- [120] Munns, R., Hare, R. A., James, R. A., Rebetzke, G. J. (2000): Genetic variation for improving the salt tolerance of durum wheat. – *Aust. J. Agric. Res.* 51(1): 69-74.
- [121] Munns, R., Richard, A. J., Andre, L. (2006): Approaches to increasing the salt tolerance of wheat and other cereals. – *J. Exp. Bot.* 57: 1025-1043.
- [122] Muranaka, S., Shimizu, K., Kato, M. (2002): Ionic and osmotic effects of salinity on single-leaf photosynthesis in two wheat cultivars with different drought tolerance. – *Photosynthetica* 40(2): 201-207.
- [123] Mutlu, S., Atici, Ö., Nalbantoglu, B. (2009): Effects of salicylic acid and salinity on apoplastic antioxidant enzymes in two wheat cultivars differing in salt tolerance. – *Biol. Planta.* 53(2): 334-338.
- [124] Nassar, R., 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.
- [125] Nongpiur, R. C., Singla-Pareek, S. L., Pareek, A. (2020): The quest for osmosensors in plants. – *J. Exp. Bot.* 71(2): 595-607.
- [126] Oyiga, B. C., Sharma, R. C., Shen, J., Baum, M., Ogbonnaya, F. C., Leon, J., Ballvora, A. (2016): Identification and characterization of salt tolerance of wheat germplasm using a multivariable screening. – *J. Agron. Crop Sci.* 472-485.
- [127] Oyiga, B. C., Ogbonnaya, F. C., Sharma, R. C., Baum, M., Léon, J., Ballvora, A. (2019): Genetic and transcriptional variations in NRAMP-2 and OPAQUE1 genes are associated with salt stress response in wheat. – *Theor. Appl. Gene.* 132(2): 323-346.
- [128] Plett DC, Moller IS (2010) Na⁺ transport in glycophytic plants: what we know and would like to know. – *Plant Cell Environ.* 33: 612-626.
- [129] Poustini, K., Siosemardeh, A. (2004): Ion distribution in wheat cultivars in response to salinity stress. – *Field Crops Research* 85(2-3): 125-133.
- [130] Qiu, Z., Guo, J., Zhu, A., Zhang, L., Zhang, M. (2014): Exogenous jasmonic acid can enhance tolerance of wheat seedlings to salt stress. – *Ecotoxicol. Environ. Saf.* 104: 202-208.
- [131] Rahaie, M., Xue, G. P., Naghavi, M. R., Alizadeh, H., Schenk, P. M. (2010): A MYB gene from wheat (*Triticum aestivum* L.) is up-regulated during salt and drought stresses and differentially regulated between salt-tolerant and sensitive genotypes. – *Plant Cell Rep.* 29(8): 835-844.
- [132] Rahnama, A., Fakhri, S., Meskarbashee, M. (2019): Root growth and architecture responses of bread wheat cultivars to salinity stress. – *Agron. J.* 111(6): 2991-2998.

- [133] Ramezani, A., Ali, N., Ali, A. A., Mahboobeh, Z. B., Tahereh, D., Mahmood, E., Hosein, A., Esmail, E. (2013): Quantitative expression analysis of TaSOS1 and TaSOS4 genes in cultivated and wild wheat plants under salt stress. – Mol. Biotechnol. 53: 189-197.
- [134] Rana, V., Ram, S., Nehra, K., Sharma, I. (2016): Expression of genes related to Na⁺ exclusion and proline accumulation in tolerant and susceptible wheat genotypes under salt stress. – Cereal Res. Commun. 44(3): 404-413.
- [135] Rao, A., Ahmad, S. D., Sabir, S. M., Awan, S. I., Shah, A. H., Abbas, S. R., Shafique, S., Khan, F., Chaudhary, A. (2013): Potential antioxidant activities improve salt tolerance in ten varieties of wheat (*Triticum aestivum* L.). – Am J Plant Sci. 4: 69-76.
- [136] Rao, G. G., Arora, S., Ramesh, N. V., Sharma, D. K. (2016): Prospects and impact of cultivating salt tolerant varieties of cotton and wheat in coastal saline soils of Gujarat. – Indian J. Soil Conser. 44(3): 308-313.
- [137] Raza, S. H., Athar, H. U. R., Ashraf, M. (2006): Influence of exogenously applied glycinebetaine on the photosynthetic capacity of two differently adapted wheat cultivars under salt stress. – Pak. J. Bot. 38(2): 341-351.
