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Responses of rice under salinity stress: A review

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Abstract

Rice (*Oryza sativa* L.) is an important staple crop that feeds more than one half of the world's population and is the model system for monocotyledonous plants. Salinity has been a key abiotic constraint devastating crop production worldwide. However, rice is very sensitive to salinity and is the most salt sensitive cereal crop with a threshold of 3 dSm^{-1} for most cultivated varieties. Even at EC as low as 3.5 dSm^{-1}, rice loses about 10% of its yield and 50% yield loss was recorded for rice at EC 7.2 dSm^{-1}. Attempts in understanding salt tolerance mechanisms has revealed several key enzymes and altered biochemical pathways inferring resistance to crop plants against salt stress. 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: rice, salinity, tolerance, screening, glycophyte, biochemical, molecular, abiotic

Introduction

Rice is considered as a major food crop across major countries worldwide. It is the 2nd most important crop in the world after wheat, covering almost 90% of area across Asia alone. 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 (Khush, 2005) [51]. It yields about one third of the total carbohydrate source. It provides the considerable amount of recommended Zinc and Niacin (Gopalan, 2007) [39]. Rice protein is biologically richest as its digestibility is very high (88%). 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 (FAO, 2008) [31]. 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. By 2050, the world's population is predicted to reach 9.6 billion people and food production needs to increase approximately 70% by 2050 or 44 million metric tons annually to provide sufficient food for this population (FAO, 2009 and FAO, 2012) [32, 33]. This is a challenge because there is very little potential for future expansion of arable lands, whereas environmental stresses affecting crop production are increasing (Tester, 2010; Eckardt, 2009 and Cominelli *et al.*, 2013) [91, 28, 23]. 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.

Salinity as an abiotic stress widely limits the crop production severely (Shannon, 1998) [86]. Salinity is a general term used to describe the presence of elevated levels of different salts such as sodium chloride, magnesium and calcium sulphates and bicarbonates in soil and water (Hoang, 2014) [42]. Salinity can develop naturally. However, human intervention has disturbed natural ecosystems, changed the hydrology of the landscape and significantly accelerated the salinisation of waterways and land. Irrigation and extensive clearing of vegetation, which bring the groundwater with soluble salts to, or close to, the soil surface, are the two major human Activities that accelerate salinity.

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 (USDA, 2016) [95], (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 (Mengel *et al.*, 2001) [59]. 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 (Munns, 2002 and FAO, 2007) [30]. Globally salt affected area accounts to about 1 billion ha of land (Fageria *et al.*, 2012) [29]. In India the scenario accounts for about 8.4 million ha land affected by salinity (Tyagi and Minta, 1998) [92]. Of the 230 million ha of the world's irrigated land, 45 million ha (20%) has been salt-affected (Munns, 2005) [66]. When growing on salt-affected soils, crops must compete with salts in the soils for water as well as to cope with ion toxification, nutritional disorders and poor soil physical conditions to survive, therefore, their productivity was reduced (Shrivastava and Kumar, 2015 and Munns and Tester, 2008) [89, 67]. Asia accounts for 90% of the world's production and consumption of rice (Virmani and llyas-Ahmed, 2008 and Khush, 2005) [51] but "Sea-level rise is already increasing rice-killing salinity in the deltas of Asian rivers, the richest rice-growing areas of the world" (Dayton, 2014). Therefore, it is crucial to enhance rice tolerance to salinity stress to enable this staple crop to provide enough food for rice-consuming communities. Although some success has been reported for enhanced salinity stress tolerance in rice, the achievements so far are quite modest. This review will discuss challenges that hinder the success of the improvement of salinity stress tolerance in rice and identify potential opportunities for enhancing salinity stress tolerance in this important crop.

Salinity is a key abiotic constraint in rice production

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 (Saqid *et al.*, 2008), delay in flowering and impaired fertility, with partial or complete grain loss resulting in poor panicle development in rice (Abdullah *et al.*, 2001; Kato *et al.*, 2008 and Rao *et al.*, 2008) [1, 49, 79], reduced P^{3+},K^+ and Ca^{2+} concentrations (Fageria *et al.*, 2012) [29], inhibition of photosynthetic activity (Netondo *et al.*, 2004; Cha-um *et al.*, 2006; Chaves *et al.*, 2009 and Moradi and Ismail, 2007) [68, 20, 21, 64].

