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Salt Tolerance in Rice: Focus on Mechanisms and Approaches

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Abstract: Salt tolerance is an important constrain for rice, which is generally categorized as a typical glycophyte. Soil salinity is one of the major constraints affecting rice production worldwide, especially in the coastal areas. Susceptibility or tolerance of rice plants to high salinity is a coordinated action of multiple stress responsive genes, which also interacts with other components of stress signal transduction pathways. Salt tolerant varieties can be produced by marker-assisted selection or genetic engineering by introducing salt-tolerance genes. In this review, we have updated on mechanisms and genes which can help in transferring of the salt tolerance into high-yielding rice varieties. We have focused on the need for integrating phenotyping, genomics, metabolic profiling and phenomics into transgenic and breeding approaches to develop high-yielding as well as salt tolerant rice varieties.

Key words: rice; mechanism; salinity; salt tolerance; yield; gene; protein

World population is increasing rapidly by every passing year and there will be a need to produce 87% more of what we are producing today especially food crops such as rice, wheat, soy and maize by 2050 (Kromdijk and Long, 2016). However, abiotic stress, which includes salinity, drought, heat and cold, critically threatens crop production and causes significant yield loss in large areas (Pareek et al, 2010; Mantri et al, 2012). Among these, soil salinity is one of the major environmental constraints to crop production and is expected to increase due to global climate changes and as a consequence of many irrigation practices. Salinity can be termed as severe abiotic stress which includes all the problems due to salts primarily by an abundance of sodium chloride from natural accumulation or irrigation (Flowers and Flowers, 2005). More than 8×10^8 hm^2 land throughout the world is affected by salinity (FAO, 2008). An average of 2 000 hm^2 irrigated land across 75 countries has been degraded by salt every year according to a study by Economics of Salt-Induced Land Degradation and Restoration (unu.edu/media-relations/releases). Salinity can be associated with higher sea levels as it brings saline water further inland and exposes more rice growing areas to salty condition (irri.org/news/hot-topics/rice-and-climate-change). Floodwater with the electric conductivity level more than 2 dS/m leads to yield loss up to 1 t/hm^2 in rice (Asch and Wopereis, 2001). Millions of hectares in South and Southeast Asia, which are well suited for rice production, are left uncultivated or grown with very low yields because of salinity (knowledgebank.irri). Accretion of salts in the soil surface is caused by different factors in different geological and climatic regions (Reynolds et al, 2001).

Plants can be primarily divided into two groups based on the effect of salt on plant growth: Crop species sensitive to soil salinity are known as glycophytes, whereas plants grown in water of high salinity or which can generally tolerate high salt

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concentrations are known as halophytes (Tuteja et al, 2011). Plants can respond to various stress as individual cells and synergistically as a whole organism. Growth reduced by salinity can be distinguished by measuring effects immediately upon addition of salt or after several days to weeks (Roy et al, 2014). Salinity affects stomatal closure which in turn causes increase in leaf temperature and inhibition of shoot elongation (Rajendran et al, 2009; Sirault et al, 2009), and these effects are clearly independent of the accumulation of salts in the shoot. This was termed as 'osmotic phase' by Munns and Tester (2008), and as a 'shoot salt accumulation independent effect' by Roy et al (2014). In response to extended salinity phase, we can observe the inhibition of growth over a period of time and premature senescence of those older leaves, which was termed as the 'ionic phase' by Munns and Tester (2008). Genotypic differences in the growth of upland rice under stress have been linked with the osmotic adjustment. Maintenance of whole plant and shoot water status, as well as mechanisms like Na^+ exclusion or maintenance of potassium in developing tissues and rapidly growing leaves, contribute to salt tolerance in rice varieties (Yeo et al, 1990).

The capacity to tolerate salinity is a key factor in plant productivity (Momayezi et al, 2009). Salinity interferes with rice growth and development, plant adaptation and stress responses. Salinity causes sterility in rice if imposed during pollination and fertilization (Pearson and Bernstein, 1959). Akbar and Yabuno (1977) found that salinity causes panicle sterility in only some rice varieties, suggesting some genetic control (Khatun et al, 1995). Comparisons between crosses involving male and female parents grown at different salinity conditions indicate that effects on the female plants dominate on pollinator plants (Khatun et al, 1995). Salinity delays heading in rice, which negatively affects a number of yield components (Grattan et al, 2002). Salinity stress affects seed germination, seedling growth, leaf size, shoot growth, shoot and root length, shoot dry weight, shoot fresh weight, number of tillers per plant, flowering stage, spikelet number, percent of sterile florets and productivity (Zeng and Shannon, 2000; Lauchli and Grattan, 2007; Moradi and Ismail, 2007; Munns and Tester, 2008; Ashraf and Akram, 2009; Hakim et al, 2010; Gupta and Huang, 2014). High salinity can lead to osmotic stress similar to physiological drought, and high salt deposition in soils makes plants increasingly difficult to acquire water and nutrients (Verslues et al, 2006). High salt reduces pollen viability of the flowering stage, which in turn determines grain yield (Khatun and Flowers, 1995; Singh et al, 2004). Growth differences among various genotypes in response to salinity are dependent on the salt concentration and the degree of salt tolerance (Eynard et al, 2005).

Understanding the mechanism of high salinity stress and subsequently developing salinity tolerant crops can be a solution for increasing food production. There is a need for developing new varieties with higher yield potential and stability across environments, climates and geographic locations. This can be done by speeding up discovery of gene and allele, and delivery of marker-assisted selection and genetic modification to crops. Multiple stress tolerance traits must be considered in breeding rice for saline environments as long-term adaptability of a variety is dependent on its level of tolerance to all the stress that occurs in its growing environment. In this review, we emphasize the need for integrated approach which employs physiology, biochemical, proteomics and molecular studies for identifying salt tolerance genes for genetic improvement of rice varieties. We have updated mechanisms underlying the nature of salt tolerance and approaches which can lead to transferring of the salt tolerance into high-yielding rice varieties.

Salinity stress responsive mechanism in rice

To increase the grain yield of rice under salinity, it is imperative to first understand the basic molecular machineries of salt tolerance. Salt tolerance is generally known as a complex quantitative trait which is controlled by multiple genes (Chinnusamy et al, 2005). Rice has been grouped as the salt susceptible cereal, especially, at its young stage (Lutts et al, 1995) and salinity confines the efficiency of production at the mature stage (Todaka et al, 2012). Rice, being transplanted crop, can alleviate the salinity at the seedling stage by management i.e. transplanting of aged seedlings but cannot avoid stress at the flowering stage. Apart from seedling stage, flowering stage is another highly sensitive growth stage which is affected by salinity stress though salt tolerance at seedling stage is independent of flowering/reproductive stage (Singh et al, 2004). Salt tolerance can be assessed by comparing the biomass production percentage in salinity versus the control conditions over a prolonged period of time (Munns et al, 2002).