- [138] Rhodes, D., Hanson, A. D. (1993): Quaternary ammonium and tertiary sulphonium compounds in higher plants. – Annu. Rev. Plant Physiol. Plant Mol. Biol. 44: 357-384.
- [139] Robin, A. H. K., Matthew, C., Uddin, M. J., Bayazid, K. N. (2016): Salinity-induced reduction in root surface area and changes in major root and shoot traits at the phytomer level in wheat. – J. Exp. Bot. 67: 3719-3729.
- [140] Rubinigg, M., Wenisch, J., Elzenga, J. T. M., Stulen, I. (2004): NaCl salinity affects lateral root development in *Plantago maritima*. – Func. Plant Biol. 31: 775-780.
- [141] Sadak, M. S. (2016): Mitigation of salinity adverse effects on wheat by grain priming with melatonin. – Int. J. ChemTech Res. 9: 85-97.
- [142] Saeidnejad, A. H., Kafi, M., Dashti, M. (2016): Ameliorative effects of spermine application on physiological performance and salinity tolerance induction of susceptible and tolerant cultivars of wheat (*Triticum aestivum*). – Arch. Agron. Soil Sci. 62: 1337-1346.
- [143] Sairam, R. K., Rao, K. V., Srivastava, G. C. (2002): Differential response of wheat genotypes to long term salinity stress in relation to oxidative stress, antioxidant activity and osmolyte concentration. – Plant Sci. 163: 1037-1046.
- [144] Salama, K. H. A., Mansour, M. M. F. (2015): Choline priming-induced plasma membrane lipid alterations contributed to improved wheat salt tolerance. – Acta Physiol. Planta. 37(8): 170.
- [145] Salama, K. H. A., Mansour, M. M. F., Hassan, N. S. (2011): Choline priming improves salt tolerance in wheat (*Triticum aestivum* L.). – Aust. J. Basic Appl. Sci. 5: 126-132.
- [146] Salama, K. H. A., Mansour, M. M., Al-Malawi, H. A. (2015): Glycinebetaine priming improves salt tolerance of wheat. – Biologia. 70: 1334-1339.
- [147] Salama, S., Trivedi, S., Busheva, M., Arafa, A., Garab, G., Erdei, L. (1994): Effects of NaCl salinity on growth, cation accumulation, chloroplast structure and function in wheat cultivars differing in salt tolerance. – J. Plant Physiol. 144: 241-247. DOI: 10.1016/S0176-1617(11)80550-X.
- [148] Sathee, L., Sairam, R. K., Chinnusamy, V., Jha, S. K. (2015): Differential transcript abundance of salt overly sensitive (SOS) pathway genes is a determinant of salinity stress tolerance of wheat. – Acta Physiol. Plant. 37(8): 1-10.
- [149] Sayed, O. (2003): Chlorophyll fluorescence as a tool in cereal crop research. – Photosynthetica 41(3): 321-330.
- [150] Seleiman, M. F., Aslam, M. T., Alhammad, Hassan, B. A., Maqbool, M. U., Chattha, M. U. et al. (2021): Salinity stress in wheat: effects, mechanisms and management strategies. – Phyton-Int. J. Exp. Bot. DOI: 10.32604/phyton.2022.017365.
- [151] Shafi, M., Zhang, G., Bakht, J., Khan, M. A., Islam, U., Khan, M. D., Raziuddin, G. (2010): Effect of cadmium and salinity stresses on root morphology of wheat. – Pak. J. Bot. 42(4): 2747-2754.

- [152] Shafiq, F., Iqbal, M., Ashraf, M. A., Ali, M. (2020): Foliar applied fullerol differentially improves salt tolerance in wheat through ion compartmentalization, osmotic adjustments and regulation of enzymatic antioxidants. – *Physiology and Molecular Biology of Plants* 26(3): 475-487.
- [153] Shahbaz, M., Ashraf, M. (2013): Improving salinity tolerance in cereals. – *Crit. Rev. Plant Sci.* 32: 237-249.
- [154] Sharma, R. (2015): Genotypic response to salt stress: I–Relative tolerance of certain wheat cultivars to salinity. – *Adv. Crop Sci. Technol.* 3: 192.
- [155] Sharma, R. (2017): Genotypic response to salt stress: II–Pattern of differential relative behaviour of salt-tolerant, moderately salt-tolerant and salt-sensitive wheat cultivars under salt stressed conditions. – *Ground Sediment & Water* 5: 205-216.
