A REVIEW ON UNDERSTANDING THE EFFECTS AND MECHANISMS OF SALINITY TOLERANCE IN RICE (*Oryza sativa* L.)

Abstract

Salinity, along with drought, is one of the key abiotic stressors that has posed a danger to the advancement and evolution of cereal crops like rice and wheat. Water shortage and a lack of irrigation water availability are the main causes of salty soil formation. Rice is salt sensitive and glycophyte, wheat is moderately salt tolerant. Wild tolerant cultivars like *Oryza coarctata* and *Oryza alta* are more tolerant than traditional cultivars such as Pokkali and Nona Bokra in rice. Salt stress affects crop plants' processes like ionic imbalance, osmotic and oxidative stress. Na^+ should be low in the shoots of the plant which is restricted by various transporters in the cell membrane of the roots in soil. High K^+ & Na^+/K^+ homeostasis should be maintained. Many RILs and NILs have been developed which acts as a donor for salinity tolerant genes. FL478 is a recombinant inbred line in which candidate genes are situated in the *Saltol* region of chromosome 1 region which is obtained by a cross between Pokkali x IR29. Increase in world's population, rice output must be increased by at least 25% by 2030 and 50% by 2050.Salinity stress is a polygenic character which involves several genes works in harmony. For evolution of salinity tolerant cultivars, we need to access the physiological, biochemical genetic responses of the crop plant which helps in transfer of candidate genes from donor parents to elite high yielding salt sensitive cultivars. Especially in rice salt tolerant mechanisms like, Ion equilibrium regulation, Adjustment of osmotic potential, Reduction of ROS, Nutrient disequilibrium, and Regulation of PGRs. Conventional, MABC, MAS and direct gene transfer by transgenic methods. This review paper's main objective is to understand the mechanisms of the crop plants to salinity effects and development of salt tolerant cultivars by modern approaches which fulfill the food scarcity of staple food crops with increasing population.

Keywords: *Saltol* QTL, Salinity, anti-transporters, Salt tolerance, PUFs, and Profiling.

