Agricultural Reviews, 38(4) 2017 : 290-296
Print ISSN:0253-1496 / Online ISSN:0976-0539

AGRICULTURAL RESEARCH COMMUNICATION CENTRE
www.arccjournals.com

Rice and its physiological and genetic basis of salt stress tolerance: A review

Bibha Rani* and V.K. Sharma

Dr. Rajendra Prasad Central Agricultural University,
Pusa-848 125, Bihar, India.

Received: 04-09-2017 Accepted: 27-10-2017 DOI: 10.18805/ag.R-1757

ABSTRACT

Climate change is causing negative impact on the rice production which is a staple food worldwide. Among cereal crops, rice is the most sensitive crop plant for salt stress. The distribution of salt-affected lands is closely related to environmental factors in particularly arid and semi-arid climates. High soil salinity is the main cause of reduction of growth and crop productivity. It is widely believed that the inhibitory effects of salt stress on plant growth are due to salt-induced osmotic stress, specific ion toxicity (Na+ and Cl- are main toxic ions), nutritional imbalance, oxidative stress and hormonal imbalance in a variety of plants, managed by independent genes at different growth stages. *SalTol* is a major quantitative trait locus (QTL) and was identified in the salt-tolerant cultivar Pokkali. Its location was detected on chromosome 1. Molecular analysis on the basis of physiological responses due to salt stress has led to identification of large number of genes induced by salt. This review will focus on salt stress environment which affect adversely to rice crop and its physiological and its related polygenic responses.

Key words: ABA-dependent pathway, ABA-independent pathway, Rice, Salt Affected Soils (SAS), *SalTol* QTL.

Rice is an important staple food crop for one third of the world's population and occupies almost one-fifth of the total land area covered under cereals (Aggarwal and Mall, 2002). It is grown under diverse cultural conditions and over wide geographical range. Most of the world's rice is cultivated and consumed in Asian region, which constitutes more than half of the global population. Approximately 11 percent of the world's arable land is planted annually to rice, and it ranks next to wheat. Rice is the most important grain with regard to human nutrition and caloric intake, providing more than one fifth of the calories consumed worldwide by the human species. Amongst the rice growing countries, India has the largest acreage accounting for about one-third of the world acreage under the crop covering about 42 million hectares of land and sharing about 43 per cent in total national food grain production. Rice is the staple food of the people of the eastern and southern parts of the country. Contributing consistently to around 45 percent of our total cereal production, rice continues to hold the key to sustained food sufficiency in our country and mainstay of diet for majority of the people as it is the livelihood for over 70 per cent of the population in the traditional rice growing regions.In Bihar, rice is cultivated on 35 lakh hectares with an annual production of about 51 lakh tonnes.

Global rice production has doubled during the last three decades, largely due to the use of improved technology such as adoption of high yielding varieties and perfection of location specific agro-techniques and crop management practices. However, considering the population growth, scientists around the world are exploring the possibilities of raising the present yield ceiling to new heights in order to achieve the targeted production. By the year 2025, 21% increase in rice production will be needed over the production of 2000 (Bhuiyan *et al*., 2002) in order to meet the demand for rice to feed the burgeoning population. Further scope of improvement in this crop for augmentation of its production basically depends on conserved use of genetic variability and diversity in plant breeding programs and use of new biotechnological tools. There is wide genetic variability available among and between wild relatives and varieties of rice, leaving a wide scope for future rice improvement programs. Salinity is one of the major constrains to productivity in rice growing areas worldwide. The productivity of rice is declining and unable to meet out for growing populationdue to adverse abiotic and soil factors, in addition to biotic factors. The possible ways to mitigate the adverse effects of salinity on rice production are reclamation of soil and develop new varieties suitable for saline soils.

Rice plants are known to tolerate salinity stress by 3 mechanisms acting upon singly or jointly (Munns *et al*., 2008; Islam *et al*., 2009). These mechanisms are exclusion, dilusion and compartmentalization. Exclusion refers to the restricted uptake of Na ion by tolerant rice varieties. Dilution effects comprised of faster growth of tolerant varieties than non-tolerant varieties under saline condition.

*Corresponding author's e-mail: bibha9rani@gmail.com

Compartmentalization refers to maintenance of high K/Na ratio. It is now established that salt tolerant varieties maintain a higher K/Na ratio compared to that in non-tolerant variety (Senguttuvel *et al*., 2010). Relatively higher amount of K than Na is probably required in the leaves for the protection of growing plants from the toxic effect of Na ion."*SalTol*", a major QTL was mapped on chromosome 1 which accounts for more than 70% of the variation in saltuptake in the population generated by crossing between salt sensitive rice variety IR29 and salt tolerant landrace, Pokkali (Lafitte *et.al*, 2004). Complex inheritance of *SalTol* QTL limit the development of salt tolerant rice line through conventional breeding methods. Genetic engineering and other biotechnological techniques has become a powerful tool in plant breeding programs since it allows the introduction of gene(s) controlling traits without affecting the desirable characteristics of anelite genotype and also overcome the problem related to linkage drag of QTL. Further Microsatellite markers have been effectively used to identify genetic variation among rice cultivars (Yang *et al*., 1994; Garland *et al*., 1999).

