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Chapter

# Insights into Physiological, Biochemical and Molecular Responses in Wheat under Salt Stress

*Hari Kesh, Sunita Devi, Naresh Kumar, Ashwani Kumar, Arvind Kumar, Pooja Dhansu, Parvender Sheoran and Anita Mann*

## Abstract

Globally, wheat is a major staple food crop that provides 20% of food calories for 30% of the human population. Wheat growth and production are significantly affected by salt stress at various stages and adversely affect germination, vegetative growth, stomatal conductance, photosynthesis, reproductive behavior, protein synthesis, enzymatic activity and finally hampered grain yield. Maintenance of low  $\text{Na}^+/\text{K}^+$  ratio, antioxidants and hormonal regulation, and accumulation of compatible osmolytes such as glycine betaine, proline and trehalose help the wheat genotypes to mitigate the negative effects of salt stress. Recent studies have reported various mechanisms at the physiological, biochemical and molecular levels to adapt the salinity stress in various ecologies. Salt tolerant genotypes can be developed by conventional breeding approaches and through biotechnological approaches. This chapter reviews the updates on mechanisms and recent approaches to structure the salt-tolerant and high-yielding genotypes.

**Keywords:** wheat, salt stress, ion homeostasis, conventional approaches, molecular breeding

## 1. Introduction

Bread wheat is a major staple food cultivated throughout the world with a global yield of 8.8 million tons [1]. Global demand for wheat is increasing day by day due to its unique features such as bio-fortified and processed products like biscuits, cookies, doughnuts, porridge and pastries [2]. However, the production and productivity of wheat have decreased due to various biotic and abiotic stresses. Different climate models estimated that wheat production could reduce by 6% due to adverse climatic conditions [3]. Among the abiotic stresses, salinity stress significantly affects the growth and production of wheat crops. Up to 40 percent yield loss worth \$ 27 billion

US annually have reported in salt-affected regions [4, 5]. Soil salinity negatively affects the morphological traits such as germination percentage, grain per spike, plant height, grain yield and harvest index [6–8]; physiological traits like relative water content, membrane stability, chlorophyll fluorescence and mineral uptake [9, 10]; biochemical traits like proline content, gluten content, protein synthesis and enzymatic activity involved in various metabolic processes [11–14]. Salinity stress disturbs the ionic balance due to the accumulation of  $\text{Na}^+$  which reduces the mineral uptake and their translocation to grains [15, 16]. Salt stress also causes the production of reactive oxygen species which hampers plant growth and development [13, 17]. Wheat grain yield reduces greatly when soil pH or electrical conductivity reaches 8.5 or 4  $\text{dS m}^{-1}$ . Salt stress creates a water deficit which makes it difficult for roots to draw water from their surroundings [18, 19]. Early-stage exposure to salt causes osmotic stress, which adversely affects the normal cell metabolism, stomatal opening and transpiration process. Long-term stress leads to ionic stress due to a high concentration of NaCl. Ionic stress causes chlorosis and necrosis of leaves and reduces photosynthesis and protein synthesis [20]. Irrigated water with the salt content of 2–3  $\text{g L}^{-1}$  or 3–5  $\text{g L}^{-1}$  reduces the grain yield of wheat by 7–13% or 13–24%, respectively [21]. To cope with these adverse effects of salt stress, plants use different mechanisms such as the exclusion of sodium ions and increase in potassium concentration, maintenance of high  $\text{K}^+/\text{Na}^+$  ratio, increased stomatal conductance and transpiration efficiency, osmotic adjustment and antioxidant defence [22–24]. Therefore, knowledge and understanding of the physiological and biochemical mechanisms are very essential for selecting and developing salt-tolerant wheat genotypes. Moreover, an integrated approach of conventional and molecular breeding can be used to improve wheat productivity and under salinity stress. Therefore, the present chapter summarizes the negative effect of salt stress, tolerance mechanism and potential breeding methods to improve the resilience in wheat.

## 2. Effect of salt stress in wheat

### 2.1 Germination

Germination is the basic and dynamic process that determines the further growth and development of plants. The seed germination process may be divided into three distinct phases. Phase one initiates with imbibition of water by dry seed, phase two causes activation of enzymatic activity and metabolic processes and phase three is a post-germination phase that includes rupturing of endosperm and radicle elongation followed by seedling establishment [25–27]. Salt stress lowers the osmotic potential of the germination medium which disrupts the normal functioning of the enzyme responsible for protein metabolism, deteriorates seed food reserves and ultimately grain yield [28]. These consequences together cause inhibition of cell expansion and cell division. Besides enzymatic imbalance, seed dormancy, hard seed coat, seed vigor and viability, temperature, moisture content and light intensity also affects the seed germination [29]. Previous studies reported that the accumulation of mucilage, callose, lignin and suberin increase the seed dormancy by limiting the permeability of water and diffusion of oxygen through the seed coat, delaying the germination process [30, 31]. Delayed and decreased germination of the wheat seed was reported at 12.5  $\text{dS m}^{-1}$  salinity level [32]. Germination percentage in wheat also depends on the type of wheat i.e. spring or winter or differences in the cultivar. For example, wheat variety Kharchia 65 was found more salt-tolerant than KRL 1–9 due to its high chlorophyll content, membrane stability

and relative water content. Significant variation in wheat cultivars was observed for percent germination, rate of germination and germination index [33, 34]. Cultivar Shakha 93 and Shakah 94 were found positive while Masr 1 was negative for most of the germination traits under salt stress condition [35]. Similarly, Charushahi et al. [36] observed complete inhibition of germination at a high salinity rate due to limited uptake of water. High salt tolerance of Al-Hussein variety at germination stage was due to high tolerance index and chlorophyll stability at different salt concentration [37].

