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REVIEW

Salinity Stress in Wheat: Effects, Mechanisms and Management Strategies

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ABSTRACT

Salinity stress is a major threat to global food production and its intensity is continuously increasing because of anthropogenic activities. Wheat is a staple food and a source of carbohydrates and calories for the majority of people across the globe. However, wheat productivity is adversely affected by salt stress, which is associated with a reduction in germination, growth, altered reproductive behavior and enzymatic activity, disrupted photosynthesis, hormonal imbalance, oxidative stress, and yield reductions. Thus, a better understanding of wheat (plant) behavior to salinity stress has essential implications to devise counter and alleviation measures to cope with salt stress. Different approaches including the selection of suitable cultivars, conventional breeding, and molecular techniques can be used for facing salt stress tolerance. However, these techniques are tedious, costly, and labor-intensive. Management practices are still helpful to improve the wheat performance under salinity stress. Use of arbuscular mycorrhizal fungi, plant growth-promoting rhizobacteria, and exogenous application of phytohormones, seed priming, and nutrient management are important tools to improve wheat performance under salinity stress. In this paper, we discussed the effect of salinity stress on the wheat crop, possible mechanisms to deal with salinity stress, and management options to improve wheat performance under salinity conditions.

KEYWORDS

Breeding techniques; oxidative stress; photosynthesis; phyto-hormones; salinity stress; wheat

1 Introduction

Globally, more than 20% of soils are salt-affected and the extent of these soils is continuously increasing owing to anthropogenic activities and climate change [1,2]. Abiotic stresses are considered to be responsible for a 50% reduction in crop production, imposing a serious threat to global food security [3,4]. As a result of the rapid increase in the global population, food production has to be increased by 70% by the end of 2050 [5]. Wheat is the important food crop which ranks first in the global grain production. It is the staple food for more than 36% of the world's population, and it provides 20% of the calories and 55% of the carbohydrates globally [6,7]. Moreover, wheat is also an important source of micro and macronutrients which are necessary for human health [8–10].

The productivity of wheat crops is negatively affected by salinity stress [11,12]. Wheat crop yield starts to decline at a salinity stress level of 6–8 dS m^{-1} [13]. According to Food and Agriculture Organization (FAO), 397 million hectares under wheat cultivation are severely affected by salinity stress, which is imposing a serious threat to food security [14]. Salinity stress causes ion toxicity and nutritional imbalance in plants, which disrupts the plant physiological processes, and consequently cause a serious reduction in final yield [15–17]. Initially, salinity stress causes a significant reduction in seed germination, and later it alters growth and reproductive behavior causing serious yield losses [18–20]. Moreover, salt stress disturbs the enzymatic activities, photosynthesis, membrane structure, hormonal balance, water, and nutrient uptake, and induces oxidative stress [21–23].

Salinity stress is a polygenic character, which is regulated by multiple genes. Exclusion of Na^+ and retention of K^+, maintenance of an optimum K^+/Na^+ ratio, osmotic adjustment, and enhanced activities of antioxidant system are vital for plants under salinity stress [24,25]. Various techniques including the introduction of desirable genes, selection of suitable genotypes [26–28], screening of genotypes, and conventional breeding techniques have been used across the globe to improve crop performance under salinity stress. However, these techniques are time consuming and costly. Under this scenario, the application of osmoprotectants, seed priming, nutrient management, and hormone application can offer promising results to manage salinity stress [6,29]. Therefore, in this review, we discussed the effect of salinity stress on the wheat crop, resistance mechanisms to salinity stress in wheat, and potential management options to enhance the resilience of wheat under such stress.

2 Effects of Salinity Stress

2.1 Effects of Salinity Stress on Wheat Germination, Growth and Yield

Germination has a key importance in the plant life cycle and it helps to determine the subsequent growth, development, and yield attributes. Salinity stress reduces seed germination and leads to a serious reduction in the final yield of the wheat crop (Fig. 1). Salt stress reduces osmotic potential, disrupts the normal functioning of enzymes necessary for metabolic activity [30], and reduced the final stand establishment and yield. Salt stress also reduces yield attributes including spikelets number, productive tillers, grain weight, and biomass yield. Plant seedlings are quite sensitive to stress conditions and seedling death also occurs due to salinity stress [31]. Root and shoot parameters are also negatively affected by salinity stress [32,33]. Guo et al. [34] observed a reduction in wheat growth under salinity stress compared to normal conditions Likewise, Zou et al. [35] observed a reduction in root and shoot lengths and their dry weight under salt stress (100 mM NaCl). Salinity stress remarkably decreases the yield of almost all the crops. However, yield reduction percentage may vary on salt-tolerant and sensitive varieties. Asgari et al. [36] examined the reduction in growth attributes of wheat which ultimately reduced wheat production. Chinnusamy et al. [37] observed a 7.1% yield reduction with each unit of increase in salinity up to 6 dSm^{-1}. Afzal et al. [38] noticed a significant reduction in seeds/spike, a thousand seed weight, and economic yield in both salt-sensitive and tolerant varieties of wheat. In conclusion, salinity stress negatively affects the metabolic processes for optimum germination; therefore, it results in a serious reduction in growth and final yield.

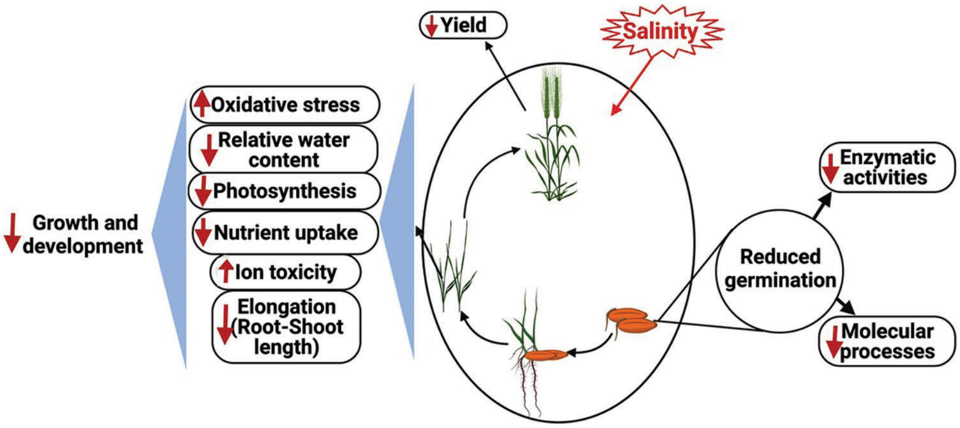

Figure 1: Effects of salinity stress on wheat crop. salinity stress reduced germination, photosynthesis, nutrient uptake, and relative water content, and induced ion toxicity and oxidative stress. therefore, it led to a reduction in growth and final yield