Climatic conditions for rice production (Production environment): Most of the rice growing areas in the world are located in the tropics (Yoshida, 1981). These areas are between the tropics of Cancer (23.50N) and the tropic of Capricorn (23.50S) and extend to as far as 490N and 350S of the latitudes. Rice also grows from sea level to an altitude of 2,500m or more (Khush, 1997). Worldwide, there are about 150 million hectares of rice, which provide around 550–600 million tons of rough rice annually (Maclean *et al*., 2002). Rice is unique among the major food crops in its ability to grow in a wide range of hydrological situations, soil types and climates.

Although, rice is primarily a tropical and subtropical crop, the best grain yields have been obtained in the temperate region. This is attributed to lower temperature during ripening, which gives more time for grain filling, long day lengths and high levels of solar energy during the ripening period (Yoshida, 1981). These phenomena are also conducive to lower grain yield obtained during the wet season versus the dry season. However, due to the prevalence of biotic and abiotic factors during dry seasons, lower grain yield is obtained in most cases as compared to the wet season.

Salt affected soils (SAS): their causes, measure and classification: Soil salinity is a major environmental constraint to crop production affecting an estimated 45 million hectares of irrigated lands and is expected to increase due to global climate changes and as consequences of many irrigation practices (Rengasamy, 2010; Munns and Tester, 2008). The deleterious effects of salt stress on agriculture yield are significant mainly because crop exhibit slower growth rates, reduced tillering and over month's reproductive development is affected (Munns and Tester, 2008). The ultimate aim of salinity tolerance research is to increase the ability of plants to maintain growth and productivity in the saline soils relative to their growth in non-saline soils in order to reduce effect of salinity on growth and yield.

Salt affected soils are widespread over the world especially in arid, semi arid and some sub-humid regions. These soils contain excessive amount of either soluble salts or exchangeable sodium or both affecting crop yields and crop production. Soil salinity and water logging are two of the main constraints present in irrigated agricultural lands. Two monsoons, southwest and northeast are prevalent in the country. The southwest monsoon mainly influences soil salinization/desalinization in arid and semiarid regions that have three distinct phases from the analysis of long-term annual weather data (1971–2008). The first phase is the hot and humid season (mid-June to September), referred to as the *"kharif"* (summer) crop period, when about 80% of the rainfall occurs. The second phase is the cool and dry season (October to March) referred to as the *"rabi"* (winter) crop period. The third phase is the hot and dry weather (April to mid-June).The winter and summer months are dry, water-deficit periods, whereas the kharif crop season has surplus water. The build-up of salts in soils is significantly influenced by wet and dry cycles set in by the monsoon and prevailing irrigation practices. From mid-April to mid-June, the land remains mostly fallow and an upward moisture flux is dominant due to high evaporative demand (5–10 mm/day), which results in a buildup of salts. The maximum possible concentration of salts in croplands (up to 12 dSm^{-1}) and non-arable lands (>12 dSm^{-1}) is observed in the pre-monsoonal period in June in waterlogged saline areas (Tyagi, 1998). With the onset of the monsoon and the planting of crops, the desalinization of the soils takes place, and salt levels reach their minimum in October. From November to February, the evaporative demands are low, but the upward flux begins to increase. This favors irrigation with saline, alkali and saline-alkali ground waters in areas of deficit canal water supply, leading to increase in soil salinity/alkalinity. The development of SAS depends on climate, topography, geology, soil mineral weathering, drainage, hydrology, irrigation source, ground water depth and quality, and management practices (Ghassemi *et al*., 1995). Accumulation of sodium or neutral salts in soils over a period leading to the formation of alkali, saline-alkali or saline soils may be compounded by natural or irrigation-induced factors, such as weathering of natural salt bearing soil minerals; irrigation with saline, saline-alkali or alkali waters; and waterlogging due to a rising ground water table. In India, the problem of salinity and alkalinity increases every year as a result of secondary salinisation. In India about 8.6 mha (Pathak, 2000) of land area is affected by soil salinity.