## 2.2 Plant growth

Salt stress severely affects wheat growth at both the vegetative and reproductive stages. Further, salt stress at the seedling stage may cause seedling chlorosis, necrosis or even death [38]. Early maturity under salt stress reduces the plumule length, leaf area and plant height [39]. Moreover, reduction in leaf size, number of leaves, root colonization, leaf expansion and dry matter of shoot were also noticed in wheat [40, 41]. The root is the first and most important organ of plants which is essential for the uptake of water and nutrient from the soil to maintain the growth and various developmental processes. Salinity inhibited growth of root and shoot dry weight, root length and diameter and root volume in wheat. Salinity reduces the root length and coleoptiles length and seedling establishment [42]. Otu et al. [43] reported a significant effect of increasing salinity level on root and shoot length, root fresh weight and elongation rate (**Figure 1**). A serious injuries effect in growth parameters of wheat like the relative growth rate of roots and leaves was seen under salt stress in



**Figure 1.** Effects of salinity stress on wheat morphological, physiological, biochemical traits and yield attributes.

comparison to normal condition [44]. Many earlier studies have reported a reduction in growth parameters like root and shoot length, seedling length, leaf area, the relative growth rate of root and shoot, fresh and dry weight of root and shoot, plant height and tillering capacity at different salinity levels [45–48] (Table 1).

Salinity level	Effects	References
5.40 and 10.60 dS m <sup>-1</sup>	Decreased chlorophyll, carotenoids and relative water content, reduced grain yield, increased hydrogen peroxides and thiobarbituric acid reactive substances	[33]
16 dS m <sup>-1</sup>	Reduction in grain filling duration and harvest index	[49]
6.85 and 12.3 dS m <sup>-1</sup>	Decreased relative water content, chlorophyll content, membrane stability index and increased hydrogen peroxide, SOD, ascorbate peroxidase (APOX) and GR	[50]
150 mM NaCl	Reduced stomatal conductance, potassium content and photosynthetic rate	[51]
0, 25, 50, 75, 100, 125, 150 mM NaCl	Decrease in root and shoot length, fresh and dry weight of roots and shoots, protein content and increase in proline content	[47]
150 and 300 mM NaCl	Increased hydrogen peroxide and lipid peroxidation, reduced glutathione and glutathione disulfide, glutathione S-transferase, decreased ascorbate content	[52]
100 and 200 mM NaCl	Declined leaf area, chlorophyll content, relative water content, grain yield, N, Fe, Mn and Mg content and increased Cu and Zn content.	[53]
150 mM NaCl	Reduced plant height, root length, shoot dry weight, glutathione (GSH), chlorophyll and carotenoid content, increased MDA, H <sub>2</sub> O <sub>2</sub> and superoxide radical.	[54]
10 mM NaCl	Reduced water potential, osmotic potential, relative water content, decreased N, P and K uptake, reduced grain yield	[55]
200 mmol L <sup>-1</sup> NaCl	Decreased net photosynthetic rate, stomatal conductance, maximum and actual photochemical efficiency of PSII and increase in intercellular CO <sub>2</sub> concentration.	[56]
10 dS m <sup>-1</sup>	Reduced membrane stability, increased MDA and hydrogen peroxide content	[57]
6.25 dS m <sup>-1</sup>	Increase in lipid peroxidation, lipoxygenase enzyme activity, H <sub>2</sub> O <sub>2</sub> content, decrease in fresh and dry weight of shoots	[58]
100 mM NaCl	increase in NADPH oxidase activity, H <sub>2</sub> O <sub>2</sub> and proline content in roots	[59]
250 mM NaCl	Increase lipid peroxidation, hydrogen peroxide and proline content, decreased relative water and chlorophyll content	[60]
0.23, 3.0, 6.0 and 12.0 dS m <sup>-1</sup>	Reduced carbon fixation, chlorophyll content, leaf area, plant height, number of vascular bundles, phloem tissue thickness and pith cavity	[61]
50, 100, and 200 mM NaCl	Decrease in level of catechin hydrate, quercetin, and benzoic acid, reduced shoot and root length, increase in epicatechin levels	[62]
50, 100, and 200 mM NaCl	Reduction in germination %, root and shoot length, total chlorophyll content and increase in MDA content	[7]
6.0 and 10.0 dS m <sup>-1</sup>	Reduced K content in roots and shoots, relative water and chlorophyll content	[8]
0, 100, and 200 mol/L NaCl	Increased Na <sup>+</sup> concentration, decreased K <sup>+</sup> concentration, decreased chlorophyll fluorescence, chlorophyll content, shoot and root length	[48]