- [156] Shi, H. Z., Quintero, F. J., Pardo, J. M., Zhu, J. K. (2002): The putative plasma membrane Na^+/H^+ antiporter SOS1 controls long-distance Na^+ transport in plants. – *Plant Cell* 14: 465-477.
- [157] Shulaev, V., Cortes, D., Miller, G., Mittler, R. (2008): Metabolomics for plant stress response. – *Physiol. Planta.* 132(2): 199-208.
- [158] Siddiqui, M. N., Mostofa, M. G., Akter, M. M., Srivastava, A. K., Sayed, M. A., Hasan, M. S., Tran, L. S. P. (2017): Impact of salt-induced toxicity on growth and yield-potential of local wheat cultivars: oxidative stress and ion toxicity are among the major determinants of salt-tolerant capacity. – *Chemosphere* 187: 385-394.
- [159] Silini, A., Cherif-Silini, H., Yahiaoui, B. (2016): Growing varieties durum wheat (*Triticum durum*) in response to the effect of osmolytes and inoculation by *Azotobacter chroococcum* under salt stress. – *Afr. J. Microbiol. Res.* 10: 387-399.
- [160] Singh, A. (2015): Soil salinization and waterlogging: a threat to environment and agricultural sustainability. – *Ecol. Indic.* 57: 128-130.
- [161] Singh, P., Mahajan, M. M., Singh, N. K., Kumar, D., Kumar, K. (2020): Physiological and molecular response under salinity stress in bread wheat (*Triticum aestivum* L.). – *J. Plant Biochem. Biotechnol.* 29(1): 125-133.
- [162] Steudle, E. (2000): Water uptake by roots: effects of water deficit. – *J. Exp. Bot.* 51(350): 1531-1542.
- [163] Sun, T., Wang, Y., Wang, M., Li, T., Zhou, Y., Wang, X., Wei, S., He, G., Yang, G. (2015): Identification and comprehensive analyses of the CBL and CIPK gene families in wheat (*Triticum aestivum* L.). – *BMC Plant Biology* 15(1): 1-17.
- [164] Tabassum, T., Farooq, M., Ahmad, R., Zohaib, A., Wahid, A. (2017): Seed priming and transgenerational drought memory improves tolerance against salt stress in bread wheat. – *Plant Physiol. Biochem.* 118: 362-369.
- [165] Tabatabaei, S. A. (2013): The effect of salicylic acid and gibberellin on enzyme activity and germination characteristics of wheat seeds under salinity stress conditions. – *Int. J. Agric. Crop Sci.* 6: 236-240.
- [166] Talat, A., Nawaz, K., Hussian, K., Bhatti, K. H., Siddiqi, E. H., Khalid, A., Anwer, S., Sharif, M. U. (2013): Foliar application of proline for salt tolerance of two wheat (*Triticum aestivum* L.) cultivars. – *World Appl. Sci. J.* 22: 547-554.
- [167] Tester, M., Davenport, R. (2003): Na^+ tolerance and Na^+ transport in higher plants. – *Ann. Bot.* 91: 503-527.
- [168] Tian, X., He, M., Wang, Z., Zhang, J., Song, Y., He, Z., Dong, Y. (2015): Application of nitric oxide and calcium nitrate enhances tolerance of wheat seedlings to salt stress. – *Plant Growth Regul.* 77: 343-356.
- [169] Tofighi, C., Khavari-Nejad, R. A., Najafi, F., Razavi, K., Rejali, F. (2017): Brassinosteroid (BR) and arbuscular mycorrhizal (AM) fungi alleviate salinity in wheat. – *J. Plant Nut.* 40: 1091-1098.
- [170] Turki, N., Harrabi, M., Okuno, K. (2012): Effect of salinity on grain yield and quality of wheat and genetic relationships among durum and common wheat. – *J. Arid Land Stud.* 22: 311-314.

- [171] Wang, W., Wang, W., Wu, Y., Li, Q., Zhang, G., Shi, R., Yang, J., Wang, Y., Wang, W. (2020): The involvement of wheat U-box E3 ubiquitin ligase TaPUB1 in salt stress tolerance. – J. Integr. Plant Biol. 62(5): 631-651.