The major ionic composition of salts is Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, $HCO3^{"}$, $CO3^{-}$, $SO4^{-}$ and $Cl^{"}$. Salt affected soils are classified into saline, saline-alkali and alkali soils on the basis of soil reaction of saturation paste (pHs) (Dregne, 1976), electrical conductivity of saturation paste (ECe), exchangeable sodium percentage (ESP) and the sodium adsorption ratio (SAR) (Richards, 1954). The Indian system of classification for characterization of SAS is essentially the same as that of the USDA (U.S. Salinity Laboratory Staff, 1954), except that the pH criterion is reconsidered from 8.5 to 8.2 because this value of pH initiates the sodication process and is associated with an ESP of 15 to 20 (Bhumbla and Abrol, 1978; Abrol *et al*., 1988). Unlike the USDA classification (see table), the Indian classification system for reclamation has classified SAS into two main categories; saline or alkali. The saline-alkali soil category is reconsidered to be saline or alkali based on a ratio of $(2CO3^{-}+HCO3^{"})/(Cl^{-}+2SO4^{-})$ or $Na^{+}/(Cl^{"}+2SO4^{-})$. If the ratio is more than 1, the saline-alkali soil is treated as alkali; if the ratio is less than 1, the soil is treated as saline (Chhabra, 2005).

Rice and its response to salinity: Rice exhibits sensitivity to salinity and its response to salinity vary with growth stage. Generally rice shows tolerance to salt stress during germination, becomes sensitive during early seedling stage, gains tolerance during vegetative growth, becomes sensitive again during reproductive and pollination stage and exhibits an increasing tolerance until maturity (IRRI 1967). Screening of crops for salinity tolerance has been carried out for a long time and different methodologies have been used for this purpose (Khan *et al*., 1997; Zeng *et al*., 2002; Ali *et al*., 2007; Salam *et al*., 2011; Shahzad *et al*., 2012). Screening under controlled conditions has given better results because of reduced environmental effects. Germplasm screening at seedling stage is simple than at vegetative or reproductive stages (Gregorio *et al*., 1997). In addition early growth stages have shown better prediction of plant's response to salinity (Wang *et al*., 2011). Although all growth stages are sensitive to salinity, seedling stage is considered as foretelling of plant's growth response to salinity (IRRI, 1967).

Physiological basis of salt tolerance: Salts decrease water potential and create water deficit problem for plant growth. In such circumstances, plants must decrease inner water potential so that it may uptake water continuously. All plant species, whether halophytes or glycophytes, face two main problems when grown in saline soils; one is ion toxicity and the other is water deficit. The salt tolerance ability varies in different crop species. It is actually based on the type of species and the extent of stress. On the basis of tolerance level, species have been divided into halophytes and glycophytes. The former can tolerate high concentrations of salt while the latter are susceptible (Maas and Nieman, 1978). Halophytes have the ability to tolerate high concentrations of Na^{+} and Cl^{-} by excluding toxic ions (Greenway and Munns, 1980). While in glycophytes, ions are present in the roots and do not move but in halophytes these ions move towards shoot and this is the way, they tolerate the toxicity of ions.There are many mechanisms by which plants limit the Na^{+} and Cl^{-} to reach the shoot (Islam, 2009).. Most of the halophytes respond to salinity through ion exclusion. In case of excessive NaCl, K^{+} and Ca^{+} ions are decreased (Lauchli and Epstein, 1990). Exclusionis an avoidance mechanism in which roots remained impermeable to salts at some extent, but after attaining the threshold level, roots loose this ability and cause damage to shoot which leads to the death of plant (greenway, 1973). Under salt stress conditions, accumulation of salt in the plant is a must. High K^{+}/Na^{+} ratio in shoot is one of the most important and effective mechanisms plants use to survive (Gorham *et al*., 1985).There are some plants which cope with the deleterious effects of salts by having more water to dilute the cell sap, while other plants distribute higher quantity of the salts in older leaves than in younger leaves (Yeo and Flowers, 1984). Therefore, plants adapt different mechanisms to get rid of it through glands (Ashraf *et al*., 2008) or via pumps at the plasma membrane of root cells (Jeschke, 1984). The intake of ions in older leaves is based on xylem transport while the export is through phloem. In case of younger leaves, intake is through both xylem and phloem that is why, in younger leaves the accumulation of ions is lesser as compared to older leaves (Flowers *et al*., 1977).

Genomics of salt stress response in rice: To improve the yield under salt stress condition, it is essential to understand the fundamental molecular mechanisms behind stress tolerance in plants. Salinity stress tolerance is a quantitative trait which is controlled by multiple genes (Chinnusamy *et al*., 2005). During the last two decades, number of genes conferring salt stress tolerance in plants has been isolated and they are involved in signal transduction and transcription regulation, ion transporters and metabolic pathways (Uddin *et al*., 2011). Salt stress evokes both osmotic stress and ionic stress which inhibits the plant's normal cell growth and division. To encounter the adverse environment, plants maintain osmotic and ion homeostasis with rapid osmotic

Table: Classification of salt affected soils used by Natural Resources Conservation Service (USDA)

Salt affected Soil Classification	pH	Electrical conductivity (dSm^{-1})	Sodium Absorption Ratio (SAR)	Exchangeable Sodium Percent(ESP)
None	7-8.5	<4	<13	<15
Sodic soil	>8.5	>4	<13	<15
Saline soil	-	<4	>13	>15
Saline-sodic soil	> or < 8.5	>4	>13	>15

and ionic signaling. Osmotic stress due to high salt rapidly increases abscisic acid (ABA) biosynthesis, thus regulating ABA dependent stress response pathway. There are several salt stress inducible genes which are ABA-independent.