2.2 Effect of Salinity Stress on Photosynthesis, Plant Water Relations and, Mineral Uptake

A plant needs optimum photosynthetic activity for its survival, which is greatly influenced by environmental conditions [39]. Photosynthesis is inhibited by the accumulation of ions (Na^+ and Cl^-) in the chloroplast and a reduction in plant water potential (Fig. 2) due to high salt stress [30]. Guo et al. [34] studied the physiological aspects of wheat under saline conditions; they observed that salinity stress led to stomatal closure, induced less CO_2 absorption, and reduced transpiration rate. Furthermore, salinity stress (320 mM NaCl) significantly reduced the photosynthetic pigments in the chloroplast [34,38] which reduced the photosynthetic efficiency and caused a serious reduction in the final productivity.

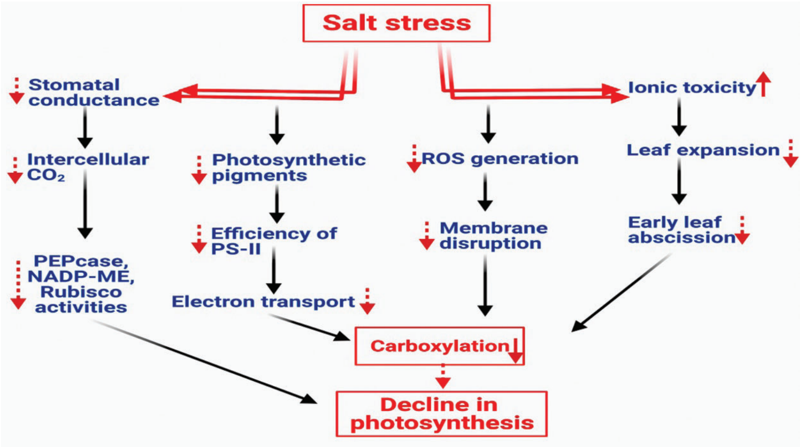

Figure 2: Possible mechanisms by which salinity stress reduces photosynthesis in wheat crop. Salt stress disturbs the balance between ROS and anti-oxidant species and causes the accretion of ROS which induces oxidative stress in the wheat crop. moreover, salinity stress increases ionic toxicity, reduces leaf growth and imposes early leaf abscission, which reduces the carboxylation and results in a reduction in photosynthesis. additionally, salinity stress also reduces the efficiency of PS-II, stomatal conductance, intercellular CO_2 and electron transportation; all of these contributes towards a reduction in photosynthesis

Moisture availability determines the physiological and metabolic processes which occur within the plant body. All the physiological and metabolic alterations in plants mainly depend on moisture availability. Due to high salinity, a plant undergoes osmotic stress that further decreases the water potential of the plant cell. Nassar et al. [40] observed a decreasing trend in relative water contents (RWC) up to 3.5% in a salt-tolerant wheat cultivar, while it was 6.7% in salt-sensitive varieties in comparison to the control. An excess of Na^+ and Cl^- ions in plants hinders the uptake of essential nutrients from the soil, which alters the plant processes. A reduction in K^+, Ca^{2+}, and Zn^{+2} uptake and an increase in Na^+ and Cl^- uptake was observed in a salt-affected wheat cultivar [34].

2.3 Salinity-Induced Oxidative Damage

Salinity stress causes stomatal closure and hinder carbon dioxide (CO_2) entrance in leaves. This restrains CO_2 fixation and enables the chloroplast to stimulate the immense levels of energy, which further develops the reactive oxygen species (ROS) [30,41–46]. These ROS cause damage to major molecules including lipid, protein, and nucleic acids [42,43]. ROS production increased under salinity [44] and induced cellular toxicity in various crop plants [30]. Salt-sensitive wheat cultivars growing under salinity conditions (5.4 and 10.6 dS m^{-1}) had more H_2O_2 and lipid peroxidation than salt-tolerant cultivars [45]. Zou et al. [35] observed that salt stress (100 mM NaCl) enhanced malondialdehyde (MDA) level up to 35% or 68% after 5 or 10 days of exposure to such stress, respectively, in wheat seedlings.

3 Mechanisms of Salinity Stress in Wheat

Wheat produces alterations at the cellular and organ level to perform best under salt stress (Fig. 3). The resistance mechanisms of salt tolerance in wheat are complex as the plant produces numerous alterations in stomatal conductance, hormonal balance, anti-oxidant defense mechanism, osmotic regulation, and ion exclusion. A comprehensive study of the above-mentioned resistance mechanisms is expressed below.

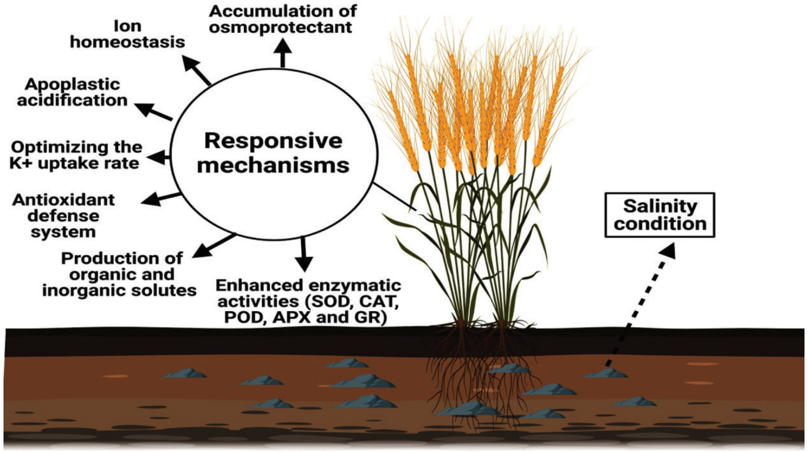

Figure 3: Responsive mechanisms of wheat crop to salinity stress. APX: ascorbate peroxidase, CAT: catalase, GR: glutathione reductase, POD: per-oxidase, SOD: superoxide dismutase

3.1 *Osmoregulation and Osmoprotection*

Plants face osmotic stress and implement a well-known strategy (osmoregulation) to lower its adverse effects [46,47]. Plants accumulate various organic compounds (sugars, polyols, amino acids, and quaternary ammonium compounds) that help to reduce the osmotic potential [48]. Osmoregulation is responsible to trigger the defense mechanism against anti-oxidant species for regulating the plant water relationship [49,50]. In nature, osmoprotectants are hydrophilic, and have a low molecular weight, and no net charge [51]. In bean plants, the salt-tolerant cultivars had high proline and amino acids with minimum protein contents as compared to the salt-sensitive varieties [52]. Various concentrations of organic and inorganic solutes result in osmotic adjustment which vary with species and cultivars [53].

