

Response of Rice under Salinity Stress: A Review Update

Bhaswati Ghosh, Nasim Ali Md* and Saikat Gantait

Faculty Centre for Integrated Rural Development and Management, School of Agriculture and Rural Development, Ramakrishna Mission Vivekananda University, Ramakrishna Mission Ashrama, Narendrapur, Kolkata 700103, India

*Corresponding author: Nasim Ali Md, Faculty Centre for Integrated Rural Development and Management, School of Agriculture and Rural Development, Ramakrishna Mission Vivekananda University, Ramakrishna Mission Ashrama, Narendrapur, Kolkata 700103, India, Tel: +91-9831941312; E-mail: nasimali2007@gmail.com

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Abstract

Salinity has been a key abiotic constraint devastating crop production worldwide. Attempts in understanding salt tolerance mechanisms has revealed several key enzymes and altered biochemical pathways inferring resistance to crop plants against salt stress. The past decades have witnessed extensive research in development of salt tolerant cultivars via conventional means, improvised by modern era molecular tools and techniques. Rice (*Oryza sativa* L) is the staple food crop across several countries worldwide. Being a glycophyte by nature, its growth is severely imparted in presence of excess salt. Rice is susceptible to salinity specifically at the early vegetative and later reproductive stages and the response of the crop to excessive salt toxicity at biochemical and molecular level as well as physiological level is well studied and documented. An understanding of the specific response of rice to ion accumulation at the toxic level can aid in identifying the key factors responsible for retarded growth and limited production of rice with the future scope of mitigating the same. The present review summarizes the differential responses of rice, in particular, to salt toxicity enumerating the detailed morphological, physiological, biochemical and molecular changes occurring in the plant. An attempt to explain salinity tolerance and its future scope and implications in screening for salt tolerance has also been elucidated in the present study.

Keywords Salinity; Biochemical marker; Chlorophyll; *Oryza sativa* L; morphological descriptor

Abbreviations

CHL: Chlorophyll, EC: Electric Conductivity, PCA: Principal Component Analysis, POD: Peroxide Dismutase, RWC: Relative Water Content, SOD: Superoxide Dismutase, STI: Salt Tolerance Index, UPGMA: Unweighted Pair Group Method Arithmetic Average

Introduction

Rice, the major food crop

Rice (*Oryza sativa* L) belongs to the family Poaceae. The basic chromosome number of rice is $n=12$. The species can be either diploid or tetraploid. In this respect, *Oryza sativa* L. and *Oryza glaberrima* L. both are diploid species ($2n=24$) [1]. The Asian cultivated rice (*Oryza sativa* L) is the first fully sequenced crop genome and is a model crop species. Rice is considered as a major food crop across major countries worldwide. As a food crop, it forms the staple food of more than three billion people accounting for about 50-80% of their daily calorie intake [2]. It yields about one third of the total carbohydrate source. It provides the considerable amount of recommended Zinc and Niacin [3]. Rice protein is biologically richest as its digestibility is very high (88%). It is the 2nd most important crop in the world after wheat, covering almost 90% of area across Asia alone. The use of the crop varies widely ranging from its use as food in cereals, snacks, brewed beverages, flour, rice bran oil to its use in religious events across India. The medicinal value of the crop adds on more to the list.

Rice cultivation has been predominant in India across ages. Rice covers a global area of 156 million hectares of land producing about

650 million tons of crop [4]. Globally covering an area of 149.15 million ha area yielding about 550.19 million tones, this food crop is being cultivated across an area of 44.6 million ha in India. India ranks first in area and second in production following China, the largest producer of rice. As an economically and industrially important crop of India, rice provides about 23% of total world rice production and 45% of the total Indian food grain production. However with the expanding population, the increase in production of the crop is the urgent need of the hour in order to keep in accord to the national food and livelihood security system. India is one of the leading exporters of rice, in specific, basmati rice.