Salt stress tolerance via ABA-dependent pathway: ABA (abscisic acid) is a major phytohormone in regulation of responses during abiotic stresses, especially drought and salt stresses. It has been well established that high salinity-induced osmotic stress increases the biosynthesis of ABA (Ye *et al*., 2012). The biosynthesis of ABA via terpenoid pathway starting from isopentenyl pyrophosphate (IPP) has been reviewed in rice. Among many genes involved in this pathway, a phytoene synthase gene, *OsPSY3* and 9-cis-epoxycarotenoid dioxygenases genes (*OsNCED3*, *OsNCED4* and *OsNCED5*) are induced one hour after salt stress and their expression is well correlated to the level of ABA in rice roots (Welsch *et al*., 2008). ABA then acts as a regulator initiating second round of signaling salt stress response in ABA-dependent pathway. Protein kinases play important roles in regulating the stress signal transduction pathways (Ouyang *et al*., 2010). Receptor-like kinases (RLKs) have important roles in plant growth, development and stress responses. Salt, drought, H_2O_2 and ABA treatments induced the expression of a putative RLK gene, *OsSIK1*. Transgenic rice plants overexpressing *OsSIK1* (*OsSIK1-ox*) showed higher tolerance to salt and drought stresses than control plants and the knockout mutants *SIK1* as well as RNA interference (RNAi) plants. Until now, at least two salt inducible MEKKs have been reported in rice. Expression of two novel MAPKs, *OsMSRMK2* and *OsMSRMK3* were induced by various environmental stresses suggesting their possible involvement in defense/stress response pathways (Agrawal *et al*., 2002). An ABA-dependent $Ca2^{+}$-dependent protein kinases (CDPKs), *OsCPK21*, have been cloned and the *OsCPK21-ox* transgenic rice exhibited higher salt stress tolerance than wild-type plant with enhanced expression of the ABA and salt-stress inducible genes such as *OsNAC6* and *Rab21* (Asano *et al*., 2011).

Salt stress tolerance via ABA-independent pathway: There are several salt stress inducible genes which are ABA-independent. These include genes for DREB1 and DREB2 TFs, some kinases, spingolipid biosynthesis enzymes (Dubey, 1984), and ROS-producing/scavenging enzymes. CBF/DREB-type genes that encode AP2/ERF domains that bind to a *cis*-acting element, DRE/CRT with a core sequence A/GCCGAC (Yamaguchi-Shinozaki and Shinozaki 2005; Todaka *et al*., 2012). *OsDREB1A*, *OsDREB1F* and *OsDREB2A* are three most important of DREB-type genes induced by salt stress and their overexpression displayed strong abiotic stress tolerance. Rice genome contains at least fourteen DREB-type genes (Wang *et al*., 2008; Mallikarjuna*et al*., 2011). Microarray analysis also revealed the expression of *OsDREB1A* and OsDREB2A genes under salt stress condition in rice which encoded proteins thought to function in stress tolerance in the plants. The genes have similar functions with the target genes of DREB1 and DREB2 proteins in *Arabidopsis* (Sakuma *et al*., 2006; Jeon and Kim, 2013). DRE-containing promoter region of *OsDHN1* is activated by protein domain encoded by *OsDREB1A* and *OsDREB1D* genes (Lee *et al*., 2013). These observations showed that the CBF/DREB type transcription factors are conserved in rice and DREB-type genes are useful for improvement of salt stress tolerance in rice genotypes.

ABA-independent kinases are also involved in salt stress tolerance. Overexpression of a CDPK, *OsCDPK7* enhanced salt stress tolerance in transgenic rice and the extent of tolerance correlated well with the level of *OsCDPK7* expression (Saijo*et al*., 2000). It was found that knockout plants of *OsGSK1*, a negative regulator gene of brassinosteroid signaling, showed enhanced tolerance to salt and other abiotic stresses suggesting that brassinosteroid plays important role for stress tolerance (Koh*et al*., 2007). *OsCPK12* gene, a member of CDPK family, negatively regulates the expression of *OsRBOHI* while it positively regulates ROS detoxification by controlling the expression of *OsAPX2* and *OsAPX8* under salt stress condition. ABA-independent ROS scavenging system is also involved in salt stress tolerance. It was found that most probably, due to the increased reducing power of ROS,a salt responsive malic enzyme gene in rice, *NADP-ME*, was overexpressed in *Arabidopsis* which resulted in enhanced salt stress tolerance (Liu *et al*., 2007).