**Table 1.**  
*Effect of salt stress on physiological, biochemical and yield attributes.*



## 2.3 Photosynthesis

Salinity stress has severed effect of various physiological processes such as respiration, membrane stability, ion toxicity and photosynthesis. The photosynthesis process involves photosynthetic apparatus, PS-I and PS-II, electron transport chain, carbon dioxide reduction pathways. Any damage at any stage leads to a reduction in the photosynthetic efficiency of a crop plant [63]. Salinity stress greatly reduces the amount of photosynthetic pigments at different salt concentrations and it was found more in salt-sensitive genotypes than tolerant. This decreased pigment content may be a due accumulation of ions in chloroplast and the high activity of chlorophyllase enzyme [64, 65]. At the vegetative stage, salt stress affects the carbohydrate synthesis while its translocation to grains during the grain filling stage [66]. Sodium chloride treatment decreases the stomatal conductance, CO<sub>2</sub> uptake required for carboxylation reaction and activity of RUBISCO (**Figure 1**) which ultimately reduces the photosynthetic efficiency [67]. Kafi [68] observed varied responses of wheat genotypes depending upon the growth stage, the concentration of salt and period of salt exposure. Stomatal conductance and reduced variable to maximum fluorescence were found major limiting factors affecting photosynthesis under salt stress. The toxic concentration of Na<sup>+</sup> and Cl<sup>-</sup> in leaves, decreases the photosynthetic rate by disrupting the chlorophyll structure and PS-II [69]. Furthermore, reduced stomatal conductance decreases the electron transport chain efficiency, which results a decline in adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH) consumption in the photosynthesis process and ultimately in quantum yield of PS-II (**Table 1**). The reduction in PS-II quantum yield was more in salt-sensitive genotypes under salinity condition [70]. All the physiological and biochemical processes are depending upon the accessibility of water. High salt concentration osmotic and ionic stress which lowers the water potential of wheat plants [71]. Relative water content reduced 3.5% intolerance while 6.7% in sensitive genotypes of wheat after six days of salt stress resulted a drastic decline in water use efficiency [72, 73]. In general, water stress at heading and after the anthesis stage significantly affects the productivity of wheat [74]. Salt sensitive wheat variety HD 2687 showed a higher decrease in chlorophyll content, membrane stability and relative water content under stress compared to Kharchia 65 indicating their salt-tolerant nature [50].

## 2.4 Mineral uptake

One of the most severe effects of salinity stress is the accumulation of Na<sup>+</sup> content in leaves over the control condition. A high concentration of Na<sup>+</sup> and Cl<sup>-</sup> ions in root zone reduces the uptake of essential cationic and anionic nutrients like calcium (Ca<sup>2+</sup>), potassium (K<sup>+</sup>) and nitrate (NO<sub>3</sub><sup>-</sup>) and decreases the amount of calcium, potassium, phosphorus and magnesium (**Figure 1**) in different plant parts [75, 76]. However, the differential response was seen for Na<sup>+</sup> concentration in winter and spring wheat. Winter-type wheat cultivars accumulate high Na<sup>+</sup> than spring type. Salt tolerant genotypes have the better ability to maintain more K<sup>+</sup> and K<sup>+</sup>/Na<sup>+</sup> ratios and accumulate less Na<sup>+</sup> in their leaves [77, 78]. The findings of Hussain et al. [55] showed that the grain yield and tolerance power of wheat can be increased by enhancing Na<sup>+</sup>/H<sup>+</sup> type antiporter. These antiporters are responsible for the transition of Na<sup>+</sup> from the cytoplasm to apoplast [79]. Moreover, tolerant genotypes have two pore K<sup>+</sup> channels and one selective cation channel for K permeability [80]. Reduced plant growth under salt stress may be due to the high plasma membrane injury due to Na<sup>+</sup> toxicity [48, 81]. Poor membrane stability due to the replacement of Ca<sup>2+</sup> by Na<sup>+</sup> causes the

influx of heavy metals [82] like  $Zn^{2+}$  and  $Cu^{2+}$ . Iron and manganese content were drastically reduced under salinity stress; however, this reduction was lesser in tolerant genotypes (**Table 1**). Salt sensitive cultivars like HD 2687 and WL 711 showed a significant reduction in magnesium, nitrogen, iron, manganese and an increase in zinc and copper. Kharchia 65 gave good performance due to its better nutrient uptake capacity and ion partitioning [53]. Shaaban and El-Nour [83] also reported a significant reduction in nitrogen, potassium, phosphorus, calcium, magnesium, iron, manganese concentration and uptake; this may be due to the increase in osmotic pressure of root when irrigated with saline water.