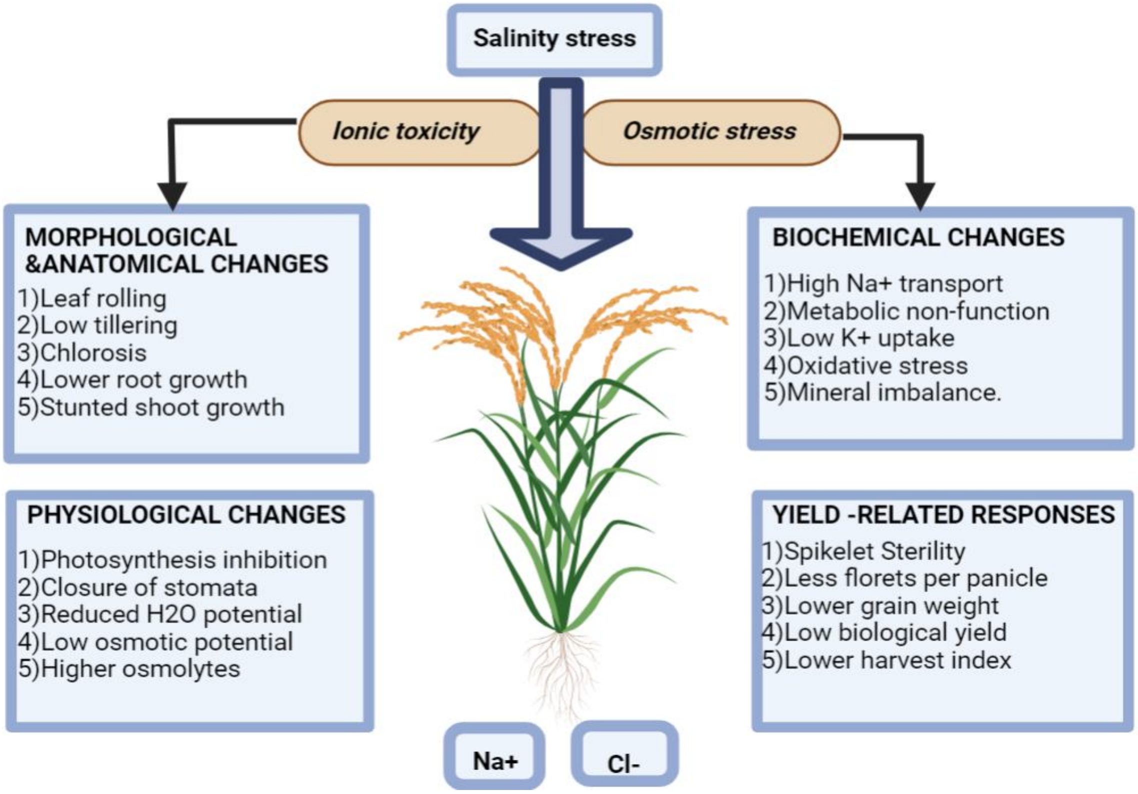
1. Introduction

Salinity affects crop plants by various processes like mainly development of osmotic stress, ionic toxicity and next to it oxidative stress and indirectly affects photosynthetic process by pigment damaging **(Munns & Tester, 2008)**. Mainly in cereals rice and wheat are the salt sensitive crops which are affected easily because these are the essential & staple food crops for more than 80% of the world's people. To produce high-yielding, salt-tolerant cultivars we need to understand various mechanisms and physiological, biochemical epigenetic responses of the plants **(Hasanuzzaman, *et al*., 2022)**. Electrical conductivity (Ec) is used to estimate salinity. **(Munns and Tester, 2008)**. In rice, salinity mainly affects at germination, seedling stage and reproductive stage, in which if Ec is 3 dS/m yield start reducing with a 12% decrease in output per unit as Ec rises **(Chinnusamy, *et al*., 2005; Reddy *et al*., 2014)**. Plants have three primary processes. a) ionic removal, b) osmotic resilience, and c) cellular resilience to salinity stress **(Munns and Tester, 2008)**.Salinity stress in rice mainly build upon Na^+ concentration and transporter's like OsHKT1;5 is a main determinant factor for salinity resilience. The genetic variability present within crop species of cultivated cereals like rice for salt resiliance is less or narrow, we use donors like land races Pokkali, FL478 and Nona Bokra which also has *Saltol* gene in the respected QTL region mainly in salinity endurance of seedlings **(Bonilla *et al*., 2002)**. Progress of varieties which have seedling stage salinity tolerance leads to growth of leaves, stems and roots that can increase yield **(Hoang, *et al*., 2016)**. In India 7mha land is pretentious by salt **(Pradhan, *et al*., 2013).** Due to the frequent use of brackish water from groundwater for irrigation, the inland is salinized **(Dolo, *et al*., 2012)**. FL478 is a recombinant inbred line which is salt tolerant used as a donor and it is evaluated from a cross between IR29 x Pokkali **(Islam, *et al*., 2012)**. In cross Nona Bokra / Koshihikari a transporter called OsHKT1;5 that regulates K^+ regulation **(Ren, *et al*., 2005)**. Early maturation, semi-dwarf, and exceptional culinary quality *Saltol* QTL from DP of FL478 was transmitted through Marker Assisted Backcross Breeding (MABB) into recurrent parent Pusa Basmati 1509 **(Yadav, *et al*., 2020)**. Until now only two high producing Basmati rice types, Pusa Basmati 1 **(Singh, *et al*., 2018)** and Pusa Basmati1121 **(Babu, *et al*., 2017b)** developed for improved seedling stage salinity tolerance through MABC **(Yadav, *et al*., 2020)**.The rice output must be increased by at least 25% by 2030 and 50% by 2050 with the increase in population growth **(Li, *et al*., 2014)**. Salinity exposure for long term in the ionic phase of plants is characterised by the buildup of Na+ and the early loss of earlier leaves **(Singh, *et al*., 2014)**. Despite their lower output and inferior seed quality, landraces have salt tolerant genes which can't be used in commercial production **(Ravikiran *et al*., 2018)**. At the early growth or seedling stage in rice, the *Saltol* QTL maintains Na+/k+ equlibrium and exhibits tolerance

(Warraich, *et al*., 2020). The advancement of salt-tolerant cultivars using both traditional breeding methods **(Krishnamurthy *et al*., 2019b)** and marker-assisted selection **(Singh, *et al*., 2016).** MAB avoids linkage drag by limiting the donor parent region through precise transfer of genes in selection of trait **(Singh, *et al.,* 2016).** On chromosome 1 of the rice crop, a few molecular markers aid in the identification of salinity resilience genes, and some *Saltol*-linked markers, including RM 3412, RM8094, AP3206, RM493 and RM10793, have been found for MAB & screening **(Ismail, *et al*., 2007)**. Pusa44 and Sarjoo52, are two high-yielding rice cultivars from India's northwest that are vulnerable to saline conditions at the seedling stage. So, increases in salt tolerance in these varieties through introgression of *Saltol* QTL which is present on chromosome number 1. In most of the plants, roots exclude Na^+ and cl^- effectively while water is taken from soil **(Munns, 2005)**. Long-term salt exposure in plants causes ionic stress, which accelerates the aging process and causes grain deformation and yellowing of the leaves **(Kumar, *et al*., 2017)**. With the effect of salinity there is interference in water transport and nutrient homeostasis which leads to osmotic stress and nutrient imbalance **(Hanin, *et al*., 2016; Zörb, *et al*., 2019)**. In cereals like rice is sensitive, wheat is moderately, and barley is most tolerant to salts **(Flowers, *et al*.,1977)**. Crops which are sensitive to saline stress are glycophytes and tolerant ones are called halophytes **(Himabindu, *et al*., 2016)**. Salinity induces stomatal closure, which rises leaf temperature and limits the development of shoots **(Rajendran, *et al*., 2009).**

2. Implications of salt stress on crop plants

Excess amount of Na^+ ion directly causes cellular damage and inhibits K^+ uptake due to which hampers photosynthetic pathway **(Xiong, *et al*., 2002)**. Ionic or mineral stress lead the way to Na^+ and Cl^- deposits in plant cells, which causes early dropping of leaves and plant death **(Maathuis, *et al*.,1999)**. Excess Na^+ in plant cell cytosol inhibits enzymatic activity, disrupting different cellular metabolisms such as synthesis of proteins, bio-molecular activities and chloroplast functions **(Horie, *et al*., 2012)**. Excess Na^+ also hampers other macro and micronutrients in cytoplasm **(Bulle, *et al*., 2016)**. Salt induced stress also dismisses cell turgor pressure in plants **(Kerepesi, *et al*., 2000)**. Reducing the cytoplasmic Na^+ level is critical to improve the saline tolerance mechanism in cereal grains like rice and wheat **(Horie, *et al*., 2012)**. Osmotic stress also causes a decline in the CO_2 assimilation capacity of plants **(Munns, *et al*., 2002)**. Ionic imbalances harden oxidative stress, which results in the build-up of reactive oxygen species (ROS) which damages lipids, enzymes, DNA & RNA **(Lalwani, & Kumar, 2022)**.



(Hasanuzzaman *et al*.,2022)

Fig. (1): **Schematic representation showing morphological, anatomical, physiological, biological and yield related responses of salt sensitive cereals under salinity.**

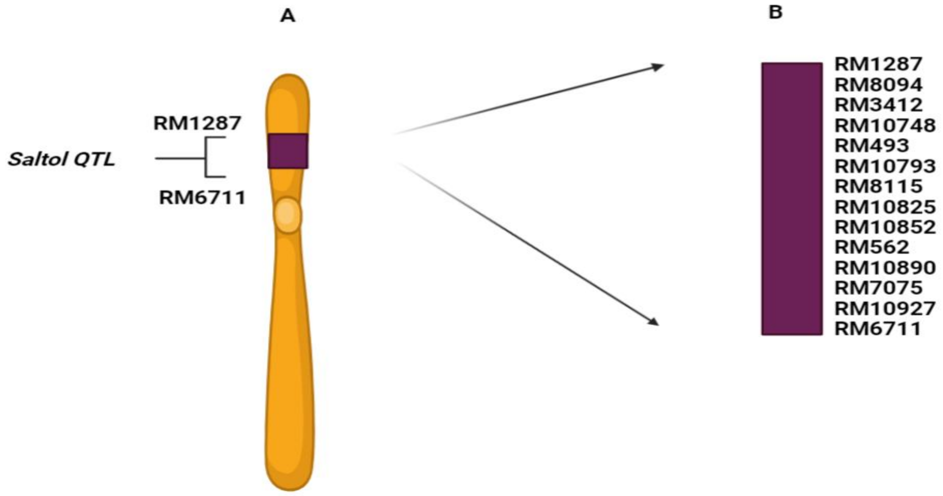
Two mechanisms exist for plants to be stressed by high salt: Higher concentrations of salinity in soil disrupt the root's ability to absorb water, as well as within the plant can be harmful, inhibits physiological and biochemical processes such as nutrition absorption and acclimatization **(Hasegawa, *et al*., 2000; Munns, 2002; Munns, *et al*.,1995; Munns & Tester, 2008)**. Shoot growth is affected by salinity, as illustrated by reduced leafy area and stunted shoot growth **(Läuchli, *et al*.,1990).** Na^+ deposits effects photosynthetic components like enzymes, chlorophyll, and carotenoid pigments in photosynthetic cells **(Dawood, *et al*., 2015).**