Molecular markers and QTL linked to rice salt tolerance: Molecular/genetic rice maps have been constructed using F_2 population or RILs derived from varieties that are genetically far apart, such as *japonica* and *indica* rice types as parents. Such a combination generated considerably more polymorphism than that between the same subspecies. Because of the ability to generate a large seed supply, RILs have been used to map several QTL in rice (Xiaon *et al*., 2003). Doubled haploid (DH) populations have also been used; however, extensive use of DH plants is limited due to difficulty in generating sufficient number of plants through anther culture. Backcrosses and other types of crosses have not been widely used in rice gene mapping. McCouch *et al*., (1988) reported the first molecular genetic map of rice using RFLP technique; various fine maps have since been released using a variety of different markers including simple sequence repeat (SSR), amplified fragment length polymorphism and random amplified polymorphic DNA (Causse *et al*., 1994; Kurata *et al*., 1995; Harushima *et al*., 1998). These as well as the genomic tools and methods that have become available such as expressed sequence tags (ESTs) from salt-stressed libraries, complete genome sequence information, development of new bioinformatics tools, expression profiling by microarrays, random and

targeted mutagenesis and complementation and promoter trapping strategies provided opportunities to characterize the salt-tolerance-related gene networks in greater depths. Zhang *et al*. (1995) mapped a major gene for salt tolerance on chromosome 7 Using F2 population derived from a salt tolerant japonica rice mutant, M-20, and the sensitive original variety 77-170A. Koyama *et al*. (2001) reported the chromosomal location of ion transport and selectivity traits that are compatible with agronomic needs. This group showed that QTL for Na^+ and K^+ transport are likely to act through the control of root development and structure and the regulation of membrane localized transport compartmentalization, respectively. Gregorio *et al*. (2002) mapped a major QTL designated *SalTol* on chromosome 1 (flanked by SSR markers RM23 and RM140) using a population generated from a cross between salt-sensitive IR29 and salt-tolerant Pokkali. Pokkali was the source of positive alleles for this major QTL, which accounted for high K^+ and low Na^+ absorptions and low Na^+ to K^+ ratio under salinity stress. A major QTL for high shoot K^+ under salinity stress in the same region of chromosome 1 was also identified (Lin et al., 2004). Mapping of *SKC1* by using finely mapped BC_2F_2 population on chromosome 1 was a major breakthrough, which maintains K^+ homeostasis in the salt-tolerant variety Nona Bokra under salt stress (Ren *et al*. 2005). This group further showed that the *SKC1* locus was able to confer salt tolerance, when transformed into salt-sensitive variety. Platten *et al*. (2013) presented data on 103 accessions from *O. sativa* and 12 accessions from *O. glaberrima*, many of which were identified as salt tolerant for the first time, showing moderate to high tolerance of salinity. The correlation of salinity-induced senescence (as judged by the Standard Evaluation System for Rice, or SES, score) with whole-plant and leaf blade Na^+ concentrations was high across nearly all accessions, and was almost identical in both *O. sativa* and *O. glaberrima*. Seven major and three minor alleles of *OsHKT1;5* were identified, and their comparisons with the leaf Na^+ concentration showed that the a*romatic* allele conferred the highest exclusion and the *japonica* allele the least.The association of leaf Na^+ concentrations with cultivar-groups was very weak, but association with the *OsHKT1;5* allele was generally strong.

CONCLUSION

Salt stress problems in field crops can effectively be mitigated through the use of tolerant rice varieties and proper management and mitigation strategies.To develop salt tolerance rice cultivars with high yield potential and grain quality is the most effective way to combat salt stress environment. It is challenging to develop salt tolerant rice through conventional breeding as salinity is polygenic trait (QTL) and unexpected linkage drag encountered in the progenies. So, it is imperative to develop salt tolerant rice genotypes usingmodern tools of biotechnology. To develop salt tolerant rice lines through molecular breeding and genetic engineering, it is indispensible to understand both physiological and molecular mechanism of salt stress response in rice. These modern techniques have just initiated another revolution to achieve the goal of food security for an exponentially increasing population worldwide.

REFERENCES

Abeysiriwardena DS and De Z (2004) A simple screening technique for salinity tolerance in rice: germination rate under stress. *International Rice Research Notes.* **29(2)**: 78-79.

Abrol IP, Yadav JSP and Masaud FI (1988) Salt- affected soils and their management, *FAO Soils Bulletin,* **39**: 93.

Aggarwal PK and Mall RK (2002) Climate change and rice yield in diverse agro-enviroments of India. *Climate change,* 52(**3**): 331-343.