- [172] Wu, H., Shabala, L., Liu, X., Azzarello, E., Zhou, M., et al. (2015): Linking salinity stress tolerance with tissue-specific Na⁺ sequestration in wheat roots. – Front. Plant Sci. 6: 71.
- [173] Xu, H., Jiang, X., Zhan, K., Cheng, X., Chen, X., Pardo, J. M., Cui, D. (2008): Functional characterization of a wheat plasma membrane Na⁺/H⁺ antiporter in yeast. – Arch Biochem. Biophys. 473: 8-15.
- [174] Yamaguchi, E., Blumwald, E. (2005): Developing salt-tolerant crop plants: challenges and opportunities. – Trends Plant Sci. 10: 615-620.
- [175] Yancey, P. H. (2005): Organic osmolytes as compatible, metabolic and counteracting cytoprotectants in high osmolarity and other stresses. – J. Exp. Biol. 208(15): 2819-2830.
- [176] Yörük, E., Keleş, E. N., Sefer, Ö., Eraslan, M. (2018): Salinity and drought stress on barley and wheat cultivars planted in Turkey. – J. Environ. Biol. 39(6): 943-950.
- [177] Yousfi, S., Serret, M. D., Márquez, A. J., Voltas, J., Araus, J. L. (2012): Combined use of $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and $\delta^{15}\text{N}$ tracks nitrogen metabolism and genotypic adaptation of durum wheat to salinity and water deficit. – New Phytol. 194: 230-244.
- [178] Zafar, S., Ashraf, M. Y., Niaz, M., Kausar, A., Hussain, J. (2015): Evaluation of wheat genotypes for salinity tolerance using physiological indices as screening tool. – Pak. J. Bot. 47: 397-405.
- [179] Zeeshan, M., Lu, M., Naz, S., Sehar, S., Cao, F., Wu, F. (2020a): Resemblance and difference of seedling metabolic and transporter gene expression in high tolerance wheat and barley cultivars in response to salinity stress. – Plants 9(4): 519.
- [180] Zeeshan, M., Lu, M., Sehar, S., Holford, P., Wu, F. (2020b): Comparison of biochemical, anatomical, morphological, and physiological responses to salinity stress in wheat and barley genotypes deferring in salinity tolerance. – Agron. 10(1): 127.
- [181] Zhang, J., Duan, X., Ding, F., Ma, H., Zhang, T., Yang, Y. (2014): Salinity induced the changes of root growth and antioxidative responses in two wheat cultivars. – Protoplasma 251(4): 771-780.
- [182] Zhang, S., Gan, Y., Xu, B. (2016): Application of plant-growth-promoting fungi *Trichoderma longibrachiatum* T6 enhances tolerance of wheat to salt stress through improvement of antioxidative defense system and gene expression. – Fron. Plant Sci. 7: 1405. DOI: 10.3389/fpls.2016.01405.
- [183] Zhao, Y., Dong, W., Zhang, N., Ai, X., Wang, M., Huang, Z., Xiao, L., Xia, G. (2014): A wheat allene oxide cyclase gene enhances salinity tolerance via jasmonate signaling. – Plant Physiol. 164: 1068-1076.
- [184] Zheng, C., Jiang, D., Liu, F., Dai, T., Jing, Q., Cao, W. (2009a): Effects of salt and waterlogging stresses and their combination on leaf photosynthesis, chloroplast ATP synthesis, and antioxidant capacity in wheat. – Plant Sci. 176: 575-582.
- [185] Zheng, C., Jiang, D., Liu, F., Dai, T., Liu, W., Jing, Q., Cao, W. (2009c): Exogenous nitric oxide improves seed germination in wheat against mitochondrial oxidative damage induced by high salinity. – Environ. Exp. Bot. 67: 222-227.
- [186] Zheng, Y., Xu, X., Simmons, M., Zhang, C., Gao, F., Li, Z. (2010): Responses of physiological parameters, grain yield, and grain quality to foliar application of potassium nitrate in two contrasting winter wheat cultivars under salinity stress. – J. Plant Nutr. Soil Sci. 173(3): 444-452.
- [187] Zhu, J. K. (2001): Plant salt tolerance. – Trends Plant Sci. 6: 66-71.
- [188] Zou, P., Li, K., Liu, S., He, X., Zhang, X., Xing, R., Li, P. (2016): Effect of sulfated chito oligosaccharides on wheat seedlings (*Triticum aestivum* L.) under salt stress. – J. Agril. Food Chem. 64: 2815-2821.