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Salt Stress Tolerance in Rice and Wheat: Physiological and Molecular Mechanism

Mohammad Hasanuzzaman

Abstract

Salinity is a major obstacle to global grain crop production, especially rice and wheat. The identification and improvement of salt-tolerant rice and wheat depending upon the genetic diversity and salt stress response could be a promising solution to deal with soil salinity and the increasing food demands. Plant responses to salt stress occur at the organismic, cellular, and molecular levels and the salt stress tolerance in those crop plant involving (1) regulation of ionic homeostasis, (2) maintenance of osmotic potential, (3) ROS scavenging and antioxidant enzymes activity, and (4) plant hormonal regulation. In this chapter, we summarize the recent research progress on these four aspects of plant morpho-physiological and molecular response, with particular attention to ionic, osmolytic, enzymatic, hormonal and gene expression regulation in rice and wheat plants. Moreover, epigenetic diversity could emerge as novel of phenotypic variations to enhance plant adaptation to an adverse environmental conditions and develop stable stress-resilient crops. The information summarized here will be useful for accelerating the breeding of salt-tolerant rice. This information may help in studies to reveal the mechanism of plant salt tolerance, screen high efficiency and quality salt tolerance in crops.

Keywords: antioxidant enzyme, Na^+/K^+ ratio, osmolytes, salt Tol gene, salinity, rice and wheat

1. Introduction

Salinity is an abiotic stress factor that has severe negative impacts on agricultural crop growth and yield potentiality [1]. The seed germination, traits of growth and yield-related components of crop plants such as rice and wheat are seriously damaged under salinity conditions [1, 2]. Currently, 230 million hectares of world's areas are used for cultivation in which 20% lands are affected by varying degree of salinity and amount of saline affected area is increasing continuously due to the effect of sea level rise, coastal subsidence, increased tidal effect and continuous reduction of river flow, particularly during dry periods [3–6]. Therefore, soil salinity is the major obstruction to crop cultivation. When the crop plants are exposed to salt-affected soil, the plants primarily develop osmotic stress and instantly inhibits the normal plant growth and development [7]. Later, ion toxicity is created in crop plants due to excess salinity level and causes imbalance in mineral

homeostasis [3]. Osmotic stress and ion toxicity are major salt-induced stresses which create secondary oxidative stress in plants and overall growth inhibition. Salinity stress also interferes with the photosynthetic process by severely damaging photosynthetic pigments [8] and ultimately results in huge loss of crop yield globally [9]. To feed up the huge global population and ensure the food and nutritional security of the rising population, it is urgent to increase the crop production at least 70% by 2050 [10].

Rice and wheat are the first two ranked cereal crops that jointly feed approximately 80% of the world's population, and are sensitive to salt stress [11, 12]. Developments of salt tolerant rice and wheat varieties is a prerequisite for salt stress management. To improve rice and wheat production, a thorough understanding of physiological response, biochemical activity, metabolism, epigenetic response, and gene expression under salt stress conditions is required. In this chapter, we discuss the salt-induced oxidative stress, osmotic stress and mineral toxicity to rice and wheat plants. Moreover, we systematically summarize the current understanding of salt-stress response and morpho-physiological and molecular mechanisms, and epigenetic response underlying salt tolerance in rice and wheat. This theoretical basis could be further useful for developing salt-tolerant and high yielding rice and wheat varieties in future.