3.2 *Ion Homeostasis*

Ionic homeostasis is a key process that regulates ion flux to maintain a low Na^+ ion concentration and building up a high K^+ concentration [44,47]. Regulating intracellular Na^+ and K^+ ions (homeostasis) is fundamental for the various enzymes' performance in the cytosol, maintaining the membrane potential as well as cell volume [44]. For equivalence Na^+ and K^+ concentration in the cytosol, plants rule out the excess salt via primary and secondary active transport [44,54], and accumulate these positively charged ions in the plasma and tonoplast membranes for the sustaining homeostasis during salt stress [54]. Various K^+ genes are down and up-regulated by saline stress [55]. For securing the cytosol from the damaging effects of Na^+ ions; the extra Na^+ is compartmentalized in the vacuole as an efficient mechanism against ion toxicity [47,54]. Cordovilla et al. [55] found a vast diversity for Na^+ and K^+ within the cytosol among various cultivars of grain crops. Plants use various affinity-based transporters found in the biological membranes for K^+ uptake [56], associated with K^+/Na^+ maintenance [57]. The extra salts are physiologically excluded from the plants as their adaptive trait for salt-resistance. The different effects of salt stress on photosynthetic and physiological attributes of wheat crop are summarized in Table 1.

Table 1: Effect of salt stress on photosynthetic and physiological attributes of wheat crop

Salinity level	Effects	References
15 dS m^{-1}	Salt stress reduced the chlorophyll and relative water contents and increased accumulation of Na^+	[39]
12.0 dS m^{-1}	Salt stress reduced the leaf chlorophyll contents and substantially changed the leaf anatomy	[40]
18 dS m^{-1}	Salt stress decreased the photosynthetic rate, stomatal conductance, and K contents while increased the electrolyte leakage and Na^+ accumulation	[41]
10 dS m^{-1}	Salt stress decreased the leaf water potential, relative water content, chlorophyll content, K^+ content and increased the Na^+ accumulation	[58]
12 dS m-1	Salt stress decreased relative water content and chlorophyll content, and produced membrane injury	[59]
6.25 dS m^{-1}	Salinity stress reduced root and shoot growth and increased accumulation of H_2O_2, lipid per-oxidation and accumulation of proline and amino acids.	[60]

High sodium concentration in plants interferes with K^+ accumulation and stomata regulation [61]. Increasing the Na^+ ion concentration in the plant vacuoles via the tonoplast pathway driven by the proton gradient is also considered a crucial strategy against salinity. As a result, plants save their essential organelles like the cytosol from an excess of sodium, thus developing a resistant mechanism against such ion [62]. Plants accumulate Na^+ ions in the vacuoles of roots via the tonoplast pathway to lower the sodium transport in the shoot [62]. Optimizing the K^+ uptake rate while reducing its omission, plants not only restrict the Na^+ entry but also take advantage of sodium exclusion from the cell under saline stress. This mechanism helps to maintain the K^+/Na^+ ratio in the cytosol [63] and ensures plant survival under salinity conditions.

3.3 Antioxidant Defense System

Reactive oxygen species (ROS), high osmotic stress and ion toxicity develop in plants due to excessive salt accumulation in the root zone of plants [43]. The ROS in plants cause the oxidation of protein degradation and alteration in deoxyribonucleic acid (DNA) sequencing [64]. Plants resistant to salt stress develop an anti-oxidative mechanism by activating various enzymes like the superoxide dismutase (SOD) and catalase (CAT) (Fig. 4) [65,66]. From numerous studies it is clear that the anti-oxidant defense system manages the oxidative damage during abiotic stress in plants [67]. A close association of anti-oxidants and salinity tolerance has been observed in wheat species [68]. Plants indicate the activities of the antioxidant enzymes under salt stress [69]. Plants have water-soluble anti-oxidants that make them strongly redox buffered [70]. Electrons react with oxygen molecules to form hydrogen peroxide (H_2O_2) as superoxide radicals [43]. Various enzymes are involved in regulating the intracellular H_2O_2. Among these, the peroxidase (POD) [70], and CAT [71] are crucial ones.

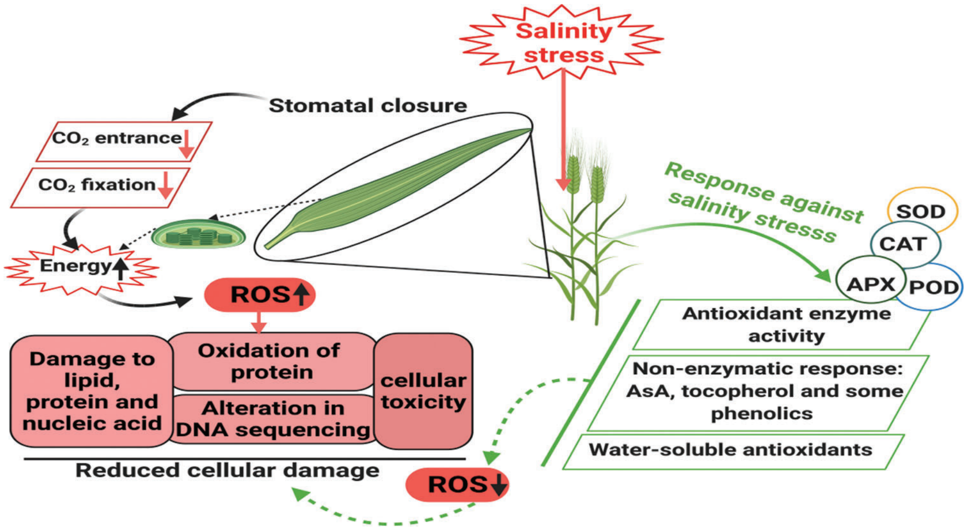

Figure 4: Salt induced oxidative stress and antioxidant defense regulation in wheat crop