3. Na^+ AND K^+ Content in Shoot and Root of Rice Varieties

Ionic concentrations of Na^+ and K^+ in the shoot and root portions of certain rice cultivars show no apparent difference in unstressed conditions but when certain varieties like PB1509 (RP) and FL478 (DP) and NILs are grown under salt stress condition show significant variation in growth of the plant. Here are some of the results in which Na^+ concentration in shoots and roots among NIL's substantially less than RP (recurrent parent), but similar to DP (donor parent). Nevertheless, concentration of K^+ in shoots and roots of NIL's is compellingly higher than recurrent parent but similar to donor parent. So, root and shoot Na^+/ K^+ ratio of NIL's was significantly lower than PB1509 but comparable and similar to FL478 **(Yadav, *et al*., 2020)**. Wild species like *Oryza coarctata* and *Oryza alta* are highly tolerant to salinity stress than check cultivars which are tolerant such as FL478, Pokkali and Nona Bokra. Tolerant native species lines displayed greater levels of Na^+ in the foliage and lower levels of accumulated Na^+ in the root region. Less Na^+ concentration in the shoot is used as a criterion for choice when breeding salinity resilience varieties in cereals **(Prusty, *et al*., 2018).**

4.*Saltol* QTL Origin and Structure

Genome wide transcriptome analysis between various rice genotypes is known for spotting of required target genes in *saltol* region in Pokkali **(Kumari, *et al*., 2009)**. *Saltol* QTL (Quantitative trait loci) is located on short arm of chromosome number 1 of an Pokkali and IR29 were crossed to create the F8 RIL population (Recombinant Inbred Line) at IRRI. The Na^+/ K^+ ratio and salt endurance at the sprouting of seed or seedling stage are the two primary effects of the *Saltol* QTL **(Gresgorio, *et al*.,1997; Bonilla, *et al*., 2002)** and also observed that under salt stress, rice seedlings have less Na^+ and higher K^+ engrossment, and lower Na^+/ K^+ ratio **(Gregorio, *et al*., 2002)**. For FL478 a (RIL) Recombinant Inbred Line, pokkali is the source for positive alleles **(Bonilla, *et al*., 2002)**. Rather the *saltol* region in FL478 was donated by IR29 **(Walia, *et al*., 2005)**. Profiling has been done for finding of required target genes in the *Saltol* region which codes for signalling related proteins (SRPs) in different genotypes of rice. Salinity Induced factors also known as PUFs (Proteins of unknown function) which codes for genes Which are also helpful in providing salinity tolerance, growth of leaves, roots and stems, viability, fertility, and early blossoming **(Soda *et al*., 2013).**



(Waziri, *et al*., 2016)

Fig. (2):

A) Chromosome 1 in which *Saltol* QTL (purple colour) is present on short arm, bound by simple sequence repeats (SSR) like RM1287 and RM6711.Central circle portion is Centromere.

B) There are 15 SSR markers are aligned within the QTL region in a position of 10.8 Mb to 16.4 Mb from RM1287 to RM6711 respectively.

In addition to these in the *saltol* region "OSAP1" zinc finger proteins and transcription factors like "HBP1b" gives salinity inducible genes **(Kumari, *et al*., 2009; Lakra, *et al*., 2015)**. MABC and MAS are the major two methods through which salt tolerant cultivars are developed like FL478 and Line IR61920 respectively. In (MABC), simple sequence repeats (SSR) and single nucleotide polymorphisms (SNP) are used in tight linkage with traits for salinity tolerance and biotic stress **(Hasan *et al*., 2015)**. MAS was used in the introduction of *Saltol* QTL from IR61920 (DP) to Novator (RP) by microsatellite markers **(Usatov *et al*., 2015).**