2. Salt stress response of rice and wheat plants

Plant showed several morphological and anatomical changes under high salinity stress conditions e.g. shorter shoot, root system impairment, total biomass reduction, shoot tip rolling, leaf chlorosis, fewer tillers per plant, lower grain weight, and fewer spikelets per panicle ultimately leading to decrease in harvest index and grain yield [13–16]. Salt stress significantly affects plant physiology and biochemical activity at germination, seedling and reproductive stages [17–19]. Excess salt causes osmotic stress and ionic toxicity on rice plants leading to overall oxidative stress and nutrient depletion [20, 21]. Plants show various morpho-physiological or biochemical changes and salt injury symptoms and even may die under high salinity stress conditions (**Figure 1**). Higher amounts of sodium ion (Na^+) directly cause cellular damage in plants and excess Na^+ in root areas inhibits K^+ uptake because of their antagonistic effect which hampered photosynthetic activity [22]. Ionic or mineral stress causes excess accumulation of sodium (Na^+) and chlorine (Cl^-) in plant cells which finally results in premature leaf senescence and often plants die by salt antagonistic effects [23, 24]. Excess presence of Na^+ in plant cells cytoplasm has an extreme inhibitory effect on enzyme activities which disrupted many cellular metabolism (e.g. protein synthesis), bio-molecular function, and photosynthesis [25–29]. Furthermore, abundance of Na^+ in the cytoplasm hampers the normal uptake and transport of potassium (K^+) and other macro- and micronutrients, for example nitrogen (N), phosphorus (P), calcium (Ca^{2+}), magnesium (Mg^{2+}), zinc (Zn^{2+}), and iron (Fe^{2+}) [25, 30–32].

Salinity-induced continuous stress diminish the plant cell turgor pressure, which in turn decreases normal cell growth, and plants must enhance enzymatic activity to adjust osmotic potential and maintain cell expansion and growth [17, 25, 32–34]. Many investigations reported that Na^+ accumulation in plant shoots is directly correlated with the rice and wheat plants' survivability under saline condition [25, 26]. Therefore, lowering the cytosolic Na^+ level is playing a vital role to enhance salt tolerance mechanisms in rice and wheat [25]. Because of osmotic stress in plants, water uptake is obstructed and due to lower water potential