Salinity: an overview

Salinity as an abiotic stress widely limit the crop production severely [5]. A saline soil is usually the reservoir of a number of soluble salts such as Ca^{2+} , Mg^{2+} , Na^+ and anions SO_4^{2-} , Cl^- , HCO_3^- with exceptional amounts of K^+ , CO_3^{2-} , and NO_3^- . A soil can be termed as saline if its EC is 4 dS/m or more [6], (equivalent to approximately 40 mM NaCl) with an osmotic pressure of approximately 0.2 MPa. Salinity is the condition when the EC is sufficient to cause yield reduction of most crops. The pH of saline soils generally ranges from 7-8.5 [7]. However, the pH in saturated soil can vary provoking severe crop damage (Table 1). The arid and semi-arid zones, characterized by low precipitation and high evaporation are the most affected due to minimum lixiviation of salt from the soil profile resulting in increased salt accumulation. Salinity prone areas found in the arid and semiarid zones are usually accounted to the accumulation of salts over ages. Moreover, weathering of the parental rocks has accelerated the process a lot [8,9]. Salinity is a well off natural phenomenon occurring near sea shores due to sea water flooding.

| Electrical conductivity (dS m ⁻¹ at 25°C) | Crop response |
|--|--|
| 0-2 | Salinity effect is practically zero |
| 4-Feb | Reduction in yield of very sensitive crops |
| 8-Apr | Reduction in yield of most crops |
| 16-Aug | Only tolerant crops produce satisfactory yield |
| >16 | Few highly tolerant crops produce satisfactory |

Table 1: Crop response to salinity influenced by electrical conductivity of saturated soil extract

Source: Adapted from [7].

However, use of irrigation and land clearing can be listed as one of the many well-known anthropogenic reasons behind salinity [10].

Salinity has been a potential threat affecting almost 900 million ha of land which nearly accounts for 20% of the globally cultivated area and also half of the total irrigated land of the world [11,12]. Globally salt affected area accounts to about 1 billion ha of land [13]. In India the scenario accounts for about 8.4 million ha land affected by salinity [14]. In India, irrigated land accounts for only 15% of total cultivated land, nevertheless, it has at least twice the productivity of rain-fed land and yields about one third of the world's consumption. In accordance to the above facts and keeping in view the present alarming scenario, development of salt tolerant genotypes is definitely an urgent need of the hour.

Salinity: A key abiotic constraint to production

Soil salinity is one of major abiotic stress devastating agricultural production worldwide (Figure 1).