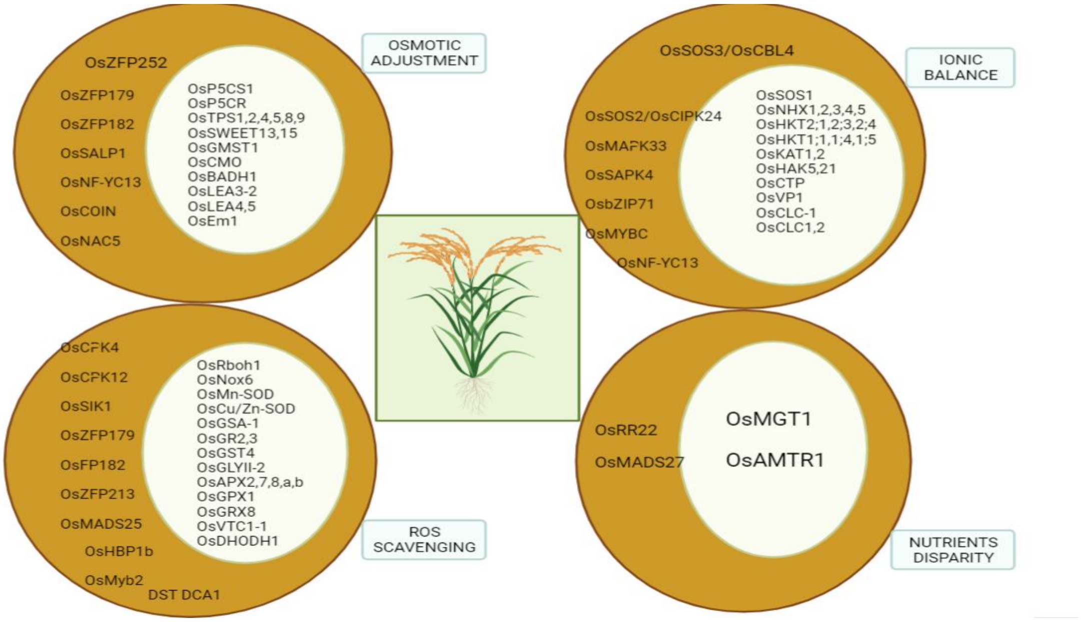
5. Salt tolerance mechanisms in Rice

a) Regulation of ionic balance

More concentration of Na^+ and Cl^+ causes salinity stress in the soil **(Munns, 2002; Ismail, *et al*., 2014)**. The ions are imported into the crop plants by various transporters at organ and cellular levels **(Deinlein, *et al*., 2014)**. Na^+ and K^+ are entranced by same transporters in the cell but compete with each other for space **(Greenway, *et al*.,1980)**. K^+ is essential for catalytic enzymes, regulation of osmosis, production of proteins, turgor pressure in cell wall and photosynthesis in leaves therefore its necessary to maintain Na^+/K^+ homeostasis which helps in growing of plants in salt stress conditions **(Lodeyro, *et al*., 2015; Fu, *et al*.,1998; Ashraf *et al*., 2004; Freitas *et al*., 2001)**. Moreover, mechanisms like decrease in cytosolic Na^+ intake, assortment of Na^+ into the vacuole and increment in Na^+ outflow, and also salt inducible enzymes, anti-transporter like OsSOS1 helps in carrying away cytoplasmic Na^+ ions into the apoplast and outflow of Na^+ from shoot respectively by increasing salinity tolerance **(Yang *et al*., 2018; El Mahi *et al*., 2019)**.The H^+ ion translocating enzyme (OsVP1) in vacuole transport H^+ from cytoplasmic fluid into vacuoles by increase in inducible H^+ gradient potential between them and promotes Na^+/H^+ exchange which enhance saline tolerance in rice **(Liu, *et al*., 2010)**. When plants are exposed to high levels of salt, their molecular signalling mechanisms are triggered, which activate both drought-induced and sodium-specific pathways **(Tester, & Davenport 2003)**.

In rice Na^+/H^+ anti-transporter (OsSOS1) situated in cell membrane helpful in lowering the Na^+/K^+ ratio at tissue level whereas the vacuole Na^+/H^+ anti-transporters (OsNHX1, OsNHX2, OsNHX3, OsNHX4, OsNHX5 and OsARP/OsCTP) has a role of compartmentalization of Na^+/K^+ to determine and development of saline tolerance in rice crop **(El Mahi *et al*., 2019; Martínez-Atienza, *et al*., 2007; Liu, *et al*., 2010; Fukuda, *et al*., 2011; Uddin, *et al*., 2008).**

In cereals some genes like Nax1 and Nax2 used as molecular markers in breeding of salinity resilience, which are situated in 2A and 5A chromosomes respectively helpful in control of Na^+ accumulation **(James *et al*., 2006; James *et al*., 2011)** and vascular Na^+/H^+ anti-transporters like TNHX1, TNHX2, and TVP1 are helpful in growth and development of seedlings in wheat through Na sequestration and PH balance **(Bulle, *et al*., 2016)**.



(Liu, *et al*., 2022)

Fig. (3): Genes involved in control of saline resilience in rice.

In rice and wheat, many genes are helpful in control of salt tolerance includes a) Ionic balance b) Nutrients disparity c) ROS scavenging d) Osmotic adjustment. The genes in the middle light-yellow colour are functional genes and the outer brown colour has regulatory genes.

The functional genes and its proteins directly protect membranes of the cell, other cell organelles and macromolecules such as DNA, RNA, proteins, carbohydrates, and fats under salinity stress conditions. The regulatory genes and its products such as activators protects crop plants from adverse effects by controlling expression of functional gene to abiotic stress **(Liu, *et al*., 2022)**.

b) Osmotic potential adjustment

Osmotic stress is caused by salt stress and synthesis of osmolytes which has an impact on osmotic modification it leads to regulation of cell turgor pressure for metabolic activity of the plant and strengthens proteins and cellular frameworks while lowering cell osmotic potential **(Yang, *et al*., 2018)**. To maintain osmotic equilibrium at the cellular level, osmolytes like proline, polyamines, soluble carbs, & proteins such as betaine and glycine from the late embryogenesis abundant (LEA) family are present **(Hare, *et al*.,1998)**. As a physiological indication of salinity tolerance, proline levels are employed. **(Liang, *et al*., 2018)**. Proline synthesis genes like OsP5CS1 and OsP5CR, monosaccharide transporter OsGMST1 and glycine betaine by OsCMO and OsBADH1 in rice would enhance the salt tolerance by accumulation **(Sripinyowanich, *et al*., 2013; Tang, *et al*., 2014)**. So as to maintain the equilibrium of sugar carbohydrates in rice under dry conditions and salinity circumstances, the outflowing transporters like OsSWEET13 and OsSWEET15 control the transit and dispersal of sugars like sucrose **(Mathan, *et al*., 2021)**. In wheat betaine helps in inhibit the Na^+ & Cl^- from roots and promotes K^+ transport to enhance salinity tolerance **(Chen, *et al*., 2007).** Plant specific membrane protein which encodes gene OsSALP1 develops salt stress tolerance by enhancing OsP5CS and proline synthesis in amply to salt stress **(Yuan, *et al*., 2016)**.