To encounter ROS activity, plants activate an antioxidant defense mechanism for their survival. Various antioxidants such as ascorbic acid (AsA), tocopherol, and some phenolics (non-enzymatic) are found in plant, which gives protection from oxidative stress. Athar et al. [72] observed less growth and photosynthetic activity due to high (150 mM NaCl) salinity, with a lower K^+/Na^+ ratio in the tissue of both sensitive and tolerant wheat cultivars. Conversely, the tolerant wheat varieties produced endogenous AsA and showed an increased CAT activity to counteract the salinity effect. Ascobin, which possesses the quality attribute of both ascorbic acid and citric acid, was found significant for producing wheat yield in a salt-induced environment [73]. In addition to the dose, the application method has a remarkable effect. Athar et al. [74] observed the different effects of AsA when it was used either as a priming agent or applied in a rooting medium or used as a foliar application against salt stress (120 mM NaCl) in wheat. AsA counteracts salinity by activating the SOD, POD, and CAT activities and photosynthesis, and more exclusion of sodium (Na^+) ions from leaves in specific cultivar [74].

3.4 Hormonal Regulation

Generally, five hormones including auxin, gibberellins, cytokinins, ethylene, and abscisic acid affect plants growth and are used externally to alleviate abiotic (salinity) stress. Amongst these hormones indole acetic acid (IAA), gibberellins (GA) and cytokinins (CK) promote plant growth whilst the rest of the hormones are known as growth retardants. Under salinity, auxin promotes wheat germination percentage, shoot dry weight along with maintaining ion homeostasis [75]. Furthermore, auxin priming has been reported to alleviate the salinity up to 15 dSm^{-1} by increasing wheat assimilation rate and sustaining the balance among various hormones [76]. On the other hand, GA priming strengthens the photosynthetic pigments and enhances plant growth and development by increasing the unit leaf surface area, thus alleviating the severe effects of salt stress in wheat [77]. Cytokinin as a priming agent, enhances wheat grain yield by promoting germination, growth, tiller-number, and a 1000 grain weight under saline conditions [78,79]. Abscisic acid (ABA) priming lowers sodium (Na^+) uptake from soil and increased chlorophyll contents [80]. Siddiqui et al. [81] observed the significant role of brassinosteroid on photosynthesis by increasing the assimilating power of wheat and boosting the photosynthetic rate under salt stress. A promising response of wheat to brassinosteroid was also observed in a salt-affected environment [82].

3.5 Molecular Mechanisms

Tetraploid wheat is relatively salt-sensitive as compared to bread wheat [83]. This is because of a lower accumulation of K^+ ions in leaves [84] controlled by the chromosome 4D specified with Kna1 loci in bread wheat [85]. Moreover, two loci, Nax1 and Nax2 are concerned for the elimination of high Na^+ ions; this was observed in genetic analysis based on populations of durum wheat and *Triticum monococcum* [86]. The HKT gene is involved in excluding Na^+ ions from wheat during salinity. But the mechanism of HKT genes for sodium-ion exclusion under salinity stress has to be further unrevealed. For instance, TaHKT1;5-D alters transcriptional programming in *Aegilops tauschii* (2n-wheat cultivar) under salt stress [87]. Byrt et al. [88] did not observe any variation in TaHKT1;5-D in hexaploid wheat cv. Bobwhite. Transcription of TaHKT1;5-D was significantly reduced in hexaploid wheat cv. JN177 under salinity [89,90]. This contradictory result arises some fundamental questions on if either the response of TaHKT1;5-D is tissue-specific [88] or based on HKT genes. The sole HKT gene is synchronized by small ribonucleic acid (RNA) and DNA methylation in Arabidopsis [91]. In addition, TaHKT1;5-D mediated salt tolerance in wheat cvs. JN177 and SR3 is also based on DNA methylation [92]. The TaHKT1;5-B1 and TaHKT1;5-B2 have a much lower transcription level than TaHKT1;5-D [88]. Xu et al. [93] noted that epigenetics might be effective in homologous transcription, and there is a need for further investigation on epigenetics of TaHKT1;5-B1 and TaHKT1;5-B2, characterized by a lower expression attributed to the TaHKT1;5-D. Furthermore, salinity tolerance regulated by HKT genes is affected by AtABI4 and OsMYBc [94,95]. Conversely, HKT gene function in complex hexaploid wheat cultivars still needs investigation to identify its function.

The performance of common wheat under salt stress conditions can be increased with the use of some imperative potential traits of wild wheat species and their related cultivars [96]. Likewise, *Thinopyrum ponticum* (tall wheatgrass) depicts tolerance against abiotic stress [97] and thus, possesses important genes to develop salt-tolerant wheat cultivars. However, a recombinant barrier hampers the production of new hybrids possessing beneficial traits by the combination of both wild and common wheat varieties [98]. Nevertheless, asymmetric somatic hybridization is the best substitute to develop a new cultivar, particularly where the inter-specific cross is not feasible [99]. With the use of this approach, a salt-tolerant wheat cultivar (Shanrong No. 3: SR3) was developed by crossing bread wheat and *Thinopyrum ponticum* [100]. Biotechnology gets a breakthrough with developing this novel cultivar, which further reveals the salt-tolerant mechanism in wheat. In genetic analysis, the polygenic effect causes homeostasis in ROS for tolerance against salinity. SR3 activates TaCHP (Zn finger transcription factor) with a greater transcription than JN177 [101], which further assists wheat cultivars to enhance POD concentration in leaves for scavenging ROS under salt stress. In another example, TaOPR1-(a gene responsible for the activation of an antioxidant defense mechanism against ROS) limits the MDA to face salinity stress [102]. In somatic hybridization; considerable epigenetic reprogramming occurs commonly known as "Genomic shock" [103]. Scientists need to evaluate the functioning of epigenetic alteration for controlling the expression of genes and they observed differences in transcript abundances of TaFLS1, TaWRSI1, and TaTIP2 between JN177 and SR3. However, it could not be explained by differences in either the promoter or the coding sequences, which were shown to vary concerning the DNA methylation level [104]. A complete investigation is needed to understand whether ROS homeostasis and its deviation among SR3 and JN177 are coupled with DNA methylation for bringing tolerance in wheat cultivars.