## 2.5 Grain yield

Grain yield in wheat depends on several agronomic and physiological traits such as tillers number, earhead length, size and number of grains, root and shoot length, chlorophyll content, membrane stability and stomatal conductance. Reduction in any of the above-mentioned traits in salt condition directly affect the grain yield of wheat. However, the percent reduction in grain yield depends on the salt concentration and tolerance power of genotypes. Hussain et al. [84] reported significant differences among the 40 genotypes of wheat under salt stress. The sensitive genotypes had fewer yields than tolerant genotypes mainly due to decreased size and number of grains and reduced tillering capacity. The tolerant genotypes produce more productive tillers, the high number of fertile spikelets and have a better capacity of photo-assimilates translocation to developing grains. Less availability of photosynthates and their translocation from source to sink (**Figure 1**) is the main reason for lower grain yield in sensitive genotypes [85, 86]. Salt stress reduced the thousand kernel weight by 20% and starch content of grains by 6% in wheat compared to control condition [87, 88]. Wheat plants grown at high salinity level  $10 \text{ dSm}^{-1}$  significantly reduced the spike length by 24%, the number of spikelets by 21%, thousand-grain weight by 70%, straw yield by 20% and grain yield by 67% [89] (**Table 1**). A number of previous studies also reported a significant decline in wheat grain yield with increasing levels of salinity [90–93]. Reduced grain yield under salt stress may be due to low germination percentage and small size and number of medium and small veins in leaves of wheat [94, 95]. As far as the wheat quality is concerned, carbohydrates, proteins, fibers and gluten index in grains declined significantly under salt stress [96]. Salt stress at the grain maturation stage promotes leaf senescence due to which protein deposition takes place in grains over starch [66]. A high reduction in protein content of wheat was observed in wheat than triticale [97].

## 3. Mechanism of salt stress tolerance

### 3.1 Ion homeostasis

Salinity stress causes an ionic imbalance in wheat by affecting the  $Na^+$  and  $K^+$  concentrations in different plant tissues. A high concentration of  $Na^+$  disturbs the uptake of nutrients like  $K^+$  and  $Ca^{2+}$  causing lesions on different plant parts with declined leaf dry weight and shoot growth. Furthermore, high concentrations of  $Cl^-$  disturb the nutrient uptake by impairing anion uptake. Antagonistic effect of  $Cl^-$  has been observed with nitrate and phosphate [98, 99] causing a reduction in wheat growth and yield. Under salt stress,  $Na^+$  is the major cause of both ionic and osmotic stress. Thus, maintaining ionic homeostasis is very essential for plant growth and

development under salinity stress. Plants maintain the ionic balance of  $\text{Na}^+$  and  $\text{Cl}^-$  inside the cell by removing excess salts via primary and secondary transport systems and their compartmentalization into vacuole [100].  $\text{Na}^+$  exclusion in plants can be achieved by different ion channels and transporters present in the cell membrane. Apart from being an essential micronutrient, K plays an important role in maintaining a low  $\text{Na}^+$  to  $\text{K}^+$  ratio. Previous studies in wheat reported a positive association of low  $\text{Na}^+$  concentration in leaves with salt tolerance. Yadav et al. [93] reported that salt stress tolerance in wheat was associated with a high  $\text{K}^+$  to  $\text{Na}^+$  ratio in roots and shoots. Low  $\text{K}^+$  to  $\text{Na}^+$  ratio in the upper leaves of wheat reduces the plant growth. The high affinity potassium transporter (HKT) gene family plays a major role in  $\text{Na}^+$  exclusion via minimizing the entry of  $\text{Na}^+$  into the roots from the soil [101]. The *Nax 1* and *Nax 2* genes belonging to the HKT gene family were initially identified in durum wheat. These genes exclude the  $\text{Na}^+$  from xylem tissues and maintain its low concentration in the leaves. The *Nax* genes have already been utilized in the breeding program for developing the salt-tolerant genotypes in durum and hexaploid wheat. The presence of the *Nax 2* gene in the durum wheat variety produced 25% more grain yield under salt stress conditions. While the presence of both *Nax 1* and *Nax 2* in bread wheat reduces  $\text{Na}^+$  concentration by 60% in leaves [102]. Salt tolerance in wheat genotypes can be achieved by down-regulation of *TaHKT 2* gene [103].

### 3.2 Osmotic protection

Osmotic stress due to high salt concentration reduces the water uptake, cell expansion in roots, growth and development of plants. Likewise, the accumulation of high Na in leaves affects the photosynthesis process which results in leaf chlorosis and necrosis [104]. Osmoprotectants such as sugars e.g. trehalose, sucrose and fructose, amino acids e.g. proline and pipercolic acid, quaternary ammonium compounds e.g. glycine betaine, pipercolate betaine, alanine betaine and hydroxyl pro betaine, polyols e.g. mannitol, sorbitol and inositol and polyamines e.g. spermidine, putrescine and spermine [105] acts as a defensive mechanism in plants by lowering the cell water potential, detoxifying reactive oxygen species, activating anti-oxidants activity and stabilizing normal structures of proteins and enzymes [106–108]. Production of compatible osmolytes in wheat plays an important role in providing tolerance against salt injury. Accumulation of glycine betaine in transgenic lines of wheat improves the salt tolerance by protecting the photosystem II reaction centers and oxygen-evolving complex thus enhancing the photosynthetic activity [109]. Salinity stress disrupts the function of the thylakoid membrane which affects the photosynthesis process and ultimately grain yield of wheat. Glycine betaine improves salt tolerance by maintaining ionic balance, increasing osmotic adjustment and neutralizing ROS [110]. Wheat seedlings treated with showed a diminished level of malondialdehyde and an enhanced level of glutathione under salt stress [111]. Exogenous application of glycine betaine increased the activities of antioxidants such as CAT and POD to neutralize ROS damage in wheat [112]. Similarly, proline is the well-known osmolytes produced under salt stress condition [113]. Proline accumulation in wheat generally found in the cytoplasm where it acts as a shield against salt injury. Exogenous application of proline significantly enhanced the root length, seedling fresh and dry weight, photosynthetic pigments and  $\text{K}^+/\text{Na}^+$  ratio and thus efficiently sustains the wheat growth under salt stress [114, 115]. Proline acts as defending agents for electron transport chain and RIBISCO enzyme from salt stress damage and increases the  $\text{CO}_2$  assimilation rate, chlorophyll content and photosynthetic rate [116]. The sugars help