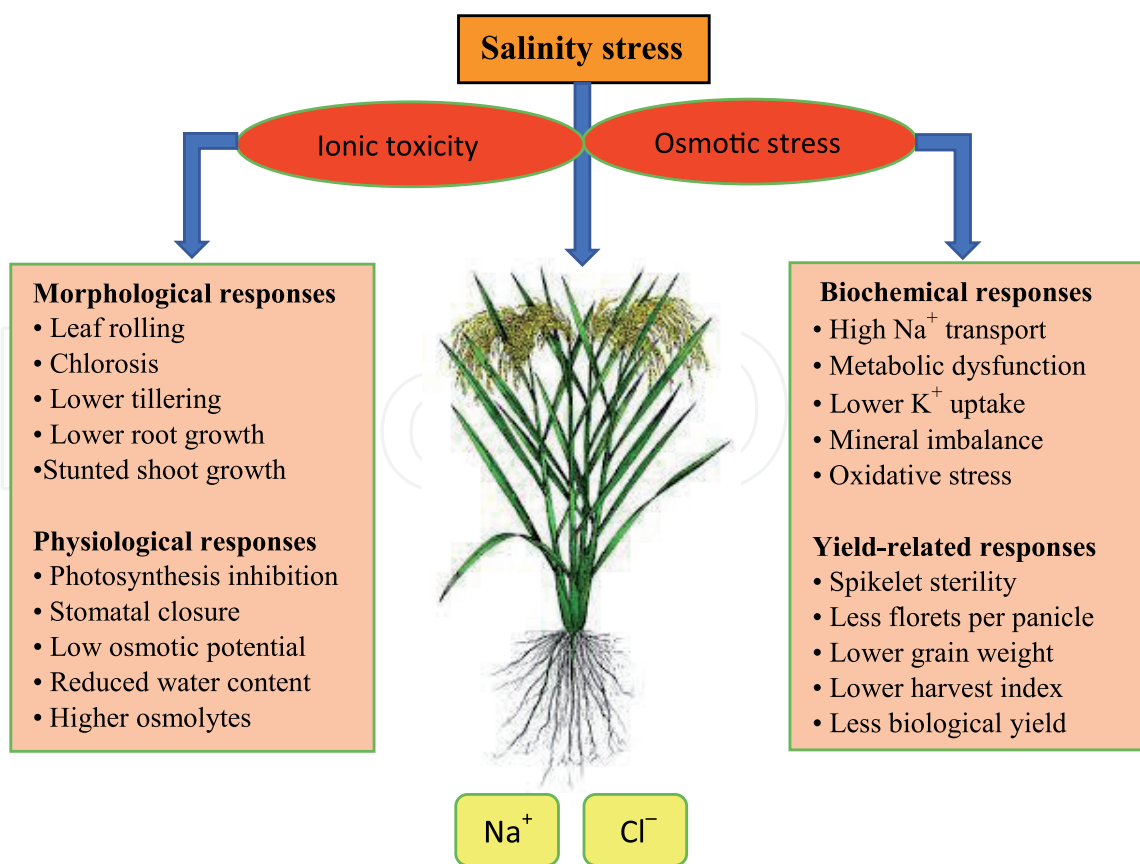


Figure 1. Schematic diagram represents the morphological, physiological, biochemical and yield associated response of rice and wheat plants under salt stress conditions. High salinity stress severely damage the plants mineral homeostasis and osmotic maintenance, thereby retarded the plant growth and developments and finally reduce crop yield.

physiological drought is created in plants. Osmotic stress also results in interruption of nutrient uptake and rapid stomatal closure, which decline the CO₂ assimilation capability of plants and highly inhibits photosynthesis [35]. Oxidative stress due to osmotic and ionic imbalance, causes higher accumulation of reactive oxygen species (ROS), which may severely damage the cellular macromolecules (e.g. DNA, lipids and enzymes) and structural components [36, 37]. Under salinity conditions, rice and wheat plants must amplify their physio-biochemical and enzymatic activity involved in the regulation of ion and osmotic homeostasis, oxidative stress, and nutritional balance [1, 23, 38, 39].

3. Salinity tolerance mechanism in rice and wheat

3.1 Maintenance of ionic homeostasis

Soil salinity induced stress in crop plants is commonly caused by high concentrations of Na⁺ and Cl⁻ [38, 39]. The ionic homeostasis must be regulated and re-established in saline stressed conditions [40]. The final determinants of salt tolerance mechanisms are different ion transporters that transport toxic ions at plant organ and cell levels [41]. Therefore, the most important fact of salinity tolerance studies is to find which transporters interfere with the entry of Na⁺ into the cell [42]. Na⁺ and K⁺ are normally transported into the plant cell by the same transporters, where these two cations compete for space [43]. Excess Na⁺ competes with K⁺ for absorption across the plasma membranes of plant cells, and K⁺ is required for the activities of several important catalytic enzymes [44].

Moreover, K^+ is essential for the preservation of cell turgor, protein synthesis, osmoregulation, normal photosynthesis [45, 46]. Therefore, the regulation and adaptation of cellular Na^+/K^+ ratio is a crucial indicator that discerns the plant's capability to survive in salinity stress conditions. Moreover, mechanisms to reduction in cytoplasmic Na^+ uptake, compartmentalization of Na^+ in the vacuole and increase of Na^+ efflux [1, 47]. It was reported that the removal of cytoplasmic Na^+ into the apoplast is due to the salt-inducible enzyme Na^+/H^+ antiporter of cell plasma membrane [3].

In the rice plants, the plasma membrane Na^+/H^+ antiporter (OsSOS1) excludes Na^+ from the shoot and roots, adjusting the lower Na^+/K^+ ratio at cellular level and developing salt tolerance in rice [48, 49]. The vacuolar Na^+/H^+ antiporters (for instance OsNHX1, OsNHX2, OsNHX3, OsNHX4, OsNHX5 and OsARP/OsCTP) contribute a necessary roles in the vacuolar compartmentalization of Na^+ and K^+ which is accumulated by cells cytoplasm and so determine salt tolerance in rice [50–52]. In wheat, the accumulation of Na^+ is controlled by the genes *Nax1* and *Nax2*, located at 2A and 5A chromosomes position, respectively [53, 54]. These are also used as molecular markers in a wheat breeding program for salt tolerance. Under salt stress, vascular Na^+/H^+ antiporter (*TNHX1*, *TNHX2*, and *TVP1*) are responsible for wheat seedling growth and development by generating the pH gradient and facilitating sodium sequestration into [31].