4. Salinity Stress Management in Wheat

The development of salt-tolerant cultivars along with appropriate agronomic practices can help to improve crop production under salt stress conditions (Fig. 5). Many opportunities exist regarding genetic diversity in gene banks exist which provides enough support to develop improved salt-tolerant cultivars characterized by a high production over the existing varieties [105,106]. The basic genetic makeup found in the genetic pool of various crop species assists breeders to make progress in developing salt-tolerant cultivars. Moreover, breeders develop salt-tolerant varieties especially for wheat and rice crop [106–108]. When developing salt-tolerant cultivars, the physiology and genetic-based traits also have considerable importance to assure the maximum yield at harvesting.

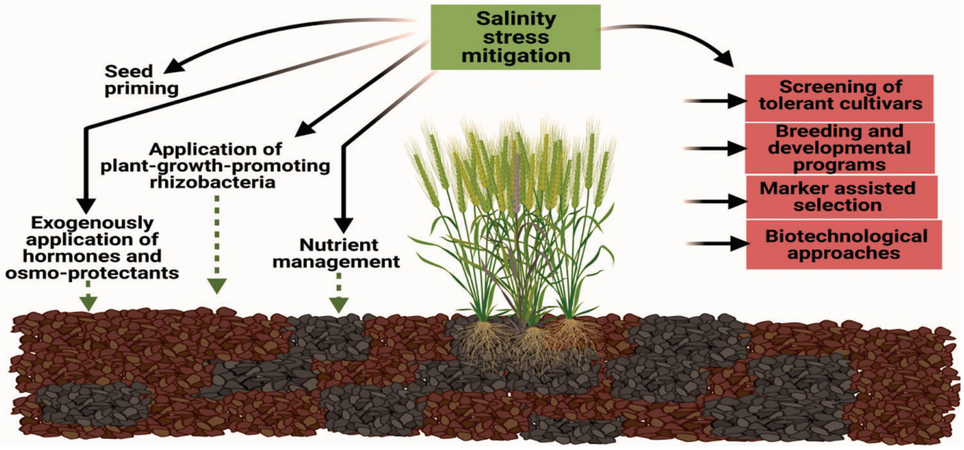

Figure 5: Strategies involved in improving the salinity tolerance in wheat crop

4.1 *Conventional Breeding*

Among all other cereals, wheat is considered a staple food in Asia; however, its yield potential is negatively affected by salinity. In response, breeders make appreciable efforts to develop salt-tolerant cultivars in Asian countries (Pakistan and India) and in Australia. However, the progress is quite slow. In Pakistan, the University of Agriculture, Faisalabad in collaboration with the Saline Agriculture Research Centre (SARC) developed the salt-tolerant lines (LU26S and SARC-1). In addition, the Central Soil Salinity Research Institute (CSSRI) introduced KRL1–4 and KRL-19 in India to cope with salinity threat. All the Indian salt-tolerant cultivars are the progeny of Kharchia 65, which was developed by Indian farmers by selection from the sodic-saline soil of Rajasthan [109]. The Indian salt-tolerant cultivar (KRL1–4) was the cross of Kharchia65 and WL711 and was a promising variety for northern India [110].

KTDH-19 being a doubled haploid wheat line was developed by crossing Kharchia65 with TW161 (a specific line for Na^+ exclusion) and gave satisfactory results under the saline condition in Spain [111], India and Pakistan [110]. Its salt tolerant ability along with an earlier maturity of three weeks caused to adopt this line in Asian countries particularly in Pakistan and India [110].

4.2 Transgenic and Biotechnological Approaches for Improving Salinity Tolerance in Wheat

In this technique a desired gene is transferred to a transgenic plant with genetic engineering to obtain the resistance against stress conditions [112,113]. Salinity tolerance is controlled by many minor genes and it is complex to transfer the desired gene for developing the desired trait in a transgenic wheat cultivar (Table 2). Genes are specific in action; the antiporter gene (*AtNHXI*) controls the overexpression of Na^+/H^+ ions in the vacuole and improves germination and biomass by lowering the leaf Na^+ concentration [114]. Free proline accumulation may increase salt tolerance in plants. An enzyme, the 1-pyrroline-5-carboxylate synthase (*P5CS*), increased the accumulation of free proline by 2.5 folds higher than the control (non-proline cultivar) to enhance salt tolerance in wheat [115].

With the use of biotechnology, wheat and other crops like rice and tobacco [116] are being equipped with salt-tolerant genes and are producing high yields [117]. Genotypic markers provide phenotypic data to explore hereditary for salt tolerance. The exact phenotypic data is the base of salt-tolerant genes [118]. Recently, advancements in DNA marker and sequencing advances have allowed high-throughput genotyping of numerous individual plant species with moderately minimal effort. Rapid strategies to assess huge amounts of genotypes are critical to completely exploit the immediate improvement of biotechnological systems and to encourage hereditary analysis of complex qualities.

In traditional selection obtaining high yields under saline conditions, the environment has various constraints including innate variables, heterogeneous soils, and climate conditions [118,119]. The physiological attributes along with genes supporting more tolerance against salinity competently discriminate in the natural environment [120]. Assessing grains' response to salt stress, scientists screened and demonstrated the effective and satisfactory results of their system on different germination media including soil, and sand [121,122], and hydroponic [119]. Particle homeostasis affects the traits involved in genetic analysis with eminent quantitative trait locus (QTLs) described by specific Na^+ and K^+ contents relieving tolerance against salinity in wheat [123] and rice [124,125].