c) Reactive oxygen species scavenging

Oxygen is essential in cellular metabolism which is converted to ROS during plant metabolic process. Excess of ROS is produced during the under-salt stress conditions e.g.: O_2, $O_2^{\,-}$, H_2O_2 and OH^- **(Qin, *et al*., 2020; Miller *et al*., 2010)**. Salt stress reactions can be triggered by low ROS production, and excessive build-up results in destruction of plasma membranes, phytotoxic reactions such as DNA mutation, peroxidation of carbs, lipids, and proteins, permanent metabolic failure, and ultimately death of cells **(Ahanger, *et al*., 2017; Miller, *et al*., 2010)**. Crop plants use antioxidants to mollify ROS stress which is of 2 types mainly a) enzymatic b) Non-enzymatic **(You, *et al*., 2015)**. Some of the enzymes that act as antioxidants are nicotinamide adenine dinucleotide phosphate oxidases (NOXs, also called as respiratory burst oxidase homologs [Rbohs]), ascorbate peroxidase (APX), catalase (CAT), glutathione peroxidase (GPXs) **(Yang, *et al*., 2018; Postiglione, *et al*., 2020; Mittler *et al*., 2017; Torres, *et al*., 2005)**. Non-enzymatic antioxidants include glutathione (GSH), ascorbic acid (ASH), phenolic compounds, tocopherol, carotenoids, glutathione (GSH), flavonoids and alkaloids **(Gill, *et al*., 2010; Borghesi, *et al*., 2011)**. CAT and APX enzymes help in removing of H_2O_2 for crop tolerance **(Ashraf, *et al*., 2004)**. Due to salt stress, rise in ROS causes lipid peroxidation in cell membranes, which makes MDA a critical product for reducing oxidative stress and boosting rice salinity tolerance **(Latef *et al*., 2021)**. From the above these studies state that removing of ROS would effectively increase the rice salt tolerance.

d) Nutrients disparity

Due to salinity stress nutritional deficiencies occur and reduces transportation of the nutrients within the plant body **(Razzaq *et al*., 2020)**. Magnesium ion transport in root zone increases OsHKT1;5 that limits Na^+ cumulation in shoots which leads to enhance in saline tolerance **(Chen, *et al*., 2017)**. In rice aminotransferase and cytokinin type -B response regulator control stress associated proteins and Zn-transporter genes respectively which maintains salinity tolerance **(Gao, *et al*., 2019)**.

e) Plant growth regulators' adjustment

In addition to above mechanisms the PGRs also help in salt tolerance. Phytohormones vary during untimely salt stress and also salinity induced signalling cascade which leads to adaptive responses. PGRs control plant growth and development in tough and difficult environmental conditions **(Van Zelm, *et al*., 2020)**. To manage and adjust to salt stress, multiple PGRs must be integrated and coordinated like (IAA) Indole acetic acid, (GA) Gibberellic acid, abscisic acid (ABA), cytokinin (CK), ethylene (ETH), brassinosteroids (BR), jasmonic acid (JA), triazoles (TR), salicylic acid (SA), which control standard growth and moderate counter to salt stress **(Sah, *et al*., 2016)**.

6) Conclusion

Salinity stress increases in salt sensitive cereals like rice and wheat which leads to a decrease in growth, development, and excess of it causes death of crop plants. So, to demonstrate salt stress there is a need to development of various tolerant varieties through MABC and MAS which stands in adverse climatic conditions. Some of the nutrients like Na+ and K+ plays important role in control of abiotic or salt stress. As Na+ increases in shoot of the crop plant which causes an imbalance in ions, oxygen levels and PGRs. In rice various transporters and genes are able to cope with salt stress by developing mechanisms like ionic homeostasis, ROS scavenging, osmotic adjustment. Genes like OsHKT1;5 located in *Saltol* QTL region is incorporated from salt tolerant fewer yielding landraces like pokkali, Nona Bokra to cultivate salt sensitive high yielding varieties by wide transcriptome analysis. Even though the mechanisms within the plant and the various conventional breeding techniques as well as modern Marker Assisted

Backcross and Marker Assisted selection techniques are developing new varieties and direct transfer of targeted genes into selected plants through genome editing like CRISPR/CAS9 and transgenic methods, as they do not accomplish the required need of growing populations and increase in salinity soils. Therefore, in staple food crops like rice and wheat, further research must be carried out to elucidate various biochemical, molecular mechanism and physiological mechanisms of salinity tolerance by modern approaches to develop climate resilient crops. There is a further need to study how to enhance and develop salinity tolerant crops.

7) References

1) Ahanger, M. A., Tomar, N. S., Tittal, M., Argal, S., & Agarwal, R. (2017). Plant growth under water/salt stress: ROS production; antioxidants and significance of added potassium under such conditions. *Physiology and Molecular Biology of Plants*, *23*, 731-744.
2) Ashraf, M. P. J. C., & Harris, P. J. C. (2004). Potential biochemical indicators of salinity tolerance in plants. *Plant science*, *166*(1), 3-16.
3) Babu, N. N., Vinod, K. K., Krishnamurthy, S. L., Krishnan, S. G., Yadav, A., Bhowmick, P. K., *et al*. (2017b). Microsatellite based linkage disequilibrium analyses reveal Saltol haplotype fragmentation and identify Novel QTLs for seedling stage salinity tolerance in rice. J. Plant Biochem. Biotechnol. 26 (3), 310–320. doi: 10.1007/s13562-016-0393-3
4) Bonilla, P., Mackell, D., Deal, K., & Gregorio, G. (2002). RFLP and SSLP mapping of salinity tolerance genes in chromosome 1 of rice (Oryza sativa L.) using recombinant inbred lines. *Philippine Agricultural Scientist (Philippines)*.
5) Borghesi, E., González-Miret, M. L., Escudero-Gilete, M. L., Malorgio, F., Heredia, F. J., & Meléndez-Martínez, A. J. (2011). Effects of salinity stress on carotenoids, anthocyanins, and color of diverse tomato genotypes. *Journal of Agricultural and Food Chemistry*, *59*(21), 11676-11682.
6) Bulle, M., Yarra, R., & Abbagani, S. (2016). Enhanced salinity stress tolerance in transgenic chilli pepper (Capsicum annuum L.) plants overexpressing the wheat antiporter (TaNHX2) gene. *Molecular Breeding*, *36*, 1-12.

7) Chen, Z. C., Yamaji, N., Horie, T., Che, J., Li, J., An, G., & Ma, J. F. (2017). A magnesium transporter OsMGT1 plays a critical role in salt tolerance in rice. *Plant Physiology*, *174*(3), 1837-1849.

8) Chen, Z., Cuin, T. A., Zhou, M., Twomey, A., Naidu, B. P., & Shabala, S. (2007). Compatible solute accumulation and stress-mitigating effects in barley genotypes contrasting in their salt tolerance. *Journal of experimental botany*, *58*(15-16), 4245-4255.