3.2 Adjustment of osmotic potential

Osmotic adjustment is critical for regulating cell turgor for the maintenance of plant metabolic activity, growth, and finally productivity [55]. Crop plants synthesize compatible osmolytes for example proline, polyamines, soluble sugars and proteins, betaine, glycine to provide osmotic balance at the cellular level [56–58]. Under salinity stress, those important osmolytes provide the plants osmotic adjustment under as they reduce osmotic potential, stabilizing proteins and finally maintain cellular structures [2, 59]. Proline, a dominant substance for osmotic adjustment, possesses high water solubility, low molecular weight and in a free state, thereby no net charge in the physiological pH range in crop plants. The plant cells tend to uptake soluble osmotic adjustment substances to mitigate salt-mediated osmotic stress caused, importantly the biosynthesis of proline is clearly activated [60]. Therefore, proline level may be used as a physiological indicator of plant stress tolerance, especially salinity [61]. Wheat *Ta-UnP*, can significantly enhance the salt tolerance of transgenic *Arabidopsis* and rice. Liang et al. [2] described that proline content in transgenic *Arabidopsis thaliana* was significantly increased for maintaining the osmotic potential and protecting plant cells from salinity stress. The proline synthesis genes *OsP5CS1* and *OsP5CR* enhances the proline production to improve the rice salinity stress tolerance [62]. A monosaccharide transporter, encoded by *OsGMST1* increases monosaccharide accumulation and develops the salt tolerance in crop plants [63]. Glycine and betaine in rice, which is synthesized by the choline monooxygenase *OsCMO* and the betaine aldehyde dehydrogenase *OsBADH1*, enhance salt tolerance by promoting glycine betaine accumulation [64, 65]. In wheat plants, some investigation proved that betaine can inhibit the transport speed and quantity of Na^+ and Cl^- from roots to the aerial parts and promote K^+ transport to enhance tolerance capability against salinity stress [33]. The salt-regulated gene *OsSALP1* encodes a small plant-specific membrane protein that develops salinity tolerance mechanism by enhancing the expression of *OsP5CS* and free proline content under salt stress [66].

3.3 ROS scavenging and antioxidant enzymes

Oxygen is one of the essential biomolecules which involves in cellular metabolism, mitochondrial respiration, and oxidative phosphorylation for energy production in plants. However, oxygen is converted into reactive oxygen species (ROS) during plants metabolic process. Plants under salt stress conditions can up-regulate the excess production of ROS e.g. O_2^- (superoxide radical), H_2O_2 (hydrogen peroxide), and OH^- (hydroxyl radical) [67, 68]. Although lower presence of ROS can act as a signal to salt stress responses, excess uptake of ROS causes cytoplasmic membrane damage, DNA mutation, peroxidation of carbohydrates, lipids and protein degradation, irreversible metabolic dysfunction, and finally cell death [68, 69]. In other crop plants, several important antioxidant enzymes and non-enzymes are activated during salinity stress to alleviate ROS stress in rice and wheat [69–71]. Various Enzymatic scavengers includes catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), glutaredoxin (GRX), glutathione peroxidase (GPX), glutathione S-transferase (GST), and glutathione peroxidases (GPXs) [1, 72–78]. Nonenzymatic scavengers include ascorbic acid (ASH), alkaloids, carotenoids, flavonoids, glutathione (GSH), phenolic compounds, and tocopherol [45, 70, 79].