Rice crop responses to salinity stress

In terms of responses to salinity stress, plants can be divided into two groups-halophyte or glycophyte-based on their level of salinity tolerance. Halophytes are plants that tolerate relatively high salt concentrations (400 mM NaCl), while glycophytes tolerate low concentrations (Maas and Nieman, 1978) [57]. Most crops are glycophytes and their growth is retarded during salinity stress. Among the cereals, rye (*Secale cereale*) is the most tolerant (threshold of 11 dSm^{-1}) and rice is the most sensitive crop plant with a threshold of 3 dSm^{-1} for most cultivated varieties (USDA, 2016) [95] whereas, generally, a soil is only considered saline (salt affected) if it has an EC above 4 dSm^{-1} (Rengasamy, 2006). Even at EC as low as 3.5 dSm^{-1}, rice loses about 10% of its yield, and 50% yield loss was recorded for rice at EC 7.2 dSm^{-1} (Umali, 1993) [93]. Plants vary greatly in their response the salinity (Table 1). The variation in response is random as salinity is a polygenic trait.

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 has been reported to be relatively tolerant to salinity stress during germination, active tillering and towards maturity, but sensitive during early seedling and reproductive stages (Heenan *et al.*, 1988 and Zeng *et al.*, 2001) [41, 105] and has resulted in reduction of crop yield and productivity (Zeng and Shannon, 2000). In case of rice, salinity is found to induce both biochemical and physiological changes causing growth inhibition and yield loss (Rao *et al.*, 2008; Colom and Vazzana, 2003; Chang and Sung, 2004; Fukuda *et al.*, 2007; Kang *et al.*, 2007 and Yang *et al.*, 2008) [79, 22, 19, 36, 48, 101]. 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 (Rergorio *et al.*, 1997; Yang *et al.*, 2008; Bhowmik *et.al.*, 2009; Haq *et al.*, 2009 and Ali *et al.*, 2014) [101, 18, 40]. An addition of as little as 50 mM NaCl in the soil can reduce rice yield significantly (Yeo and Flowers, 1986) [103].

Table 1: Crop response to salinity influenced by electrical conductivity. Source: (Umali, 1993)

Electrical conductivity ($dS\ m^{-1}$ at 25°C)	Crop response
0-2	Salinity effect is practically zero
2-4	Reduction in yield of very sensitive crops
4-8	Reduction in yield of most crops
8-16	Only tolerant crops produce satisfactory yield
>16	Few highly tolerant crops produce satisfactory

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 (Rahman *et al.*, 2000) [77]. 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

(Netondo *et al.*, 2004 and Baker, 2008) [68, 15]. Salinity has been reported to decrease leaf area tremendously and also showed profound changes in leaf anatomy in rice grown in-vitro (Bahaji *et al.*, 2002) [14] or in greenhouse (Wankhede *et al.*, 2010) as verified by Wankhede *et al.* (2013). The ultra-structural observations briefed by Rahman *et al.* (2000) [77] also ensured the inhibitory effect of salt on leaf thus hampering the photosynthetic efficiency: swelling of thylakoids followed by disruption of chloroplastids. 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 (Garcia *et al.*, 1997 and Yeo *et al.*, 1999) [37, 102], (b) selective ion uptake (Flowers and Yeo, 1986 and Asch *et al.*, 1997) [103, 12] and (c) regulation of K^+/Na^+ ratio (Rajarathinam *et al.*, 1988; Pandey and Srivastava, 1991; Rahman *et al.*, 2001 and Flowers and Yeo, 1981) [78, 70, 76, 34].

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 Flowers and Yeo (1981) [34]. A strong correlation was suggested between sodium content, ratio of K^+/ Na^+ with seedling growth and grain yield under salt stress (Khatun *et al.*, 1995; Lutts *et al.*, 1995 and Ankita and Cabuslay, 1990) [50, 55]. 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) (Zeng and Shannon, 2000; Lutts *et al.*, 1995; Yancey *et al.*, 1982) [55, 100]. Ashraf (1994) [13] 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 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 defence system and the components being directly or indirectly involved in the process.

Response of rice 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 (Munns and Tester, 2008) [67]. The initial osmotic effect in plants refers to the lowered water potential to the increased concentration of salt with an enhanced osmotic potential. 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 (Jones, 1981; Ali *et al.*, 1999 and Lutts *et al.*, 1996) [45, 5, 56]. Proline accumulation in rice has also been reported by (Bandurska, 1993) [16] suggesting its active roles in osmotic adjustment, shielding the enzymes and membranes, also providing energy and nitrogen for utilization during exposure to salinity (Perez *et al.*, 1993 and Cram, 1976) [72, 24].