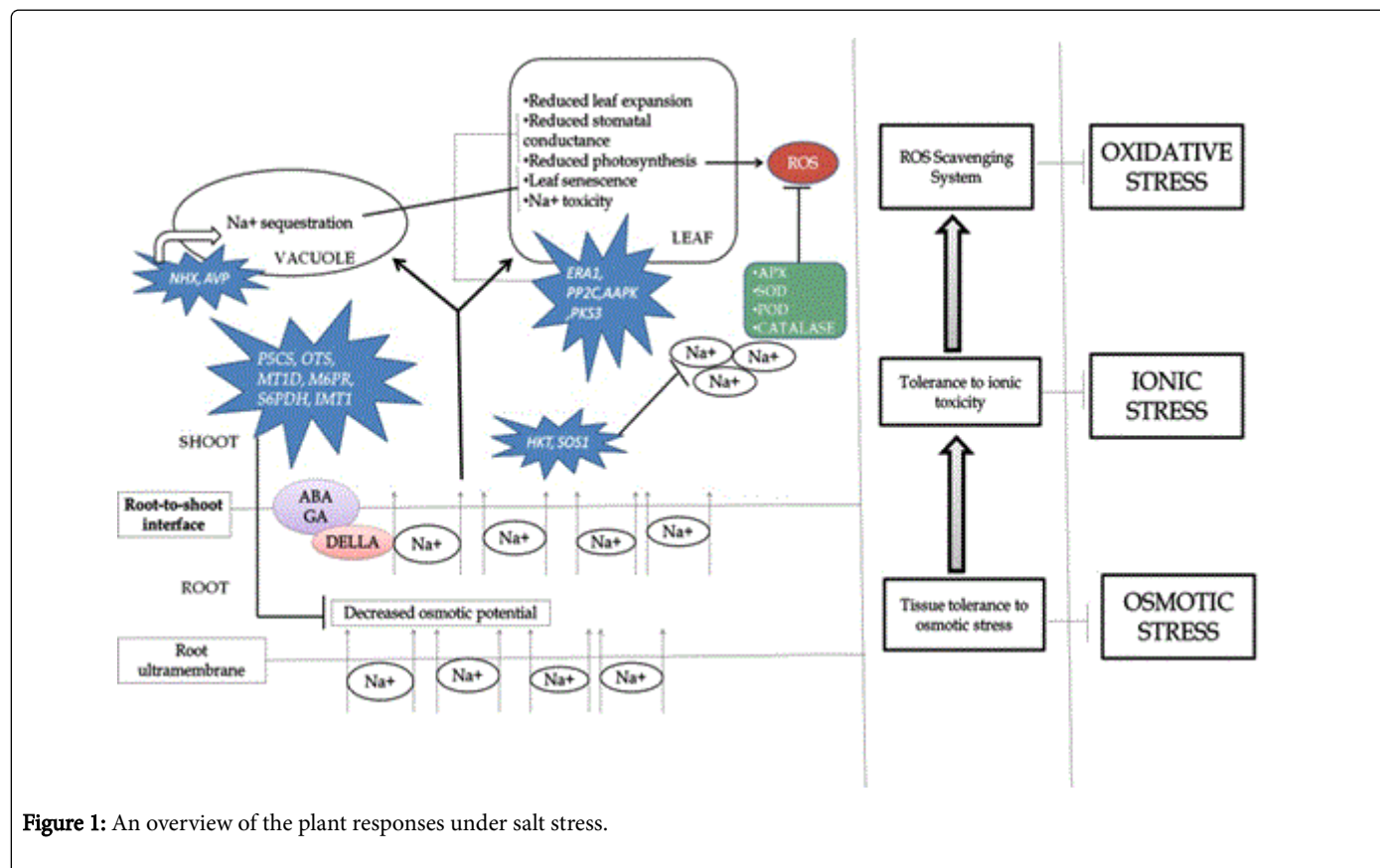


Figure 1: An overview of the plant responses under salt stress.

Globally, salt affected area accounts for about 800 million ha of land. Interestingly, this figure covers more than 6% of total global area. Of the 1500 million ha of dry land farming, 32 million ha (2%) are accounted to be salt effected at varying degrees by secondary salinity and to date more than 45 million ha (20%) of the total irrigated land (accounting about 230 million ha) is saline [4].

Soil salinity as an abiotic stress can be traced back in time even when human civilization did never existed or did not even started agriculture as an occupation. However, the devastating effect of it has been aggravated with the practice of irrigation and cultivation.

The effects of salinity in plants are many and interfere greatly with the yield and production of the crops. Salinity affect the plants mainly by imparting two types of stresses: Osmotic Stress (initial stage: caused due to increased osmotic potential of rhizosphere due to high salt concentration) and Ionic Stress (final stage: toxicity resulted by high ionic concentration). The destructive effects of salinity include retarded plant growth due to increased Na⁺ concentration [15], delay in flowering and impaired fertility, with partial or complete grain loss resulting in poor panicle development in rice [16-19], reduced P³⁺, K⁺ and Ca²⁺ concentrations [13], inhibition of photosynthetic activity [20-23].

Plants vary greatly in their response to salinity. The variation in response is random as salinity is a polygenic trait. NaCl being the most soluble and predominant salt, almost all plants have adapted mechanisms to regulate its concentration. It may be via preferential selection of ions, such as K^+ and NO_3^- commonly present in low concentrations or via effective exclusion of Na^+ and Cl^- by roots [24]. Halophytes, the natural flora of highly saline soils evolved against glycophytes by this exclusion principle mainly. For example, sea barley grass, *Hordeum marinum*, excludes both Na^+ and Cl^- only after it reaches the threshold of 450 mM NaCl [25]. An exclusive salt tolerance mechanism (presence of vesiculated hairs on their surface also known as trichomes) has also been reported in *Atriplex halimus*, a well known salt tolerant species, for adaptation to salinity stress by accumulating excess salts inside the hairs and thereby protecting the leaf parenchyma and vascular tissues [26].

The differential tolerance to salt toxicity in cereals ranges from barley (*Hordium vulgare*) being the most tolerant followed by Bread Wheat (*Triticum aestivum*), durum Wheat (*Triticum turgidum* ssp. durum) with rice being the most sensitive (*Oryza sativa*) [10]. Strikingly this difference in response is much more in dicotyledonous relatives than in the monocots.