Catalase (CAT) and glyoxylic acid-circulating is found in plant peroxisomes and bodies, respectively, which is one of the main enzymes that remove H_2O_2 and APX. Studies revealed that CAT is a main enzyme for scavenging H_2O_2 and is essential for H_2O_2 tolerance of crop plants [45]. The increment of ROS in the crop plant leads to lipid peroxidation in the cell membrane during higher and continuous salinity stress. Superoxide dismutase (SOD), the first line of defense of the plant antioxidant enzyme system, can eliminate the excess superoxide anions in the cells. SOD can disproportionate O_2 to form H_2O_2 and diminish the toxicity of the superoxide anion. Ascorbate peroxidase (APX) is one of the main enzymes that remove excess H_2O_2 in cells Chloroplast APX mainly removes the H_2O_2 produced by the Miller reaction. Malondialdehyde (MDA) is the key product of membrane lipid peroxidation when plants are under salt stress, and its content represents the degree of cell membrane damage [80] Therefore, MDA content can indicate plant salt stress and salt tolerance. OsAPX2, OsAPX7, OsAPx8, OsAPXa, and OsAPXb increase APX activity, lower H_2O_2 and malondialdehyde (MDA) levels, decrease oxidative stress damage, and enhance rice tolerance to salt stress [81–84]. Glutathione responsive rice glyoxalase II (OsGLYII-2) functions in salinity adaptation by maintaining better photosynthetic efficiency and increasing the antioxidant pool [85]. All these studies suggest that enhancing ROS-scavenging ability can efficiently increase the salt tolerance of rice and wheat.

3.4 Regulation of RGRs under salinity stress

Phytohormone levels fluctuate downstream of the early salt signaling phase, and the salt-induced signaling cascade eventually leads to adaptive responses [14]. Phytohormones are important endogenous chemical signals that regulate plant growth and development in both ideal and challenging environments [14]. Multiple phytohormones must be integrated and coordinated in order to respond and adapt to salt stress, such as abscisic acid (ABA), indole acetic acid (IAA), cytokinins (CK), ethylene (ETH), jasmonic acid (JA), gibberellic acid (GA), cytokinin (CK), and salicylic acid (SA), brassinosteroids (BR), triazoles (TR) which regulate normal growth and mediate responses to abiotic stress [14, 38, 86–88].

4. Salt stress tolerant gene in rice and wheat

Seed germination, seedling growth and development, vegetative and flowering stage growth, fruit setting, and root system structural development are all harmed by high saline levels. Crop yields will eventually suffer as a result of this phenomenon [89]. Modern agricultural research includes the use of biotechnological technologies and genetic engineering to study crop tolerance mechanisms, explore tolerant genes, and cultivated varieties of tolerant crops using molecular biology, molecular genetics, and other methods. The goal of plant tolerance research is to develop tolerant cultivars; nevertheless, the mechanism of plant stress tolerance is a difficult problem to solve. We can offer strategies to avoid salt damage and increase salt tolerance of plants based on basic research and a full understanding of the mechanisms of salt stress and salt tolerance of plants. A number of genes involved in salt stress have been investigated in order to better understand the salt tolerance process. It is hypothesized that overexpression of a single gene can increase transgenic plants' salt tolerance. *A. thaliana* plasma membrane Na⁺/H⁺ antiporter gene SOS1 and vacuolar Na⁺/H⁺ antiporter gene AtNHX1 can considerably improve the salt tolerance capacity of the transgenic plants [90]. Researchers found that AtSAT32 transgenic plants have higher salt tolerance and activity of vacuolar H transport pyrophosphatase in high salt environments after overexpressing AtSAT32 in *A. thaliana*. The AtSAT32 mutant, on the other hand, is extremely sensitive to salt [91]. Furthermore, through rice ABA-dependent regulatory mechanisms, the rice OsbZIP71 gene can considerably improve transgenic plant tolerance to high salt and drought [92]. Plant tolerance can also be improved by increasing the activity of antioxidant enzymes and increasing the degree of antioxidant metabolism in plants. The use of genetic engineering to create highly effective transgenic plants makes it possible to investigate the role of antioxidant enzymes in the scavenging of active oxygen. In numerous transgenic plants, the necessity of scavenging active oxygen has been demonstrated, and overexpression of SOD, APX, GR, and GAT improves plant tolerance to oxidative stress. The SOD isoenzyme has been the subject of the most extensive investigation among the numerous antioxidant enzymes [93]. Wheat salt tolerance gene research could lead to the utilization of saline soil and the expansion of wheat planting areas, resulting in higher wheat yields. Wheat salt tolerance genes have been studied extensively by researchers, with some successes. Wheat genes Ta-UnP, TaZNF, TaSST, TaDUF1, and TaSP have been shown in lab research to improve the salt tolerance of transgenic plants [1, 94–97]. Furthermore, ectopic expression of the wheat TaCIPK14 gene increases transgenic tobacco's salt tolerance [98]. Bread wheat with TaHKT1;5-D has a high salt tolerance [99]. The ability to tolerate salt is a multi-gene trait. Hundreds of thousands of genes and dozens of physiological systems are usually involved in its regulation. -As a result, research into the huge number of salt-tolerant genes is required. The study of salt-related gene function provides a theoretical foundation for increasing the stress signal network and improving rice and wheat plant tolerance to stress.