Soluble sugars and starch has been observed to serve as an osmoticum in a number of plants as a response to salinity (Popp and Smirnoff, 1995 and Amirjani, 2011) [73, 9]. An increase in sugar content in shoots has been reported by Hurry *et al.* (1995) [43] 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 (Dubey and Singh, 1999 and *Sakamoto et al.*, 1998) [27, 83]. The toxic effects of salinity are masked by accumulation of glycine betaine in rice as being reported by Pareek *et al.* (1997) [71]. 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 Proteins accumulating in plants grown under saline conditions act as a storage form of nitrogen which is re-utilized in absence of stress (Jha and Singh, 1997; and Akbar and Yabuno, 1975) [44, 2]. 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 signalling

Salinity tolerance at the gene or molecular level started with the aim to bred for salinity tolerance and develop salt tolerant lines. Genetic diversity analysis of several genotypes were thus employed to screen for salinity tolerance by various molecular markers: RFLP and SSLP mapping by Kanawappe *et al.* (2011), RAPD and SSR analysis by, morpho-molecular evaluation of landraces by Rikke and Johnson (1998) [80]. 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 (Ron and Weller, 2007 and Bechtold *et al.* 1993) [81. 17] and ‘insertional mutagenesis’ (Salvi and Tuberosa, 2005 and Rabbani *et al.*, 2003) [84, 75]. Several genes were identified in rice induced by high salinity levels as elaborated by Urao *et al.* (1999) [94] in the course of monitoring the expression profile of rice under stress, which included genes like salT, catalase and several denovo genes.

The first breakthrough was achieved by Hoang *et al.* (2014) [42] where a major QTL ‘saltol’, has been mapped on chromosome I in an F_8 recombinant inbred lines (RIL) population of Pokkali x IR29 cross, 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 (Sabouri and Sabouri, 2008) [82]; 5 major QTLs: qRL-7 for root length, qDWRO-9a and qDWRO-9b for dry weight root, qBI-1a and qBI-1b for biomass (Koyama *et al.*, 2014) [52]. Separate QTLs being identified each for sodium uptake, potassium uptake, and sodium:potassium selectivity (Lin *et al.*, 2004) [53]; 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 (Mohammadi *et al.*, 2013) [63] and many more. A total of 35 QTLs were identified by Mohammadi *et al.* (2008) [62] in an F_2 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 (Apel and Hirt, 2004; Logan, 2005 and Asada, 1999) [10, 54, 11].

Defence system of rice against salinity stress

Plant defence 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 (Munns and Tester, 2008) [67].

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) (Sharma and Dubey, 2007 and Dionisiosese and Tobita, 1998) [87, 26]. The oxidative damage caused is a measure of poise between the formation of ROS and its subsequent removal by the anti-oxidative scavenging system (Asada, 1999 and Demiral and Turkan, 2005) [11, 25]. The active role of the anti oxidative system has also been observed in roots of rice cultivars differing in salt tolerance (Mandhania, 2006; Mittal and Dubey, 1991; Kalir *et al.,* 1984 and Sheoran and Garg, 1979) [58, 61, 46, 88]. Asada (1999) [11] 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 (Kalir *et al.*, 1984) [46]. An increase in peroxidase activity in salt-tolerant cultivars under salt stress has been recorded by various researchers (Garg *et al.*, 2002; Mishra *et al.*, 2013 and Sarkar *et al.*, 2013) [38, 60, 85]. In rice, differential opinions are being established as far as oxidative responses are being concerned. Noble and Rogers (1992) [69] reported an increase in SOD activity, APX activity and GPX activity, however reporting an decrease in CAT activity with increased exposure to salinity levels. An anticipation of the above results was however elucidated by Al-khatib *et al.* (1993) [8] where an increased CAT activity and decreased SOD and POX activity was observed in salt tolerant lines.

Conclusion

Rice is the major food crop cross across several countries globally. 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 very sensitive to salinity even at EC as low as 3.5 dSm^{-1}, rice loses about 10% of its yield and 50% yield loss was recorded for rice at EC 7.2 dSm^{-1}. The plant defence system in rice includes arrest and alleviation of the harmful effects of salt toxicity at physiological, biochemical and molecular levels. 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.

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