Table 2: Traits considered important for salinity stress in wheat

Gene category	Function	References
AtHKT1 (Na^+ antiporter)	AtHKT1 expressed in the root stele and leaf vasculature and it reduced Na^+ accumulation	[126,127]
AtNHX1 (Na^+/H^+)	Reduced cytosolic Na+ by sequestration of Na^+ in the vacuole	[114]
Nax2 and *Kna1* (*HKT1;5* genes)	Increased Na^+ exclusion	[128]
AKT1 AKT2 and KAT1 (potassium transporters)	Increased the K^+ transport by exclusion of Na^+	[126]
Pyrroline-5-carboxylate synthetase 'P5CS	Increased proline concentration to counter effects of salt stress	[115]

QTL mapping plays a vital role in examining genetics and producing the complicated plant traits [129]. Our understanding of the complexities of the plant characters is appreciably increased with the use of QTLs for agronomic traits [130]. Marker selection results in an improvement in notable QTLs that have assisted the breeders fundamentally [131] and pyramiding the various apposite forms of genes (alleles) [132]. The basic principle for genes exploring for salt tolerance is based on QTL mapping (biparental), which mainly focuses on the single dividing population incidental from parental genotypes (homozygous) in wheat [133], rice [134], and other grains crops [135]. The HKT group is associated with salinity tolerance in the Knal loci and Nax1 plus Nax2 were encoded with some locus found in common wheat [85]. Some constraints were faced regarding bi-parental QTL mapping that was inefficient for exploring the allelic cultivars in the gene pool and affecting the quality traits [136]. Bi-parental QTL mapping can only exhibit the genes responsible for characterization which normally lies in the range of 10 to 30 cm [137]. Moreover, these chromosomal alleles could demonstrate a few thousand genes [138]. Thus, obviously effective and successful QTLs that are being cloned highlighted with more than one gene [139]. Toconquer the utilization of inherited variability for salt tolerance, further research is mandatory to establish the right mapping sequence for germplasm.

In association mapping interpretation of disequilibrium linkage with phenotypic connection occurs. Differentiation among different loci, which carried the complex genetic information, is also possible and supported with association mapping. Distinctive markers linked with phenotypes and carried gene of interest are used in this technique [140]. Thudi et al. [141] reported the use of association mapping for plant genetics and made underutilization for gene sequencing [142]. Linking disequilibrium and accretion of various genetic makeups determine the use of association mapping [139]. All the possible recombinant events that take place during the crop life span and distribution patterns of small linkage barriers are studied with association mapping [143]. Moreover, their functions based on actual QTLs variation occurs on allele manipulation of the desired character under observation during association mapping of the crop gene pool. Linkage, disequilibrium (LD) informs non-arbitrary association among various alternative forms of genes present on the typical polymorphic locus and thus has a fundamental importance in association mapping. An association mapping group includes vast land regions, areas of adjustment with an upright representation of its evolutionary history typically non-arbitrary because of familial relatedness and distinctive sorts of structure [140]. Association mapping identifies marker quality [144] and requires the proper apparatus to use this technique, which clarifies the complexities [145]. It is necessary to accumulate all the elements associated with mapping and to merge them in the desirable form of a model suitable for markers used within sub-populations [146].

Conventional breeding is time consuming and causes many complexities in polygenic traits. A breeder generally does not phenotypically analyze the crop selecting from the back cross due to varying germ plasmas. Thus, to manage salt stress in tolerant cultivars, breeders use marker-assisted selection for QTL analyses based on polymorphic traits of parental lines [143]. An efficient marker has to be developed to deal with salinity in plants. The genome in major cereals (rice, barley, sorghum, and soybean) has been sequenced, and it has progressed towards a next-generation sequencing (NGS) to modify the genetic maps for obtaining tolerance in plants. Despite these successful models, marker-assisted selection has few constraints at the end of undesirable traits coming from wild donors causing mutants in the genetic programs of cultivars and non-significant results at the farm level. However, NGS is a promising approach in determining molecular markers relatively quicker for obtaining high-density genetic maps. Furthermore, it is necessary to boost salt-resistant QTLs preparation to address salt stress, which can only be achieved with the use of NGS.

4.3 Use of Plant-Growth-Promoting Rhizobacteria (PGPR) to Manage Salinity Stress

Microorganisms are usually colonized in the rhizosphere and they enhance germination, root and shoot length, increase mineral uptake, and yield [147–150], and enhance tolerance against abiotic stress (salinity) [151,152]. Under abiotic stress, many beneficial effects of salt-tolerant rhizobacteria were observed [153,154]. Plant growth is negatively affected by salinity, whereas the function and composition of soil beneficial bacteria also decreased [155]. Saline soils deteriorate the soil structure formed by the soil microbial community near the region of the rhizosphere with a declining quantity and quality of the root exudates [156]. Many strains of PGPR *(S. rhizophila* e-p10, *P. fluorescens* SPB2145, *P. chlororaphis* TSAU 13, *Serratia plymuthica* RR2–5–10, *P. putida* TSAU1, *P. extremorientalis* TSAU20, *P. fluorescens* PCL1751, and *P. aureofaciens* TSAU22) induced tolerance against salinity [154,157]. Thus, with the use of these strains, wheat can withstand and perform better with optimum yields under saline stress environments [158,159]. PGPR improve germination rate and growth attributes [160], a thousand-grain weight and grain production [161]. Salt-tolerant rhizobacteria isolated from wheat roots were responsible for increasing root length under saline conditions [162]. Use of PGPR for seed inoculation increased root and shoot length of crops (tomato, pepper, canola, bean, and lettuce) along with increasing their dry biomass, fruiting, and grain yield by enhancing tolerance against salinity [163,164]. Furthermore, PGPR caused osmotic adjustment during saline conditions which also helped to mitigate the adverse effects of salinity stress [165].

4.4 Ameolative Role of AMF against Salinity Stress

Plants under salt-stressed environments undergo hypertonic as well as the hyperosmotic conditions that lead to plant death. Arbuscular mycorrhizal fungi (AMF) are persistent in soil, play a significant role in improving soil health [166], and increases plant growth during salinity [167–169]. AMF enable plants to improve their water and mineral nutrient uptake, increase photosynthesis and accumulation of osmolytes under salt stress [170,171]. Plants with colonized AMF have morphological, physiological, and nutritional changes for normal activities during salinity [172]. In addition, AMF also increase mineral and water uptake [167,173] and water use efficiency (WUE) [170]. However, such development mainly depends upon the type of AMF species that is used for inoculation under saline conditions [174].