4.1 Epigenetic response to abiotic stress in rice and wheat

Histone post-transcriptional modifications, histone variations, DNA methylation, and non-coding RNAs are examples of chromatin state modification which can arrange diverse chromatin states that epigenetically define specific transcriptional outputs. The identification of epigenetic markers and their effect on plant response to abiotic stressors has been made easier because to recent advances in the field of -omics of important crops.

Recent research using –omics technologies have found a link between changed DNA methylation patterns and varied gene expression across the genome in three rice cultivars with variable susceptibilities to increasing salt and drought stress [100]. DNA methylation alterations were seen in both salt-tolerant and salt-susceptible rice varieties upon exposure into high salinity [101]. DNA immunoprecipitation with the 5-methylcytosine antibody and high throughput sequencing (MeDIP-seq) were used to determine the genome-wide methylation status of a salt resistant rice variety under increased salinity in a recent study [102]. These research identified new epigenetic variables and target genes linked to rice's response to salt stress, which could be used to improve resistance under salt stress conditions. The role of miRNAs in rice response to abiotic stress has been the subject of a lot of research over the last few years [103–106]. Rice tolerance to salt stress was boosted by overexpression of a *miR156*, while the expression of transcription factor target genes like *SQUAMOSA PROMOTER BINDING PROTEIN LIKE-9 (SPL9)* and *DIHYDROFLAVONOL-4-REDUCTASE (DFR)* which mostly associated with developmental processes was reduced [107].

Based on 850 RNA-seq data collected from 32 tissues sampled at different growth stages and/or under different stress treatments, an analysis of the wheat whole genome expression pattern (e.g. “expression atlas”) found higher average methylation status in low expressed genes [108]. Gardiner et al. [109] discovered that methylation patterns in wheat are not evenly distributed across the A, B, and D subgenomes, indicating that methylation patterns in progenitor species are different. In recent years, several research on epigenetic modifications in wheat in response to abiotic stress have been published. Wheat drought stress response has been linked to heterochromatic small interfering RNA (hc-siRNA) and micro RNAs (miRNA), both tiny regulatory RNAs [110]. For example, 2055 putative sites for 113 conserved durum miRNAs and 131 targets for four novel durum miRNAs that may contribute to genotypic stress tolerance have been found [111]. Differential epigenetic modifications in certain genes such as HKTs (high-affinity potassium transporters) were discovered in the shoots and roots of wheat genotypes with variable levels of susceptibility to salt stress [112].

5. Conclusion

Salinity stress is the one of the main abiotic factors that limits crop growth, development and yield. In this chapter, we briefly summarize how crop plants, especially rice and wheat respond to salinity induced osmotic, ion, and oxidative stresses and collect a significant number of studies and progress on the effects of salt stress on plants. Much research was undertaken to clarify physiological and biochemical and molecular mechanisms of plants salt tolerance applying molecular biology and biotechnological approach which will further explain the plant salt-tolerance mechanism and provide sufficient theoretical guidance for the future cultivation of salt stress tolerance rice and wheat. Moreover, by understanding the role of epigenetics in gene expression under abiotic stress could provide guidance in the development of climate-smart crops. Further enhancing plant salt tolerance and rich salt tolerant crop plants still need further study.

Conflict of interest

No

Notes/thanks/other declarations

No

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