in the regulation and stabilization of the native structure of proteins and enzymes which enables their normal functioning. These sugars may contribute up to 50% of osmoregulation in leaves of glycophytes. It is reported that galactose plays a major role in ascorbic acid pathways and enhances salt tolerance in wheat [117].

### 3.3 Antioxidants

Salinity stress disrupts the availability of CO<sub>2</sub> in leaves and electron transport chain in mitochondria and chloroplast due to which reactive oxygen species like singlet of oxygen (<sup>1</sup>O<sub>2</sub>), superoxide radicle (O<sub>2</sub><sup>-</sup>), hydroxyl radicle (OH<sup>-</sup>) and hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) are produced [118, 119]. Accumulation of these ROS at high concentrations is extremely harmful to plants. Chloroplast, mitochondria and peroxisomes are the primary site of ROS production. Photosystem I and II in chloroplasts, respiratory complex I and III in mitochondria and glycolate oxidase in peroxisomes are the major source of ROS generation [120–123]. ROS cause protein oxidation, lipid peroxidation, damage to nucleic acid, inhibition of enzyme activity and programmed cell death [124]. Lipid peroxidation is caused by the oxidative burst of the cell membrane which can be estimated by the content of malondialdehyde (MDA). Lipid peroxidation increases electrolyte leakage, disturbs membrane permeability and activates the oxidation of protein and DNA. Up to 73% increase in MDA content at 300 mM and 35% increase at 100 mM have been observed when wheat plants exposed to salinity stress [52]. Plants have the natural defense system antioxidant to detoxify the harmful effect of ROS. The enzymatic antioxidants are catalase (CAT), superoxide dismutase (SOD), peroxidase (POX), ascorbate peroxidase (APX), glutathione reductase (GR), glutathione peroxidases (GPX), dehydro-ascorbate reductase (DHAR) and mono-dehydro-ascorbate reductase (MDHAR) while non-enzymic antioxidants are glutathione (GSH), ascorbate (AsA), tocopherol and carotenoids [124, 125]. Sairam et al. [33] reported an increased concentration of catalase in both salt-tolerant and sensitive cultivars of wheat. Mandhania et al. [126] observed enhanced activity of SOD and CAT in wheat which detoxify H<sub>2</sub>O<sub>2</sub> and break it down as H<sub>2</sub>O and O<sub>2</sub> under salt stress. Tolerant wheat genotypes produced a high concentration of AsA and catalase to counter the effect of salinity in comparison to sensitive genotypes [45]. Likewise, exogenous applications of ferulic acid, caffeic acid and sinapic acid up-regulate the CAT and POX activity in stresses plant of tolerant genotypes. These phenolic acids decrease the H<sub>2</sub>O<sub>2</sub> and MDA content in roots and shoots of both sensitive (cv. HD 2329) and tolerant (cv. Kharchia local) cultivars [57].

## 4. Approaches for salt stress tolerance

### 4.1 Conventional breeding

Genetic improvement for grain yield, quality traits, biotic stress and abiotic stress including salinity stress are the major breeding objective in wheat. Different methods such as screening of genotypes, pedigree method, hybridization, genetic transformation and marker-assisted breeding have been used in for increasing salt tolerance in wheat. Target breeding for salt stress is mainly done in India and Pakistan. The salt-tolerant genotypes in India are KRL 19, KRL 1–4, KRL 210, KRL 213 and KRL 283 developed by Central Soil Salinity Research Institute, Karnal (India). Almost all the tolerant genotypes in India are developed using Kharchia 65 as donor parent.

Kharchia 65 is collected from Kharchi in Pali district of Rajasthan possessing very high salinity and sodicity tolerance. KRL 1–4 developed in 1990 using the pedigree method from a cross between Kharchia 65 and WL 711 [127]. KRL 19 (PBW 255/KRL 1–4) which can tolerate salinity up to EC 5–7 dSm<sup>-1</sup> was released in 2000. It has yield potential in saline soil is 2.5–3.5 ton ha<sup>-1</sup>. KRL 210 (PBW 65/2\*Pastor) and KRL 213 (Cndo/r143//Ente/Mexi-2/3 *Aegilops squarrosa* (taus)/4/Weaver/5/2\*Kauz) were released in 2010 with yield potential 3.0–5.0 ton ha<sup>-1</sup>. KRL 283 (CPAN 3004/Kharchia 65//PBW 343) was released in 2018 using bulk selection method [128] with yield potential up to 41 q ha<sup>-1</sup>. Apart from the released variety, genetic stock of salt-tolerant wheat lines i.e. KRL 35, KRL 99 and KRL 3–4 have been registered with NBPGR. Similarly, two varieties LU26S and SARC-1 were developed in Pakistan by Saline Agriculture Research Cell (SARC) at Faisalabad and one variety Sakha 8 was developed in Egypt by Agricultural Research Centre at Giza [128]. KTDH a double haploid line with good Na<sup>+</sup> exclusion ability was a product of a cross between Kharchia 65 with TW161. This line matured early and performed average under saline conditions of Spain [129].