Plant exposure to high salinity produces excessive MDA which decreases membrane stability and increases lipid peroxidation [168,175–177]. AMF inoculated plants reduce MDA production with increased anti-oxidant enzymatic activity under salinity stress [178,179]. Studies show that anti-oxidant enzymes were active in AMF colonized plants over un-inoculated plants and showed promising results under salt stress conditions [180–182]. High chlorophyll content was observed in AMF inoculated plants during salt stress that enhanced the photosynthesis rate for carbohydrate production [171,183].

Availability of essential mineral nutrients to plants impedes salinity [184,185]. AMF colonized plants absorb plenty of minerals [186] facilitating a high water uptake [187] and increasing their growth under salt-stressed conditions [188]. Hormones like auxins (IAA, ABA) and gibberellins (GA) improve plant growth. The concentration of these plant growth regulators decreased under salt stress, whilst their concentration was significantly increased on AMF inoculated plants under salinity [178–179,189]. The combined use of PGPR and AMF increased nutrient uptake [190], water absorption, and grain production under saline conditions [191]. The synergistic effect of both PGPR and AMF enables plants to cope with various biotic as well as abiotic stress conditions. Further research is needed for getting the best combination of PGPR and AMF for obtaining a maximum plant production under biotic and abiotic stressed environments.

4.5 Use of Exogenously Applied Hormones and Osmoprotectants to Mitigate Salinity Stress in Wheat

Hormones are chemicals produced in plants and they regulate normal plant functioning, development, and tolerance against various stresses especially under salinity [192]. Moreover, the external use of different synthesized plant hormones (Auxin, CK, ABA, GA, and brassinosteroids) mitigates the effect of various abiotic stresses. Auxin improves germination and shoot dry weight while maintaining ionic homeostasis in salinity; thus, it is well-known as a growth promoter [75]. It alleviates salinity up to 15 dS m^{-1} with a balanced hormonal concentration in the plant and enhances yield by improving assimilation rate in salt-sensitive and salt-tolerant wheat cultivars [76]. GA_3 priming brings improvement in photosynthetic pigments, and leaf and plant growth under salinity stress conditions [193]. ABA primed seeds expresseshigh salinity tolerance with high chlorophyll production and decreased Na^+ uptake [80]. High wheat grain yield was observed with the application of brassinosteroid under salt stress [82,194].

Plants produce numerous compatible solutes to survive against ionic, oxidative as well as osmotic stress [195]. These osmolytes include proline, glycine-betaine (GB), β-alanine betaine, dimethylsulfoniopropionate (DMSP), choline, polyols, and sugars [trehalose (Tre), sorbitol, and mannitol] as shown in Table 3. Effective results were observed with the exogenous application of osmoprotectants to alleviate salt and metal stresses on plants [196–198]. Proline, being an osmoprotectant, helps in osmotic adjustment as well as detoxification of ROS, and strengthening the photosystem II structure [199,200]. Various anti-oxidant enzymes (SOD, POD, and CAT) trigger their activities with exogenous applied GB and significantly improve the salinity tolerance of *T. aestivum* [201]. In another experiment GB application (10 and 30 mM) increased germination and calcium and chlorophyll contents in shoots and leaves, and improved salinity tolerance [202]. Likewise, exogenous proline (60 ppm) up-regulated endogenous hormones (GA, IAA) and down-regulated MDA, and improved salinity tolerance in wheat [203].

Table 3: Accumulation of osmolytes in wheat during a salt-stressed environment

Salt stress	Osmolytes	Functions	References
8.6 dSm^{-1}	Sugars	Increase in soluble sugars increased the osmotic potential, and protected plants from oxidative stress by activating anti-oxidant enzymes.	[34]
150 mM	Proline	Proline accumulation increased plant growth, osmotic adjustment, protected cell membrane, and increased the activities of antioxidants to scavenge ROS. Moreover, proline also increased chlorophyll and K^+ contents, CO_2 assimilation rate, stomatal conductance, and sub-stomatal CO_2 concentration.	[204–206]
200 mM	Glycinebetain	Glycinebetain increased the photosynthetic rate, membrane stability efficiency of PS-II and water use efficiency.	[207]
65 mM	Trehalose	Trehalose maintained osmotic balance and increased relative growth rate, chlorophyll content, biomass production, K^+ accumulation and K^+/Na^+ ratio.	[208,209]

Rao et al. [210] suggested that increased production of Pro and GB mitigated the damaging effects of salt stress by activating antioxidant enzymes. The application of trehalose improved the Pro and K^+ accumulation, and the ratio of K^+/Na^+ and stabilized the protein and lipid structure [211,212]. Mannitol lowers lipid peroxidation by amplifying the antioxidant (POD, SOD, APX, CAT, and GR) enzymes, and thus reverses the harmful effects of salinity [213]. Melatonin protects the cell membrane and increases the activities of antioxidants under stress conditions [214]. In conclusion, hormone and osmoprotectant applications improve antioxidants activities, photosynthetic efficiency, membrane stability, and detoxifies ROS, thus leading to substantial improvement under salinity stress.

4.6 Role of Seed Priming under Conditions of Salt Stress

Seed priming is an economical and cheap approach that gives promising results for getting a maximum production under salt stress conditions [215]. Seed priming improves germination rate and seedling establishment in wheat and other crops [32,216–218]. The positive effects of seed priming can be due to the availability of adenosine triphosphate (ATP), enzymatic activation, and *de-novo* synthesis of some substances that promote germination [219]. Seed priming is a reliable, simple, inexpensive, and low-risk technique [220,221]. Various priming techniques such as hydro-priming (soaking the seeds in water), osmo-priming (soaking the seeds in nutrient, hormone, or chemical solutions), and halo-priming (soaking the seeds in a salt solution) have been developed to increase the speed of germination, seedling establishment and crop production [222]. Seed priming has been shown to effectively increase germination and seeding emergence of many crops in the tropics and subtropics, particularly under salt stress conditions [223].