Ali Z., Salam A, Azhar FM and Khan IA (2007) Genotypic variation in salinity tolerance among spring and winter wheat (*Triticumaestivum* L.) accessions. *S. Afr. J. Bot.* 73:70–75.

Asano T, Hakata M, Nakamura H, Aoki N, Komatsu S, Ichikawa H, Hirochika H and Ohsugi R (2011) Functional characterisation of OsCPK21, a calcium-dependent proteinkinase that confers salt tolerance in rice. *Plant Mol. Biol.,* **75**:179–191.

Ashraf M, Athar HR, Harris PJC and Kwon TR (2008). Some prospective strategies for improving crop salt tolerance. *Adv. Agron.*, **97**: 45-110.

Aslam M, Qureshi RH and Ahmed N (1993) A rapid screening technique for salt tolerance in rice. Plant Soil, **150:** 99–107.

Bhuiyan NI, Paul NR and Jaber MA (2002) Feeding the extra millions by 2025: challenges for rice research and extension in Bangladesh, Proceedings of the Workshop on Modern Rice Cultivation in Bangladesh, **29-**31: 4-23.

Bhumbla DR and Abrol IP (1978) Saline and sodic soils. In: Soils and rice. International Rice Research Institute, Manila, Philippines, 719-738.

Causse M, Fulton T, Cho Y, Ahn S, Chunwongse J, Wu K, Xiao J, Yu Z, Ronald P, Harrington S, Second G, McCouch S, Tanksley S (1994) Saturated molecular map of the rice genome based on an interspecific backcross population. *Genetics,* **138:** 1251–1274.

Chhabra R (2005) Classification of salt-affected soils. *Arid Land Research and Management*.**19**: 61-79.

Chinnusamy V, Jagendorf A, and Zhu JK (2005) Understanding and improving salt tolerance in plants. *Crop Science*, **45:** 437-448.

Cramer GR and Bowman DC (1999) Kinetics of maize leaf elongation 1. Increased yield threshold limits short-term, steady-state elongation rates after exposure to salinity. *J. Exp. Bot.,* **42:** 1417-1426

Dregne HE (1976) Soils of Arid regions. Elsevier. Amsterdam.

Flowers TJ, Troke PF and Yeo AR (1977) Mechanism of Salt tolerance in halophytes, *Annual Rev. of Plant Physiol*., **28:** 89–121.

Garland, S.H., Lewinm L., Abedinia, M., Henry, R. and Blakeney, A. (1999). The use of microsatellite polymorphisms for the identification of Australian breeding lines of rice (*Oryza sativa* L.). *Euphytica* **108**: 53–63.

Ghassemi F, Jakeman AJ, and Nix HA (1995) Salinization of land and water resources: Human causes, extent, management and case studies. CAB International, Wallingford, UK.

Gorham J (1994) Salt tolerance in the Triticaceae: K/Na discrimination in some perennial wheat grasses and their amphiploids with wheat. *J. Extp. Bot*. **45:**441-447.

Gorham J, WynJone RG and McDonnelle (1985) Some mechanisms of salt tolerance in crop plants. *Plant and soil,* **89**(**1**): 15-40.

Greenway H (1973). Salinity, plant growth and metabolism. *J. Aust. Agric. Sc.* **39:** 24-34

Greenway H and Munns R (1980) Mechanism of salt tolerance in non-halophytes. Annual Rev. *Plant Physiol.,***31**: 149-190.

Gregorio GB, Dharmawansa S and Mendoza RD (1997) Screening rice for salinity tolerance. IRRI Discussion Paper Series NO.22: 2-23, International Rice Research Institute,Manila, Philippines.

Gregorio GB, Senadhira D, Mendoza RD, Manigbas NL, Roxas JP and Guerta CQ (2002) Progress in breeding for salinity tolerance and associated abiotic stresses in rice. *Field Crops Res*.,**76:** 91–101.

Harushima Y, Yano M, Shomura A, Sato M, Shimano T, Kuboki Y, Yamamoto T, Lin SY, Antonio BA, Parco A, Kajiya H, Huang N, Yamamoto K, Nagamura Y, Kurata N, Khush GS, Sasaki T (1998) A high-density rice genetic linkage map with 2275 markers using a single F2 population. *Genetics,* **148:** 479–494.

IRRI (1967) Annual Report. Los Banos. Laguna, Philippines. p: 308.

Islam MT (2009) Physiological basis of salt tolerance in crop plants and salinity management strategies. *Bangladesh Soc. Agric. Sci. Technol,* **6**(**1**): 185-190.

Jeon J and Kim J (2013) Cold stress signaling networks in Arabidopsis. *J. Plant Biol.*, **56:** 69–76.