## 4.2 Molecular breeding

Salt stress is a major constraint in wheat production and productivity worldwide. Salt stress causes the accumulation of Na<sup>+</sup>, Cl<sup>-</sup> ions and reactive oxygen species which disrupts the nutrient uptake, hormonal balance leads to a reduction in growth and development of wheat plants. Salt stress tolerance is a polygenic trait governed by multiple QTLs and interaction effects. Understanding the inheritance pattern of salt tolerance is the major step in developing the improved genotypes for salinity stress. Identification of QTLs with major effects helps in marker-assisted selection of salt-tolerant wheat genotypes. Several QTLs associated with salt tolerance-related traits have been mapped in wheat. A major QTL for salt tolerance was identified on linkage group 4DL controlling K/Na ratio in wheat [130]. To enhance the salt tolerance capacity, two major Na<sup>+</sup> exclusion genes *Nax 1* and *Nax 2* have been introgressed into durum wheat from *Triticum monococcum* [131, 132]. Genetic analysis mapped *Nax 1* and *Nax 2* locus on the long arm of linkage group 2A and 5A, respectively. Both of the genes were also introgressed into *Triticum aestivum* cv. Westonia from durum wheat and showed reduced Na<sup>+</sup> concentration in leaves [133]. In a RIL mapping population between Pasban 90 x Frontana, a total 60 QTLs for various physiological traits related to salinity tolerance has been identified on linkage group 1B, 1D, 2A, 2B, 2D, 3A, 3B, 3D, 4A, 4B, 4D, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7B and 7D. Out of these, one for chlorophyll a, three for proline content, four each for osmotic potential, superoxide dismutase, chloride content, five each for relative water content and water potential, six for membrane stability index, seven for total chlorophyll and eight for chlorophyll b [134]. Low Na<sup>+</sup> and high K<sup>+</sup> content in leaves is an important cellular mechanism that help the plant to withstand under salt stress condition [73, 135]. For Na content, 3 QTLs were identified by Amin and Diab [136], one by Asif et al. [137], eight by Devi et al. [138], six by Hussain et al. [104], five by Ilyas et al. [134], one by Lindsay et al. [139], four by Masoudi et al. [140] and six by Xu et al. [141]; for K content, four QTLs were detected by Amin and Diab [136], two by Devi et al. [138], five by Hussain et al. [104], four by Ilyas et al. [134], ten by Masoudi et al. [140], and eight by Xu et al. [141]; for K/Na ratio six QTLs were mapped by Amin and Diab [136], two by Asif et al. [137], four by Ilyas et al. [134], twelve by Masoudi et al. [140] and three by Xu et al. [141] (**Table 2**).

Traits	Gen	No. of QTLs	Linkage group	References
Na conc.	DH	3	2B, 4B, 5D	[136]
K conc.		4	2B, 2D, 3D, 5D	
K/Na ratio		6	2B, 2D, 3B, 4A, 5B, 7A	
Growth rate		5	1A, 2A, 2B, 3A, 4A	
Leaf fresh weight		5	3A, 3B, 4B, 5B, 5D	
Leaf dry weight		3	1D, 4B, 5D	
Water content		2	3D, 5B	
No. of spikes/plant		5	2B, 4B, 5B, 7D	
No. of spikelets/spike		6	1D, 2B, 3B, 4B, 5B, 7D	
No. of grains/plant		5	1B, 1D, 2B, 3B, 5D	
Grain weight/plant		5	1D, 2B, 3B, 3D, 5B	
Total dry weight		6	1D, 2A, 3A, 4B, 5D	
Shoot growth	RILs	3	5A, 7B	[137]
Na accumulation		1	2A	
Chloride accumulation		3	1A, 2A, 3A	
K/Na ratio		2	2B, 2D	
Germination %	RILs	5	2A, 2B, 4A, 6D, 7B	[142]
Germination index		5	2A, 2B, 4A, 6D, 7B	
Seedling vigor index		5	2A, 2B, 4A, 6D, 7B	
Root length		12	1B, 2A, 2D, 3B, 3D, 4D, 5A, 5B, 6A, 6B, 6D	
Shoot length		5	2D, 3D, 5D, 6D, 7B	
Seedling fresh weight		7	1D, 2A, 2D, 3B, 3D, 6A, 6B	
Seedling dry weight		5	1B, 2B, 5B, 5D, 6A	
Sodium content	RILs	8	1B, 2D, 5D, 6A, 7D	[138]
Potassium content		2	1B, 2D	
Proline content		3	2D	
Plant height		6	2D, 6A	
Length of ear head		3	5D, 6A, 6B	
Thousand-grain weight		3	2D	
Grain yield		4	1A, 2D, 6A, 7D	
Tiller number per plant		3	2D, 4D, 6A	
Number of earhead		1	4D	
Days to heading		2	2D	
Days to anthesis		1	2D	