A study of salt tolerance mechanism has been possible with a comparative analysis of the patterns of response between a wild type and the natural halophytic relative. In this regard, light has been thrown into the mechanism of salinity tolerance when *Arabidopsis thaliana* was being compared with its wild halophytic relative *Thellungiella halophilla*. The contrasting responses highlighted their selective tolerance to salt: *Arabidopsis* ceased its growth in presence of the constant exposure to 100 mM salt whereas [27] endured almost little or no effect on the growth rate of *Thellungiella* [28].

Effect of salinity stress in rice crops

Rice is a crop with great economic importance [29,30] and is cultivated across 114 countries globally [31]. However, the abiotic and biotic stresses can reduce its yield. This problem will be worse in attention to increase of global population and food sources deficiency [32]. Rice is susceptible to salinity, specifically, at the early vegetative and later reproductive stages [5,33]. Rice genotypes show wide variations in salinity tolerance due to additive gene effects [34]. Studies indicated that rice is more resistant at reproductive and grain filling than at germination and vegetative stages [35], as well as low levels of salinity can increase the resistance of rice to higher and lethal salinity levels [36]. At present, salinity is the second type of stress and is the most predominant hindrance to rice production after drought [37]. The effects of salinity on the growth and yield of rice in field have been well studied including the study of genotypic variance for salt tolerance amongst the paddy germplasm [38-40].

Response of rice under salinity

With the aim of generating salt-tolerant rice cultivars, several morpho-physiological studies have been accomplished till date. The main focus of such an approach was to maximize the genetic diversity between parental genotypes. Response of plants to salinity is a random and natural process. Rice as a crop has been reported as sensitive in the seedling and reproductive stages [23,41] and has resulted in reduction of crop yield and productivity [16]. In case of rice, salinity is found to induce both biochemical and physiological changes causing growth inhibition and yield loss [19,42-45]. Several physiological parameters

have been studied in the process of evaluation of true salt tolerant lines to understand the drastic effects of salt accumulation at physiological level: plant height, plant dry weight, leaf injury and $Na^+ - K^+$ ratio [37,46-49].

The effect of salinity on rice is many fold, leading to inhibition of germination, difficulties in crop area establishment, leaf area development, decrease in dry matter production, delay in seed set and also even sterility can occur [40,50]. It has been well documented that the effect of salinity on seedling growth, seedling establishment, grain yield components such as spikelet number, tiller number has successively lead to a reduction in grain yield [51-54]. A wide range of variation has been reported between and within different rice varieties in response to salinity [50,55] checked for varying floodwater salinity tolerance among a number of paddy varieties and reported that floodwater electrical conductivity (EC) reduced germination rate by almost 50% and yield by 80% for the most susceptible cultivar in accordance to the highest salinity level imposed. Further, salinity also resulted in a decrease of the spikelet number per panicle, 1000 grain weight and increased sterility, regardless of the season and development stage.

Morpho-physiological response

Resistance to salinity stress does not rely on a single trait and thereby understanding of the tolerance mechanisms should employ the study of the response of rice under stress. A study of the response of rice to salinity began with the understanding of the underlying physiological mechanisms associated with plant defense mechanisms being activated during stress. The effect of salinity on plants is initiated by the osmotic effect characterized by lowered osmotic potential followed by later ionic effect causing ion toxicity. Studies conducted to interpret the response of rice at physiological level indicated chloroplast and mitochondria to be the most vulnerably affected organs among others [56]. Hence, chlorophyll content, changes in chlorophyll fluorescence (Fv/Fm) and membrane permeability are efficient and potential indicators for understanding the inhibitory effect of salt on the photosynthetic efficiency [20,57]. Salinity has been reported to decrease leaf area tremendously and also showed profound changes in leaf anatomy in rice grown in-vitro [58] or in greenhouse [59] as verified by [60]. The ultra-structural observations briefed by [56] also ensured the inhibitory effect of salt on leaf thus hampering the photosynthetic efficiency: swelling of thylakoids followed by disruption of chloroplasts. Salinity was observed to exert severe detrimental effect on the mesophyll tissue even stretching its harmful effects to the vascular bundles. Evaluation of the response of the crop plant at later stages was to comprehend the toxic ionic effect of salt on the plants. The toxic effect of accumulation of sodium salt are mainly mitigated by the plant via (a) salt exclusion [61,62], (b) selective ion uptake [63,64] and (c) regulation of K^+/Na^+ ratio [66-69]. A study of the root ultra-structure elucidated the penetrating effect of salinity on rice and the response of the crop plant with an increased rate of vacuolation and vesiculation decreasing mucilage production in treated plants compared to control as observed by [69]. A strong correlation was suggested between sodium content, ratio of K^+/Na^+ with seedling growth and grain yield under salt stress [51,52,70]. Evaluation of different cultivars was precised at morpho-physiological level by estimating parameters like tiller number, leaf area, panicle length, root length, biomass, dry weight, RGR (Relative Growth Rate), RWC (Relative Water Content) [16,52,70-72]. Yancey et al. [73] observed an increased level of leaf RWC in paddy under salinity and suggested the role of osmo-protectants in preventing cell injury from