Jeschke WD (1984) K^+-Na^+ exchange at cellular membranes, intracellular compartmentation of cations, and salt tolerance. In Salinity tolerance in plants: Strategies for Crop Improvement. Ed. R C Staples. Wiley, New York. pp. 37-66.

Khan MSA., Hamid A and Karim MA (1997) Effect of sodium chloride on growth photosynthesis and mineral ions accumulation of different types of rice (Oryza sativa L.) *J. Agron. Crop Sci*., **179**(**3**): 11-17.

Khush GS (1997). Oryza: From Molecule to Plant, 25-34.

Koh S, Lee SC, Kim MK, Koh JH, Lee S, An G, Choe S and Kim SR (2007) T-DNA tagged knockout mutation of rice OsGSK1, an orthologue of Arabidopsis BIN2, with enhanced tolerance to various abiotic stresses. *Plant Mol. Biol*. **65:** 453–466.

Koyama ML, Levesley A, Koebner RM, Flowers TJ and Yeo AR (2001) Quantitative trait loci for component physiological traits determining salt tolerance in rice. *Plant Physiol.*, **125:** 406–422.

Kurata N, Nagamura Y, Yamamoto K, Harushima Y, Sue N, Wu J, Antonio BA, Shomura A, *et al.* (1994) A 300 kilobase interval genetic map of rice including 883 expressed sequences. *Nat. Genet.* **8:**365–372.

Lauchli A (1984) Salt exclusion: an adaptation of legumes for crops and pastures under saline conditions. In Salinity tolerance in plants: Strategies for Crop Improvement. Ed. R C Staples. pp. 171-187. Wiley, New York.

Lauchli A and, Epstein E. (1990). Plant responses to saline and sodic conditions. In: Tanji K. K. Tanji, (ed.), Agricultural Salinity Assessment and Management. Am Soc Civil Engrs New York. pp. 113-137. ASCE manuals and reports on engineering practice No, 71. p. 113–137 ASCE New York.

Lee SC, Kim SH and Kim SR (2013) Drought inducible OsDhn1 promoter is activated by OsDREB1A and OsDREB1D. *J. Plant Biol.* **56:** 115–121.

Lin HX, Zhu MZ, Yano M, Gao JP, Liang ZW, Su WA, Hu XH, Ren ZH, Chao DY (2004) QTLs for Na+ and K+ uptake of the shoots and roots controlling rice salt tolerance. *Theor. Appl. Genet.,* **108:**253–260.

Liu S, Cheng Y, Zhang X, Guan Q, Nishiuchi S, Hase K and Takano T (2007) Expression of an NADP-malic enzyme gene in rice is induced by environmental stresses; over-expression of the gene in Arabidopsis confers salt and osmotic stress tolerance. *Plant Mol. Biol.* **64:** 49–58.

lsch R, Wust F, Bar C, Babili SA and Beyer P (2008) A third phytoene synthase is devoted to abiotic stress-induced abscisic acid formation in rice and defines functional diversification of phytoene synthase genes. *Plant Physiol.,* **147:** 367–380.

Maas EV and Nieman (1978) Physiology of Plant Tolerance to Salinity. 13: 277. Maas EV and Nieman RH (1978) Physiology of Plant Tolerance to salinity. In: Crop Tolerance to Suboptimal Land Conditions, [Jung, G.A. (Ed.)] American Society of Agronomy, Madison, WI., pp 277-299.

Maclean JL, Dawe DC, Hardy B and Hettel GP (2002) Rice Almanac, third edition, IRRI, Los Banos, Phillipins, 1-253.

Mallikarjuna G, Mallikarjuna K, Reddy MK and Kaul T (2011) Expression of OsDREB2A transcription factor confers enhanced dehydration and salt stress tolerance in rice. *BiotechnolLett.,* **33:** 1689–1697.

McCouch SR, Kochert G, Yu ZH, Wang ZY, Khush GS, Coffiman WR, Tanksley SD (1988) Molecular mapping of rice chromosomes. *Theor. Appl. Genet.*, **76:** 815–829.

Munns R and Tester M (2008) Mechanisms of salinity tolerance. Annual Rev.Plant Biol., **59**: 651-681.

Ouyang SQ, Liu YF, Liu P, Lei G, He SJ, Ma B, Zhang WK, Zhang JS and Chen SY (2010) Receptor-like kinase OsSIK1 improves drought and salt stress tolerance in rice plants. Plant J., **62:** 316–329.

Pathak PS (2000) Agro forestry: A tool for arresting land degradation. *Indian Farming*, **49**(**11**): 15-19.

Pearson GA, Ayers SD and Eberhard DL. (1966) Relative salt tolerance of rice during germination and early seedling development. *Soil Sci.,* **102**:151-156.