Traits	Gen	No. of QTLs	Linkage group	References
Shoot height	RILs	8	1D, 2B, 3A, 3B, 5B	[143]
Shoot fresh weight		11	1A, 1D, 2A, 3B, 4B, 5B, 6B	
Shoot dry weight		5	1A, 3B, 6A, 6B	
Chlorophyll content		7	2B, 5A, 6B, 7B, 7D	
Root boron conc.	F2	3	2A, 2B, 3D	[104]
Root calcium conc.		3	3B, 6B	
Root copper conc.		2	1D, 7B	
Root iron conc.		3	2A, 6A, 6B	
Root potassium conc.		3	2A, 4B, 3D	
Root magnesium conc.		1	5A	
Root manganese conc.		3	2A, 6B	
Root sodium conc.		3	2A, 6A, 7A	
Root phosphorus conc.		1	7B	
Root sulfur conc.		5	2A, 3B, 6B, 7B	
Root zinc conc.		3	2A, 6A, 7A	
Shoot boron conc.		3	3B	
Shoot calcium conc.		2	6A, 6B	
Shoot potassium conc.		2	2A, 6A	
Shoot magnesium conc.		2	2A, 6B	
Shoot manganese conc.		1	4B	
Shoot sodium conc.		3	2A, 7A	
Shoot phosphorus conc.		2	4B, 1D	
Shoot sulfur conc.		3	1A, 2A, 4B	
Shoot zinc conc.		1	7B	
Relative water content	RIL	5	2A, 4A, 7A, 7B	[134]
Membrane stability index		6	3A, 3D, 4A 5B, 7B, 7D	
Water potential		5	2A, 5B, 5D, 6A, 6B	
Osmotic potential		4	2B, 5D, 7A, 7B	
Total chlorophyll		7	1B, 3D, 5B, 6A, 6B, 6D, 7D	
Chlorophyll a		1	7D	
Chlorophyll b		8	1D, 3A, 3B, 4A, 6B, 7A, 7B	
Proline content		3	1B, 4B, 7A	
Superoxide dismutase		4	1B, 1D, 2A, 6D	
Sodium content		5	1D, 2A, 2B, 3B, 6B	
Potassium content		4	2B, 4A, 5A, 6A	
Chloride content		4	1D, 2B, 3B, 7A	
Na/K		4	1D, 2D, 3A, 4D	
Sodium exclusion	F2	1	2A	[139]



Traits	Gen	No. of QTLs	Linkage group	References
Salt tolerance index	RIL	3	3A, 4D, 5A	[144]
Fresh weight of radicle		1	4D	
Dry weight of radicle		3	3A, 3B, 7A	
Fresh weight of plumule		2	3A, 3B	
Dry weight of plumule		1	4D	
Salt injury index		5	3A, 5B, 6B, 6D	
Root fresh weight index		2	4A, 6D	
Shoot fresh weight		6	2A, 2B, 3B, 3D, 4A	
Plant fresh weight index		5	3B, 3D, 4A, 7B	
Root dry weight index		2	3D, 6D	
Shoot dry weight index		2	1A, 3B	
Plant dry weight index		5	2A, 3B	
Root/shoot length ratio		8	1A, 2A, 2D, 3A, 3D, 6A, 6D	
Chlorophyll content		2	3D, 7A	
Shoot height	RIL	7	1A, 1B, 4A, 4B, 6B, 7B	[140]
Shoot fresh weight		9	1A, 1B, 3A, 3B, 6B	
Shoot dry weight		7	1A, 1B, 3A, 3B, 7B	
Chlorophyll content		6	1B, 1D, 3B, 6A, 6B, 7B	
Salt injury index		5	1B, 3B, 6A, 6B	
Shoot Na <sup>+</sup> conc		3	1B, 3B, 5A	
Shoot K <sup>+</sup> conc		3	2A, 2B	
Shoot Na <sup>+</sup> /K <sup>+</sup>		6	1B, 2D, 3A, 3B, 5A	
Root Na <sup>+</sup> conc		1	7A	
Root K <sup>+</sup> conc		7	1A, 2B, 3B, 3A, 4A	
Root Na <sup>+</sup> /K <sup>+</sup>		6	1A, 2B, 3A, 3B, 7D	
Na <sup>+</sup> translocation from roots to shoots		3	1B, 2B, 3B	
K <sup>+</sup> translocation from roots to shoots		2	4A	
Maximal root length	RIL	4	1B, 5A, 6A, 7B	[141]
Shoot height		3	4A, 4B, 5A	
Root dry weight		3	2D, 3B, 5A	
Shoot dry weight		1	2A	
Total dry weight		2	2A, 2D	
Chlorophyll content		1	5B	
Root K <sup>+</sup> conc		4	1D, 5A, 5B	
Root Na <sup>+</sup> conc		2	2B, 3B	
Root K <sup>+</sup> /Na <sup>+</sup> concentration		3	4B, 5B, 7D	
Shoot K <sup>+</sup> conc		4	2B, 3B, 4B, 6A	
Shoot Na <sup>+</sup> conc		2	5A, 7A	