salt stress-induced dehydration. An understanding of the STI (Salt tolerance index) evaluating indigenous landraces at the morpho-biochemical level has been reported by [49] implicating the importance of landraces as probable sources for de-novo genes inferring tolerance to them as being observed in the study. Thus, the evaluation of different cultivars at morpho-physiological level enabled to build up a comprehensive idea about the several physiological mechanisms operating in the crop plant as a response to salt stress but failed to provide an insight about the exact pathways and defense system and the components being directly or indirectly involved in the process.

Response at the biochemical level

The effect of salinity on crop plants may be categorized as a two-fold process: an initial osmotic effect followed by ionic stress when salt accumulation reaches its toxic level [10]. The initial osmotic effect in plants refers to the lowered water potential to the increased concentration of salt with an enhanced osmotic potential. One of the important plant defenses is the osmotic adjustment in plants accomplished via accumulations of high concentrations of inorganic ions or low molecular weight organic solutes. These compatible osmolytes found in higher plants are actually certain low molecular weight sugars, organic acids, polyols. They also include nitrogen containing compounds such as amino acids, amides, imino acids, proteins and quaternary ammonium compounds. Studies indicated that proline, which occurs widely in higher plants, assimilates in larger amounts in salt stressed plants [39,74,75]. Proline accumulation in rice has also been reported by [76] suggesting its active roles in osmotic adjustment, shielding the enzymes and membranes, also providing energy and nitrogen for utilization during exposure to salinity [77,78].

Soluble sugars and starch has been observed to serve as an osmoticum in a number of plants as a response to salinity [79,80]. An increase in sugar content in shoots has been reported by [81] and also an increased starch content in roots been showed in the roots of rice which contributes to the osmotic adjustment to the crop exposed to salinity by maximizing sufficient storage reserves to prop up the primary metabolism [82,83]. The toxic effects of salinity are masked by accumulation of glycine betaine in rice as being reported by [84]. These compounds are reported to have active role in osmotic adjustment, fortification of the cellular macromolecules, nitrogen storage. They are important to balance the cellular pH, detoxify the cells and scavenge the ROS species.

The other way to respond against salinity is alteration or accumulation of protein level. Exposure to salinity can result in denovo protein synthesis or an up-regulation of the process to increase the concentration of certain proteins already present in the plant [85]. Proteins accumulating in plants grown under saline conditions act as a storage form of nitrogen which is re-utilized in absence of stress [86-88]. Protein synthesis is also destined to play an active role in osmotic adjustment. A significant increase in soluble protein content and positive correlation has been ensured in tolerant rice seedlings compared to the sensitive ones.

Response at molecular level: targeted approach and cellular signaling

Attempts to understand salinity tolerance at the gene or molecular level started with the aim to bred for salinity tolerance and develop salt tolerant lines. Earlier studies on salinity tolerance mechanisms

revealed the complexity of salinity as an abiotic stress and that there do exists not only inter-species variation in plant in response to this stress but also inter-varietal differential response as far as rice being concerned as a crop [87-90]. Genetic diversity analysis of several genotypes were thus employed to screen for salinity tolerance by various molecular markers: RFLP and SSLP mapping by [91], RAPD and SSR analysis by [92], morpho-molecular evaluation of landraces by [93]. In order to define the complexity and the nature of the inheritance of salinity in rice, several studies were conducted which included conventional techniques such as positional cloning [94,95] and 'insertional mutagenesis' [96,97]. Several genes were identified in rice induced by high salinity levels as elaborated by [98] in the course of monitoring the expression profile of rice under stress, which included genes like salt, catalase and several denovo genes.