9) Chinnusamy, V., Jagendorf, A., and Zhu, J. K. (2005). Understanding and proving salt tolerance in plants. Crop Sci. 45, 437–448. doi: 10.2135/cropsci2005.0437

10) Dawood, M. G., & El-Awadi, M. E. (2015). Alleviation of salinity stress on Vicia faba L. plants via seed priming with melatonin. *Acta Biológica Colombiana*, *20*(2), 223-235.

11) Deinlein, U., Stephan, A. B., Horie, T., Luo, W., Xu, G., & Schroeder, J. I. (2014). Plant salt-tolerance mechanisms. *Trends in plant science*, *19*(6), 371-379.

12) Dolo, J. S. (2012). *Screening for tolerance to salinity: a case study with seven rice varieties from Africa rice center and Ghana* (Doctoral dissertation).

13) El Mahi, H., Pérez-Hormaeche, J., De Luca, A., Villalta, I., Espartero, J., Gámez-Arjona, F., ... & Quintero, F. J. (2019). A critical role of sodium flux via the plasma membrane Na+/H+ exchanger SOS1 in the salt tolerance of rice. *Plant Physiology*, *180*(2), 1046-1065.

14) Flowers, T. J., Troke, P. F., & Yeo, A. R. (1977). The mechanism of salt tolerance in halophytes. *Annual review of plant physiology*, *28*(1), 89-121.

15) Freitas, J. B. S., Chagas, R. M., Almeida, I. M. R., Cavalcanti, F. R., & Silveira, J. A. G. (2001). Expression of physiological traits related to salt tolerance in two contrasting cowpea cultivars. *Documentos Embrapa MeioNorte*, *56*, 115-118.

16) Fu, H. H., & Luan, S. (1998). AtKUP1: a dual-affinity K^+ transporter from Arabidopsis. *The Plant Cell*, *10*(1), 63-73.

17) Fukuda, A., Nakamura, A., Hara, N., Toki, S., & Tanaka, Y. (2011). Molecular and functional analyses of rice NHX-type Na^+/ H^+ antiporter genes. *Planta*, *233*, 175-188.

18) Gao, S., Xiao, Y., Xu, F., Gao, X., Cao, S., Zhang, F., ... & Chu, C. (2019). Cytokinin-dependent regulatory module underlies the maintenance of zinc nutrition in rice. *New Phytologist*, *224*(1), 202-215.

19) Gill, S. S., & Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant physiology and biochemistry*, *48*(12), 909-930.

20) Greenway, H., & Munns, R. (1980). Mechanisms of salt tolerance in nonhalophytes. *Annual review of plant physiology*, *31*(1), 149-190.

21) Gregorio, G. B., Senadhira, D., Mendoza, R. D., Manigbas, N. L., Roxas, J. P., & Guerta, C. Q. (2002). Progress in breeding for salinity tolerance and associated abiotic stresses in rice. *Field Crops Research*, *76*(2-3), 91-101.

22) Gresgorio, G. B., Senadhira, D., & Mendoza, R. D. (1997). Screening Rice for Salinity tolerance. IRRI. *Dis paper*, (22).

23) Hanin M, Ebel C, Ngom M, Laplaze L, Masmoudi K (2016) New insights on plant salt tolerance mechanisms and their potential use for breeding. Front Plant Sci 7:1787. https://doi.org/10.3389/ fpls.2016.01787

24) Hare, P. D., Cress, W. A., & Van Staden, J. (1998). Dissecting the roles of osmolyte accumulation during stress. *Plant, cell & environment*, *21*(6), 535-553.

25) Hasan, M. M., Rafii, M. Y., Ismail, M. R., Mahmood, M., Rahim, H. A., Alam, M. A., ... & Latif, M. A. (2015). Marker-assisted backcrossing: a useful method for rice improvement. *Biotechnology & Biotechnological Equipment*, *29*(2), 237-254.

26) Hasanuzzaman, M. (2022). Salt stress tolerance in rice and wheat: Physiological and molecular mechanism. *Plant Defense Mechanisms*, 33.

27) Hasegawa, P. M., Bressan, R. A., Zhu, J. K., & Bohnert, H. J. (2000). Plant cellular and molecular responses to high salinity. Annual Review of Plant Physiology and Plant Molecular Biology, 51, 463-499.

28) Himabindu, Y., Chakradhar, T., Reddy, M. C., Kanygin, A., Redding, K. E., & Chandrasekhar, T. (2016). Salt-tolerant genes from halophytes are potential key players of salt tolerance in glycophytes. *Environmental and Experimental Botany*, *124*, 39-63.

29) Hoang, T. M. L., Tran, T. N., Nguyen, T. K. T., Williams, B., Wurm, P., Bellairs, S., & Mundree, S. (2016). Improvement of salinity stress tolerance in rice: challenges and opportunities. *Agronomy*, *6*(4), 54.

30) Horie, T., Karahara, I., & Katsuhara, M. (2012). Salinity tolerance mechanisms in glycophytes: An overview with the central focus on rice plants. *Rice*, *5*(1), 1-18.

31) Islam, M. R., Gregorio, G. B., Salam, M. A., Collard, B. C., Singh, R. K., & Hassan, L. (2012). Validation of SalTol linked markers and haplotype diversity on chromosome 1 of rice. *Molecular Plant Breeding*, *3*(10).

32) Ismail, A. M., Heuer, S., Thomson, M. J., and Wissuwa, M. (2007). Genetic and genomic approaches to develop rice germplasm for problem soils. Plant Mol. Biol. 65, 547–570. doi: 10.1007/s11103-007-9215-2

33) Ismail, A., Takeda, S., & Nick, P. (2014). Life and death under salt stress: same players, different timing. *Journal of experimental botany*, *65*(12), 2963-2979.

34) James, R. A., Blake, C., Byrt, C. S., & Munns, R. (2011). Major genes for Na+ exclusion, Nax1 and Nax2 (wheat HKT1; 4 and HKT1; 5), decrease Na+ accumulation in bread wheat leaves under saline and waterlogged conditions. *Journal of experimental botany*, *62*(8), 2939-2947.

35) James, R. A., Davenport, R. J., & Munns, R. (2006). Physiological characterization of two genes for Na^+ exclusion in durum wheat, Nax1 and Nax2. *Plant physiology*, *142*(4), 1537-1547.

36) Kerepesi, I., & Galiba, G. (2000). Osmotic and salt stress-induced alteration in soluble carbohydrate content in wheat seedlings. *Crop science*, *40*(2), 482-487.