**Table 2.**  
QTLs associated with salt tolerance related traits in wheat.

### 4.3 Salt-tolerant genes

One of the approaches to improve salinity tolerance is the identification of genes playing a significant role in the tolerance mechanism. Till now massive information about tolerant genes, transcription factors that are either up-regulated or down-regulated have been identified using genomic or transcriptomics approaches. There is increasing evidence for the involvement of dehydrin and expansion proteins, transcription factors like TaSRG, TaMYB2A, TaNAC29, TdERF1 and Sodium antiporter, transporters and vacuolar pyrophosphatase in the salt stress response in wheat [145–147]. Some of the examples of salt-responsive genes are listed in **Table 3**.

Gene	Protein	Function	References
DHN-5	Dehydrin	Higher seed germination and growth rate, high proline contents, and lower water loss	[148]
TNHX1 and TVP1	Sodium antiporter and vacuolar pyrophosphatase	High relative water and K <sup>+</sup> content,	[149, 150]
TaSTRG		Higher fresh weight, chlorophyll content, proline and soluble sugar contents	[151]
TaMYB2A	Transcription factor	High membrane stability, water retention capacity, high photosynthetic efficiency	[145]
TmHKT1;4-A2 and TmHKT1;5-A	Na <sup>+</sup> transporters	TmHKT1;4-A2 excludes Na <sup>+</sup> from the xylem in roots and leaf sheaths; mHKT1;5-A excludes Na <sup>+</sup> from the xylem only in the roots	[152]
TaSC	Calcium-dependent protein kinase	High germination rate, seedling length, K <sup>+</sup> /Na <sup>+</sup> ratio and proline content	[153]
TaEXPB23	Expansins	Root elongation, improved water retention ability reduced osmotic potential	[154]
TaERF3	Ethylene-response factor	Accumulation of proline and chlorophyll increased while and H <sub>2</sub> O <sub>2</sub> content decreased	[146]
TaNAC29		TaNAC29 enhance salt tolerance by reducing H <sub>2</sub> O <sub>2</sub> production, membrane damage and by enhancing the antioxidant (SOD, POD, APX and CAT) activity	[155]
TdERF1	Ethylene-response factor	Maintain high membrane stability, and soluble sugar content	[147]
TNHXS1 and TVP1	Sodium antiporter and vacuolar pyrophosphatase	Higher biomass, chlorophyll content and catalase (CAT) activity, more K <sup>+</sup> and less Na <sup>+</sup> content	[155]
TMKP1	Mitogen-activated protein kinase phosphatases	Increased antioxidants activities, namely SOD, CAT and peroxidase, reduced MDA and H <sub>2</sub> O <sub>2</sub>	[156]
TaPUB1	Ubiquitin-protein ligase	higher germination rate, less reduction in chlorophyll, higher photosynthetic capacity and antioxidants activity and lower Na <sup>+</sup> /K <sup>+</sup> ratio	[88]
TaEXPA2	Expansin proteins	higher germination rates, longer root length, more lateral roots, higher survival rates and more green leaves, lower Na <sup>+</sup> but higher K <sup>+</sup>	[157]

**Table 3.**  
*Genes conferring salt tolerance in wheat.*

These transcription factors can change the gene expression by specific binding in the promoter region of a large number of genes. Rong et al. [146] characterized the function of ethylene response factor TaERF3 and observed that overexpression of TaERF3 improved the salt and drought tolerance in wheat. Electrophoretic mobility shift assay showed that TaERF3 protein interacted with the GCC-box present in the promoters of seven TaERF3-activated stress-related genes, suggesting that TaERF3 positively regulated wheat adaptation responses to salt and drought stress through the activation of stress-related genes. Similarly, Up-regulation of bZIP genes was found insensitive and down-regulation in tolerant cultivar of wheat under salinity stress [158]. Overexpression of TaEXPA2 an  $\alpha$ -expansin gene of wheat provides salt tolerance in transgenic lines of tobacco. The enhanced salt tolerance was associated with improved relative water content, selective ion absorption and increased antioxidant activity. Moreover, ABA signaling positively participated in regulating the TaEXPA2-enhanced salt stress tolerance but how ABA participates in regulating salt stress tolerance needs to be studied further [157].

### Author details


Hari Kesh<sup>1</sup>, Sunita Devi<sup>1</sup>, Naresh Kumar<sup>1</sup>, Ashwani Kumar<sup>1\*</sup>, Arvind Kumar<sup>1</sup>, Pooja Dhansu<sup>2</sup>, Parvender Sheoran<sup>1</sup> and Anita Mann<sup>1</sup>

1 ICAR – Central Soil Salinity Research Institute, Karnal, India

2 ICAR – Sugarcane Breeding Research Institute, Regional Center, Karnal, India

\*Address all correspondence to: ashwani.kumar1@icar.gov.in

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