The response of plants to combat salinity stress is initiated by their ability to sense the initial osmotic stress or osmo-sensing. Though the physiological mechanisms throw light to the modification taking place in the tissue or cellular level, which is actually measured phenotypically by quantifying the Na^+/K^+ ratio, however, control at genetic level and the regulatory pathway solely formed the backbone behind understanding of the induced signaling pathway in response to this stress. With an aim to achieve the same, experiments conducted on different mutants of *Arabidopsis thaliana*, came forth with several regulatory genes and important pathways: *Arabidopsis thaliana* histidine kinase, *ATHK1*: candidate osmosensor [99], CDPKs (Ca^+ dependent protein kinases: *OsCDPK7* being identified in response to salinity in rice by Sajio et al.); MAPKs (Map kinases: *OsMAPK5* being identified in rice whose suppression led to hypersensitivity to salinity by [99,100]; SOS pathway (*SOS1*, *SOS2*, *SOS3*: [101]). These multiple genes governing the regulation of the response of the plants to salinity stress ensured the polygenic character of salinity as a trait. Thereby, work initiated to identify QTL (Quantative trait loci) related to salt tolerance. The first breakthrough was achieved by [37] where a major QTL 'saltol', has been mapped on chromosome I in an F8 recombinant inbred lines (RIL) population of Pokkali X IR29cross, using amplified fragment length polymorphism (AFLP) markers. In recent years, QTL analysis in rice helped in mapping several QTLs related to several characters correlated with salinity: QTLs mapped on chromosome 1 and 2 for shoot growth [102]; 5 major QTLs: *qRL-7* for root length, *qDWRO-9a* and *qDWRO-9b* for dry weight root, *qBI-1a* and *qBI-1b* for biomass [103]. Separate QTLs being identified each for sodium uptake, potassium uptake, and sodium:potassium selectivity [104]; 8 QTLs accounting each of three for three traits of the shoots, and each of five for four traits of the roots at five chromosomal regions [105] and many more. A total of 35 QTLs were identified by [106] in an F2 mapping population derived from a Sadri/FL478 cross, the major QTL clusters being mapped in chromosomes 2, 4 and 6 for multiple traits under salinity stress. Identification of QTL for salinity tolerance opened a new horizon in the study of salinity and the plant response to cope up with this stress thereafter. Studies are being conducted to formulate and identify different alleles whether associated with the respective QTLs for salinity [107-109].

Defense system of rice against salinity stress

Plant defense mechanisms to combat the toxic effect of salt stress can be categorized into three processes viz. a) Tolerance to osmotic stress via osmotic adjustment, b) Na^+ exclusion from leaf blades by selective ion uptake and also regulation of uptake of sodium ions at molecular level, c) Tissue tolerance, i.e. tolerance of tissue to accumulated Na^+ , or in some species, to Cl^- via compartmentalization

of absorbed or accumulated salt [10]. In addition to osmotic stress and ionic stress plants are subjected to oxidative stress which is caused mainly due to the inhibitory action of salinity on photosynthesis. In order to cope up with the upcoming photo-inhibitory effects plants undergo modification in their metabolic pathways such as heat debauchery by the xanthophyll pigments and electron transfer to oxygen acceptors (not water) which can result in the formation of ROS (reactive oxygen species). The later response is however mitigated by an initiation of the up regulation of several regulatory enzymes for such as superoxide dismutase, ascorbate peroxidase, catalase, and the various peroxidases [105-109]. The enzymatic antioxidant defense system of plants is inclusive of Superoxide dismutase (SODs), peroxidases, Catalases, and the enzymes of the ascorbate–glutathione cycle: Ascorbate peroxidase (APX), Monodehydro-ascorbate reductase (MDHAR), Dehydro-ascorbate reductase (DHAR), and Glutathionereductase (GR) while non-enzymatic antioxidants include: Ascorbate (AsA) and Glutathione (GSH) [110,111]. The oxidative damage caused is a measure of poise between the formation of ROS and its subsequent removal by the antioxidative scavenging system [109,112]. The active role of the anti oxidative system has also been observed in roots of rice cultivars differing in salt tolerance [113-116]. Sese and Tobita [109] reported a significant decrease of SOD activity in the salt-susceptible varieties whereas an increase in SOD activity in the salt-tolerant variety in response to salt treatment [115]. An increase in peroxidase activity in salt-tolerant cultivars under salt stress has been recorded by various researchers [117-119]. In rice, differential opinions are being established as far as oxidative responses are being concerned. Mishra et al. [120] reported an increase in SOD activity, APX activity and GPX activity, however reporting a decrease in CAT activity with increased exposure to salinity levels. An anticipation of the above results was however elucidated by [121] where an increased CAT activity and decreased SOD and POX activity was observed in salt tolerant lines.