37) Krishnamurthy, S. L., Sharma, P. C., Gautam, R. K., Singh, R. K., Singh, Y. P., Mishra, V. K., *et al*. (2019b). Notification of crop varieties and registration of Germplasm: Variety CSR56 (IET 24537). Indian J. Genet. 79 (2), 512–513.

38) Kumar S, Beena AS, Awana M, Singh A (2017) Physiological, biochemical, epigenetic, and molecular analyses of wheat (Triticumaestivum) genotypes with contrasting salt tolerance. Front Plant Sci 8:1151. https://doi.org/10.3389/fpls.2017.01151

39) Kumari, S., Panjabi nee Sabharwal, V., Kushwaha, H. R., Sopory, S. K., Singla-Pareek, S. L., & Pareek, A. (2009). Transcriptome map for seedling stage specific salinity stress response indicates a specific set of genes as candidate for saline tolerance in Oryza sativa L. *Functional & Integrative Genomics*, *9*, 109-123.

40) Lakra, N., Nutan, K. K., Das, P., Anwar, K., Singla-Pareek, S. L., & Pareek, A. (2015). A nuclear-localized histone-gene binding protein from rice (OsHBP1b) functions in salinity and drought stress tolerance by maintaining chlorophyll content and improving the antioxidant machinery. *Journal of plant physiology*, *176*, 36-46.

41) Lalwani, Z., & Kumar, P. (2022). Oxidative stress in plants: A delicate balance between life and death.

42) Latef, A. A. A., Hasanuzzaman, M., & Tahjib-Ul-Arif, M. (2021). Mitigation of salinity stress by exogenous application of cytokinin in faba bean (Vicia faba L.). *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, *49*(1), 12192-12192.

43) Läuchli, A., & Epstein, E. (1990). Plant responses to saline and sodic conditions. In K. K. Tanji (Ed.), Agricultural salinity assessment and management, (pp. 113-137). New York: American Society of Civil Engineers.

44) Li, J. Y., Wang, J., & Zeigler, R. S. (2014). The 3,000 rice genomes project: new opportunities and challenges for future rice research. *Gigascience*, *3*(1), 2047-217X.

45) Liang, W., Ma, X., Wan, P., & Liu, L. (2018). Plant salt-tolerance mechanism: A review. *Biochemical and biophysical research communications*, *495*(1), 286-291.

46) Liu, C., Mao, B., Yuan, D., Chu, C., & Duan, M. (2022). Salt tolerance in rice: Physiological responses and molecular mechanisms. *The Crop Journal*, *10*(1), 13–25. https://doi.org/10.1016/j.cj.2021.02.010

47) Liu, S., Zheng, L., Xue, Y., Zhang, Q., Wang, L., & Shou, H. (2010). Overexpression of OsVP1 and OsNHX1 increases tolerance to drought and salinity in rice. *Journal of Plant Biology*, *53*, 444-452.

48) Lodeyro, A. F., & Carrillo, N. (2015). Salt stress in higher plants: mechanisms of toxicity and defensive responses. *Stress Responses in Plants: Mechanisms of Toxicity and Tolerance*, 1-33.

49) Maathuis, F. J., & Amtmann, A. N. N. A. (1999). K^+ nutrition and Na^+ toxicity: the basis of cellular K^+/Na^+ ratios. *Annals of botany*, *84*(2), 123-133.

50) Martínez-Atienza, J., Jiang, X., Garciadeblas, B., Mendoza, I., Zhu, J. K., Pardo, J. M., & Quintero, F. J. (2007). Conservation of the salt overly sensitive pathway in rice. *Plant physiology*, *143*(2), 1001-1012.

51) Mathan, J., Singh, A., & Ranjan, A. (2021). Sucrose transport in response to drought and salt stress involves ABA-mediated induction of OsSWEET13 and OsSWEET15 in rice. *Physiologia plantarum*, *171*(4), 620-637.

52) Miller, G. A. D., Suzuki, N., Ciftci-Yilmaz, S. U. L. T. A. N., & Mittler, R. O. N. (2010). Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant, cell & environment*, *33*(4), 453-467.

53) Mittler, R. (2017). ROS is good. *Trends in plant science*, *22*(1), 11-19.

54) Munns, R. & Tester, M. (2008). Mechanisms of salinity tolerance. *Annu. Rev. Plant Biol.*, *59*, 651-681.

55) Munns, R. (2002). Comparative physiology of salt and water stress. *Plant, cell & environment*, *25*(2), 239-250.

56) Munns, R. (2005). Genes and salt tolerance: bringing them together. New Phytol. 167:645– 63

57) Munns, R., Schachtman, D., & Condon, A. (1995). The Significance of a Two-Phase Growth Response to Salinity in Wheat and Barley. Functional Plant Biology, 22(4), 561-569.

58) Postiglione, A. E., & Muday, G. K. (2020). The role of ROS homeostasis in ABA-induced guard cell signaling. *Frontiers in plant science*, *11*, 968.

59) Pradhan, B. (2013). *Influence of drought and salinity on metabolic processes in different wheat varieties* (Doctoral dissertation, University of North Bengal).

60) Prusty, M. R., Kim, S. R., Vinarao, R., Entila, F., Egdane, J., Diaz, M. G., & Jena, K. K. (2018). Newly identified wild rice accessions conferring high salt tolerance might use a tissue tolerance mechanism in leaf. *Frontiers in Plant Science*, *9*, 417.

61) Qin, H., & Huang, R. (2020). The phytohormonal regulation of Na+/K+ and reactive oxygen species homeostasis in rice salt response. *Molecular Breeding*, *40*(5), 47.

62) Rajendran, K., Tester, M., & Roy, S. J. (2009). Quantifying the three main components of salinity tolerance in cereals. *Plant, cell & environment*, *32*(3), 237-249.

63) Ravikiran, K. T., Krishnamurthy, S. L., Warraich, A. S., and Sharma, P. C. (2018). Diversity and haplotypes of rice genotypes for seedling stage salinity tolerance analyzed through morpho-physiological and SSR markers. Field Crops Res. 220, 10–18. doi: 10.1016/j.fcr.2017.04.006

64) Razzaq, A., Ali, A., Safdar, L. B., Zafar, M. M., Rui, Y., Shakeel, A., ... & Yuan, Y. (2020). Salt stress induces physiochemical alterations in rice grain composition and quality. *Journal of food science*, *85*(1), 14-20.