Platten JD, Egdane JA and Ismail AM (2013) Salinity tolerance, Na^+ exclusion and allele mining of HKT1;5in Oryza sativa and O. glaberrima: many sources, many genes, one mechanism**.** *BMC Plant Bio.,* **13:** 32-48.

Ren ZH, Gao JP, Li LG, Cai XL, Huang W, Chao DY, Zhu MZ, Wang ZY, Luan S, Lin HX (2005) A rice quantitative trait locus for salt tolerance encodes a sodium transporter. *Nat. Genet.,* **37**:1141–1146.

Rengasamy (2010) Soil processes affecting crop production in salt-affected soils. Funct. *Plant Bio.,***37**: 613–620.

Richards LA (1954) Saline and Alkali Soils: Diagnosis and Improvement. USDAAgriculture Research Service Handbook 60.

Saijo Y, Hata S, Kyozuka J, Shimamoto K and Izui K (2000) Overexpression of a single Ca2+ dependent protein kinase confers both cold and salt/drought tolerance on rice plants. Plant J. 23: 319–327.

Sakuma Y, Maruyama K, Osakabe Y, Qin F, Seki M, Shinozaki K, et al. (2006) Functional analysis of an Arabidopsis transcription factor, DREB2A, involved in drought-responsive gene expression. *Plant Cell,* **18:** 1292–1309.

Salam A, Ali Z, and Aslam M (2011) Sodium chloride tolerance in rice at early seedling growth: genotypic variability, identification and selection. Pak. J. Bot., 43: 2701–2705.

Senguttuvel P, Raveendran M, Vijayalakshmi C, Thiyagarajan K, Bapu JRK and Viraktamath BC (2010) Molecular mechanism of salt tolerance for genetic diversity analysed in association with Na^+/K^+ ratio through SSR markers in rice. *Int. J. Agric. Res*., **5:** 708-719.

Shahzad A, Ahmad M, Iqbal M, Ahmed I and Ali GM (2012) Evaluation of wheat landrace genotypes for salinity tolerance at vegetative stage by using morphological and molecular characters of different types of rice (Oryza sativa L.). *J. Agron. Crop Sci.*, **179:** 163-169.

Todaka D, Nakashima K, Shinozaki K and Yamaguchi-Shinozaki K (2012) Towards understanding transcriptional regulatory networks in abiotic stress responses and tolerance in rice. *Rice,* **5**:6.

Tyagi NK (1998) Managing salinity through conjuctive use of water resources. *Eco. Modelling*. **40(1**): 11-24.

Uddin MK, Juraimi AS, Ismail MR, .Hossain MA, Othman R and Rahim AA (2011) Effect of salinity stress on nutrient uptake and chlorophyll content of tropical turfgrass species. AJCS, 5(**6**): 620-629.

Wang Q, Guan Y, Wu Y, Chen H, Chen F and Chu C (2008) Overexpression of a rice OsDREB1F gene increases salt, drought, and low temperature tolerance in both Arabidopsis and rice. *Plant Mol Biol.,* **67**:589–602.

Wang Z, Wang J, Bao Y, Wu Y, and Zhang H (2011) Quantitative trait loci controlling rice seed germination under salt stress. *Euphytica,* **178:** 297–307.

Xiong L and Yang Y (2003) Disease resistance and abiotic stress tolerance in rice are inversely modulated by an abscisic acid–inducible mitogen-activated protein kinase. *Plant Cell,* **15:**745–759.

Yadav R, Courtois B, Huang N, McLaren G (1997) Mapping genes controlling root morphology and root distribution in a doubled haploid population of rice. *TheorAppl Genet.,* **94:**619–632.

Yamaguchi-Shinozaki K and Shinozaki K (2005) Organization of cis-acting regulatory elements in osmotic- and cold-stress-responsive promoters. *Trends Plant Sci.*,**10**: 88–94.

Yang GP, SaghaiMaroof MA, Xu CG, Zhang Q and Biyashev RM (1994) Comparative analysis of microsatellite DNA polymorphism in landraces and cultivars of rice. *Mol Genet Genomics* **245:**187-194.

Ye N, Jia L and Zhang J (2012) ABA signal in rice under stress conditions. *Rice.,* **5**(1): 1-9.

Yeo AR and Flowers TJ (1984) Mechanism of salinity resistance in rice and their role in physiological criteria in plant breeding. In: R. C. Staples and G. H. Teonniessen, eds., Salinity Tolerance in Plants. John Wiley and Sons, New York. 151-170.

Zeng L, Shannon MC and Grieve CM (2002) Evaluation of salt tolerance in rice genotypes by multiple agronomic parameters. *Euphytica,* **127**(**2**): 235-245.

Zhang GY, Guo Y, Chen SL, Chen SY (1995) RFLP tagging of a salt tolerant gene in rice. *Plant Sci.,* **110:** 227–224.