The implication: screening against salinity stress

Differential salinity sensitivity at various growth stages is one of the factors affecting salt tolerance phenotypes. Generally, rice plants is very sensitive to salinity at young seedling stages and less sensitive at reproductive stages [70,52]. To assess the response of germplasm to salinity a proper screening technique is required. In paddy, the screening can be done at its two salt sensitive stages. Screening at seedling stage is a rapid method and based on simple criteria. Screening can be done at field level or in laboratory condition. The former one is difficult because of presence of soil heterogeneity, climatic factors and other environmental factors which may itself interfere with the physiological processes. Environmental influence is a very complicated factor intertwining salt tolerance. Any environmental changes such as humidity and temperature will affect evapo-transpiration and further influence ion transport [5]. This makes the evaluation of the phenotypes at field conditions very difficult. So screening under laboratory condition has many advantages over field screening.

A combined pleiotropic effect of different factors alters plant growth and development at three levels of the plants viz. physiological, biochemical and molecular level. Primitive works done ensured screening for salinity tolerance based on agronomic characters. Thus, early experiments conducted on development of salt tolerant genotypes solely relied on conventional selection and breeding techniques [5,74,120-124]. which included screening at the morphological level based on several physiological and agronomical characters.

Morphological screening can be done using the parameters described as effective salinity indices like root length, shoot length, plant biomass, shoot Na^+/K^+ ratio [38,39,125,126]. The morphological screening can be started at least after 10 days of exposure to saline solution for screening properly the tolerant genotypes from susceptible [37]. However screening for salinity tolerance based on agronomic characters may not prove to be practicable and fruitful technique because they are highly influenced by the environment. The understanding of the salt tolerance mechanisms and furthermore the assessment of salt tolerance is expected to be much more well defined by screening the genotypes at the biochemical level as undertaken by many scientists [75,81,112,119,125,126]. It provided an idea about the potential indicators of salt tolerance at the whole plant, tissue or cellular level. The identification of the metabolic sites affected by salt stress and, conversely, the mechanisms utilized by plants to survive salinity stress has also been well understood. Molecular screening for salt tolerance in rice accounts for the recent approaches for understanding the response of rice under salt stress and thereby mines useful alleles responsible for salt tolerance [91,107,127-129]. The identification of saltol QTL in 2010 by Thomson et al. has widened the horizon for further work and development as far as genetic approach is being concerned [130-135].

Conclusion

Salinity as an abiotic stress is the second most devastating phenomenon after draught and interfering with the production and yield of rice globally. Rice is the major food crop cross across several countries globally. With the increased population worldwide the demand for rice is also increasing in accordance. Rice, a glycophyte, by nature is susceptible to salinity and show wide and vivid response against the detrimental effects of increased salt accumulation. The plant defense system in rice includes arrest and alleviation of the harmful effects of salt toxicity at physiological, biochemical and molecular levels. A comprehensive study of the manifold works done to apprehend the effect of salinity and the response of the crop in turn has been illustrated here. Due to the polygenic nature of the stress, it has been very meticulous to comment in particular about the exact mechanism by which mitigation of the same is achieved. However, a number of metabolic pathways, enzyme complexes, regulatory genes and QTLs have been enumerated till date to throw some light on the various particular responses at various stages of this abiotic stress. With respect to the devastating effect of salinity on this staple food crop, it is very important assimilate the knowledge of the response of the crop towards salinity. This will aid in future work of improvement towards salinity tolerance and breeding for salinity tolerance. A number of works are being conducted across globally to understand salinity and the complex mechanisms of rice to mollify the same. In this regard, it is of prior importance to have an upshot of all the works going on to understand salinity and its effect on rice. This review is a minor attempt to summarize the salient contributions and breakthroughs made in this area in the course of understanding the response and thus the plant defense to fight salinity as a stress.

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