Increased germination rates and better seedling establishment led to higher levels of salt stress tolerance and crop yields when the seeds were primed [221]. Afzal et al. [224] observed the effect of hydro-priming on salt-sensitive (MH-97) and salt-tolerant (AUQAB-2000) wheat cultivars under salinity (15 dSm^{-1}). They noted seed priming increased tolerance against salinity. Osmopriming of seeds with AsA has been reported to increase endogenous AsA content and CAT activity, which increased salt stress tolerance in wheat [225]. Increased germination rate, early seedling establishment, ABA and Pro accumulation, and plant growth were demonstrated by osmo-priming seeds with 0.05 mM salicylic acid (SA) in wheat [226]. Calcium chloride ($CaCl_2$) used as a priming agent (halopriming) reduced Na^+ concentration and increased accumulation of K^+ ions that helped to maintain ion homeostasis and salt tolerance in wheat [227]. Moreover, halo-priming also increased the activities of SOD and CAT that detoxified the ROS under salt stress [228]. Phyto hormones are also used as priming substances that induces salinity tolerance. IAA seed priming enhanced amylase activity that triggers the germination process [229] and deteriorates the inhibitory effects of salt stress in wheat production [224]. Photosynthetic pigments (chl a and b) and osmotic adjustment were increased with SA priming (100 mgL^{-1}) in a wheat cultivar during salt stress [230]. The positive response of wheat by lowering Na^+ and Cl^- ions while accumulating K^+ and Ca^{2+} contents under salt stress was observed with GA (150 mgL^{-1}) priming [76]. Furthermore, it also enabled wheat to increase its germination rate and seedling growth and contributed to a marked increase in its final production.

4.7 Nutrient Management to Improve Salinity Tolerance

Plant nutrients are vital for getting an optimum yield. However, the limited supply of essential nutrients along with a poor soil fertility reduce crop production globally [31]. Sixty percent of soils across the globe are deficient in nutrients; therefore, it is necessary to have satisfactory soil nutrient levels to obtain a maximum yield [231]. Nutrients are essential to alleviate the effects of different abiotic stresses including salinity. Plants use various nutrients including (1) nitrogen (N) and magnesium (Mg) in the photosynthetic process [232], (2) phosphorous (P) for ATP generation, and (3) potassium (K) for stomatal regulation enzyme activation [233,234]. Researchers found a positive response of plants with the use of various mineral nutrients against abiotic stresses; amongst them, tolerance in plants against salinity is acquired with the plenty use of silicon (Si) and potassium (K) [235,236]. Exogenously applied potassium (K) increases salt tolerance in wheat by increasing photosynthetic efficiency, photosynthetic pigments, and antioxidant enzymes activities [237–239]. Foliar application of phosphorous (P) enhances leaf area index and plant biomass, and reduces salinity-induced damages [240]. Nitrogen is an essential part of energy (ATP), and vital for carbon metabolism [241]. Conversely, plants with nitrogen deficiency are susceptible to oxidative damage. Less enzyme activity because of low magnesium (Mg) concentrations occurs in the chloroplast, and it alters the photosynthetic efficiency in salt-affected soils [242,243]. A low Boron concentration improves the antioxidant defense mechanism in wheat and lessens the effect of ROS [233]. ROS production during salt-stress can be minimized with selenium (Se) application [244], and foliar-applied zinc (Zn) enhances grain production in wheat under salt stress conditions [245–250]. All these findings suggest that an adequate nutrient supply is essential for maintaining optimum growth yield and under salinity stress. In Table 4., the salt-induced oxidative stress and antioxidant defense regulations in wheat are presented.

Table 4: Salt-induced oxidative stress and antioxidant defense regulation in wheat

Salinity stress	Oxidative stress	Anti-oxidant defense regulation	References
10 dSm^{-1}	Salt stress induces accumulation of ROS and increases MDA contents	CAT and APX activities were up-regulated to counter the effects of oxidative stress	[251]
100 mM	Salt stress induces accumulation of hydrogen peroxide and superoxide	CAT, SOD, and APX activities were considerably up-regulated to scavenge ROS	[252]
120 mM	Salinity stress induces oxidative and osmotic stresses	Activities of POD, SOD and CAT significant increased to mitigate the effects of salt-induced damages	[253]
100 mM	Salt stress induces accumulation of ROS and MDA	DOS, POD, CAT, APX and GR activities were considerably increased to mitigate the effects of salt stress	[254]
300 mM	Salt stress induces increase in H_2O_2 and O_2^- concentrations	Wheat plants increased SOD, POD, CAT and proline activities to increase salt tolerance	[255]

Note: CAT: catalase, GR: glutathione reductase, POD: Peroxidase, SOD, superoxide dismutase, APX: ascorbate peroxidase, ROS: reactive oxygen species.

5 Conclusions and Prospects

Wheat is the world's most popular and consumed cereal crop. However, salinity stress is a major threat to global wheat production, food, and nutritional security. Salt stress negatively affects seed germination, plant growth, photosynthesis, ATP production, water relationships, nutrient uptake and yield because of a salt-induced oxidative stress and ionic and hormonal imbalances. Wheat crop shows a wide range of morphological, physiological, and molecular responses under salinity stress. The physiological and molecular mechanisms are very important because they can help the breeders to develop salt tolerance in wheat. These mechanisms against salinity stress are well understood in wheat. However, a better understanding is still needed in many fields, especially in understanding the physiological basis of assimilate partitioning from plant sources to sinks. Additionally, more studies are needed to study the response of roots to salinity stress involving the root-shoot signaling and corresponding impacts on the nutrient and water uptake. Genetic manipulation of salt-tolerant traits is also an important approach to improve salinity tolerance in wheat crops. However, genetic manipulation requires the collaboration of physiologists, breeders, and agronomists to find sustainable ways to improve salinity tolerance in wheat. Moreover, there is a need to assess the wild relatives and accessions of wheat crops having strong salinity tolerance. Modern techniques including molecular markers, genetic engineering, and QTL mapping have contributed to an understanding of the complex salinity traits in wheat. However, there is a large extent for further improvement. As the genotype and environment interactions are still poorly understood, QTL identified under specific conditions cannot perform well in different conditions. Likewise, transgenic plants developed for salinity tolerance may not perform well at the field level. Therefore, research findings need further validation of developed materials at the farmer field scale. The use of plant growth-promoting rhizobacteria and arbuscular mycorrhizal fungi can also help to improve wheat responses under salt stress. However, future investigations are needed to find out the mechanisms lying behind the reduction of the effects of salinity stress by these microbes. Additionally, exogenous application of osmo-protectants, phytohormones, seed priming, and nutrient management can also help to (1) improve salt tolerance in wheat. All these efforts would help to alleviate the negative effects of salinity stress on wheat crops, and (2) contribute to an improved wheat productivity and food security.

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