65) Reddy, A. M., Francies, R. M., Rasool, S. N., and Reddy, V. R. P. (2014). Breeding for tolerance stress triggered by salinity in rice. Int. J. Appl. Biol. Pharm. Technol. 5, 167–176.

66) Ren, Z. H., Gao, J. P., Li, L. G., Cai, X. L., Huang, W., Chao, D. Y., ... & Lin, H. X. (2005). A rice quantitative trait locus for salt tolerance encodes a sodium transporter. *Nature genetics*, *37*(10), 1141-1146.

67) Sah, S. K., Reddy, K. R., & Li, J. (2016). Abscisic acid and abiotic stress tolerance in crop plants. *Frontiers in plant science*, *7*, 571.

68) Singh, D. P., & Sarkar, R. K. (2014). Distinction and characterisation of salinity tolerant and sensitive rice cultivars as probed by the chlorophyll fluorescence characteristics and growth parameters. *Functional plant biology*, *41*(7), 727-736.

69) Singh, R., Singh, Y., Xalaxo, S., Verulkar, S., Yadav, N., Singh, S. (2016). From QTL to variety- Harnessing the benefits of QTLs for drought, flood and salt tolerance in mega rice varieties of India through a multi-institutional network. Plant Sci. 242, 278–287. doi: 10.1016/j.plantsci.2015.08.008

70) Singh, V. K., Singh, B. D., Kumar, A., Maurya, S., Subbaiyan, G. K., Vinod, K. K., *et al*. (2018). Marker-Assisted Introgression of Saltol QTL Enhances Seedling Stage Salt Tolerance in the Rice Variety “Pusa Basmati 1”. Int. J. Genomics doi: 10.1155/2018/8319879. Article ID 8319879.

71) Soda, N., Kushwaha, H. R., Soni, P., Singla-Pareek, S. L., & Pareek, A. (2013). A suite of new genes defining salinity stress tolerance in seedlings of contrasting rice genotypes. *Functional & integrative genomics*, *13*, 351-365.

72) Sripinyowanich, S., Klomsakul, P., Boonburapong, B., Bangyeekhun, T., Asami, T., Gu, H., ... & Chadchawan, S. (2013). Exogenous ABA induces salt tolerance in indica rice (Oryza sativa L.): the role of OsP5CS1 and OsP5CR gene expression during salt stress. *Environmental and Experimental Botany*, *86*, 94-105.

73) Tang, W., Sun, J., Liu, J., Liu, F., Yan, J., Gou, X., ... & Liu, Y. (2014). RNAi-directed downregulation of betaine aldehyde dehydrogenase 1 (OsBADH1) results in decreased stress tolerance and increased oxidative markers without affecting glycine betaine biosynthesis in rice (Oryza sativa). *Plant molecular biology*, *86*, 443-454.

74) Tester, M., & Davenport, R. (2003). Na+ tolerance and Na+ transport in higher plants. *Annals of botany*, *91*(5), 503-527.

75) Torres, M. A., & Dangl, J. L. (2005). Functions of the respiratory burst oxidase in biotic interactions, abiotic stress and development. *Current opinion in plant biology*, *8*(4), 397-403.

76) Uddin, M. I., Qi, Y., Yamada, S., Shibuya, I., Deng, X. P., Kwak, S. S., ... & Tanaka, K. (2008). Overexpression of a new rice vacuolar antiporter regulating protein OsARP improves salt tolerance in tobacco. *Plant and cell physiology*, *49*(6), 880-890.

77) Usatov, A. V., Alabushev, A. V., Kostylev, P. I., Azarin, K. V., Makarenko, M. S., & Usatova, O. A. (2015). Introgression the saltol QTL into the elite rice variety of Russia by marker-assisted selection. *American Journal of Agricultural and Biological Science*, *10*(4), 165-169.

78) Van Zelm, E., Zhang, Y., & Testerink, C. (2020). Salt tolerance mechanisms of plants. *Annual review of plant biology*, *71*, 403-433.

79) Walia, H., Wilson, C., Condamine, P., Liu, X., Ismail, A. M., Zeng, L., ... & Close, T. J. (2005). Comparative transcriptional profiling of two contrasting rice genotypes under salinity stress during the vegetative growth stage. *Plant physiology*, *139*(2), 822-835.

80) Warraich, A. S., Krishnamurthy, S. L., Sooch, B. S., Vinaykumar, N. M., Dushyanthkumar, B. M., Bose, J., & Sharma, P. C. (2020). Rice GWAS reveals key genomic regions essential for salinity tolerance at reproductive stage. *Acta Physiologiae Plantarum*, *42*, 1-15.

81) Waziri, Aafrin & Kumar, Pravin & Purty, Ram Singh. (2016). Saltol QTL and their role in salinity tolerance in rice. Austin Journal of Biotechnology & Bioengineering. 3. 1-5.

82) Xiong, L., & Zhu, J. K. (2002). Molecular and genetic aspects of plant responses to osmotic stress. *Plant, Cell & Environment*, *25*(2), 131-139.

83) Yadav, A. K., Kumar, A., Grover, N., Ellur, R. K., Krishnan, S. G., Bollinedi, H., ... & Singh, A. K. (2020). Marker aided introgression of ‘Saltol’, a major QTL for seedling stage salinity tolerance into an elite Basmati rice variety ‘Pusa Basmati 1509’. *Scientific reports*, *10*(1), 1-15.

84) Yang, Y., & Guo, Y. (2018). Elucidating the molecular mechanisms mediating plant salt-stress responses. *New Phytologist*, *217*(2), 523-539.

85) You, J., & Chan, Z. (2015). ROS regulation during abiotic stress responses in crop plants. *Frontiers in plant science*, *6*, 1092.

86) Yuan, X., Sun, H., Tang, Z., Tang, H., Zhang, H., & Huang, J. (2016). A novel little membrane protein confers salt tolerance in rice (*Oryza sativa* L.). *Plant molecular biology reporter*, *34*, 524-532.

87) Zörb C, Geilfus CM, Dietz KJ (2019) Salinity and crop yield. Plant Biol 21:31–38. https://doi.org/10.1111/plb.12884