



# A Review on Understanding the Effects and Mechanisms of Salinity Tolerance in Rice (*Oryza sativa* L.)

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## Authors' contributions

This work was carried out in collaboration between all authors. Author MPKR designed the study, performed the statistical analysis, wrote the protocol, and wrote the first draft of the manuscript. Authors NT, HSJ and BK managed the analyses of the study. Author DMK managed the literature searches. All authors read and approved the final manuscript.

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## 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

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affects crop plants' processes like ionic imbalance, osmotic and oxidative stress.  $\text{Na}^+$  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  $\text{K}^+$  &  $\text{Na}^+/\text{K}^+$  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; 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 [54]. 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 [26]. Electrical conductivity ( $E_c$ ) is used to estimate salinity [54]. In rice, salinity mainly affects at germination, seedling stage and reproductive stage, in which if  $E_c$  is 3 dS/m yield start reducing with a 12% decrease in output per unit as  $E_c$  rises [9 and 65]. Plants have three primary processes. a) ionic removal, b) osmotic resilience, and c) cellular resilience to salinity stress [54]. Salinity stress in rice mainly build upon  $\text{Na}^+$  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 resilience 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 [4]. Progress of varieties which have seedling stage salinity tolerance leads to growth of leaves, stems and roots that can increase yield [29]. In India 7mha land is pretentious by salt [59]. Due to the frequent use of brackish water from groundwater for irrigation, the inland is salinized [12]. 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 [31]. In cross Nona Bokra / Koshihikari a transporter called OsHKT1;5 that regulates  $\text{K}^+$  regulation [66]. 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 [83]. Until now only two high producing Basmati rice types, Pusa Basmati 1 [70] and Pusa Basmati1121 [3] developed for improved seedling stage salinity tolerance through MABC [83]. The rice output must be increased by at least 25% by 2030 and 50% by 2050 with the increase in population growth [44]. Salinity exposure for long term in the ionic phase of plants is characterised by the buildup of  $\text{Na}^+$  and the early loss of earlier leaves [68]. Despite their lower output and inferior seed quality, landraces have salt tolerant genes which can't be used in commercial production [63]. At the early growth or seedling stage in rice, the *Saltol* QTL maintains  $\text{Na}^+/\text{K}^+$  equilibrium and exhibits tolerance [80]. The advancement of salt-tolerant cultivars using both traditional breeding methods [37] and marker-assisted selection [69] MAB avoids linkage drag by limiting the donor parent region through precise transfer of genes in selection of trait [69]. 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 [32]. 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  $\text{Na}^+$  and  $\text{Cl}^-$  effectively while water is taken from soil [56]. Long-term salt exposure in plants causes ionic stress, which accelerates the aging process and causes grain deformation and yellowing of the leaves [38]. With the effect of salinity there is interference in water transport and nutrient homeostasis which leads to osmotic stress and nutrient imbalance [23 and 87]. In cereals like rice is sensitive, wheat is moderately, and barley is most tolerant to salts [14]. Crops which are sensitive to saline stress are glycophytes and tolerant ones are called halophytes [28]. Salinity induces stomatal closure, which rises leaf temperature and limits the development of shoots [62].

## 2. IMPLICATIONS OF SALT STRESS ON CROP PLANTS

Excess amount of  $\text{Na}^+$  ion directly causes cellular damage and inhibits  $\text{K}^+$  uptake due to which hampers photosynthetic pathway [82]. Ionic or mineral stress lead the way to  $\text{Na}^+$  and  $\text{Cl}^-$  deposits in plant cells, which causes early dropping of leaves and plant death [49]. Excess  $\text{Na}^+$  in plant cell cytosol inhibits enzymatic

activity, disrupting different cellular metabolisms such as synthesis of proteins, bio-molecular activities and chloroplast functions [30]. Excess  $\text{Na}^+$  also hampers other macro and micronutrients in cytoplasm [6]. Salt induced stress also dismisses cell turgor pressure in plants [36]. Reducing the cytoplasmic  $\text{Na}^+$  level is critical to improve the saline tolerance mechanism in cereal grains like rice and wheat [30]. Osmotic stress also causes a decline in the  $\text{CO}_2$  assimilation capacity of plants [55]. Ionic imbalances harden oxidative stress, which results in the build-up of reactive oxygen species (ROS) which damages lipids, enzymes, DNA & RNA [41].

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 [27,55,54 and 57]. Shoot growth is affected by salinity, as illustrated by reduced leafy area and stunted shoot growth [43].  $\text{Na}^+$  deposits effects photosynthetic components like enzymes, chlorophyll, and carotenoid pigments in photosynthetic cells [10].

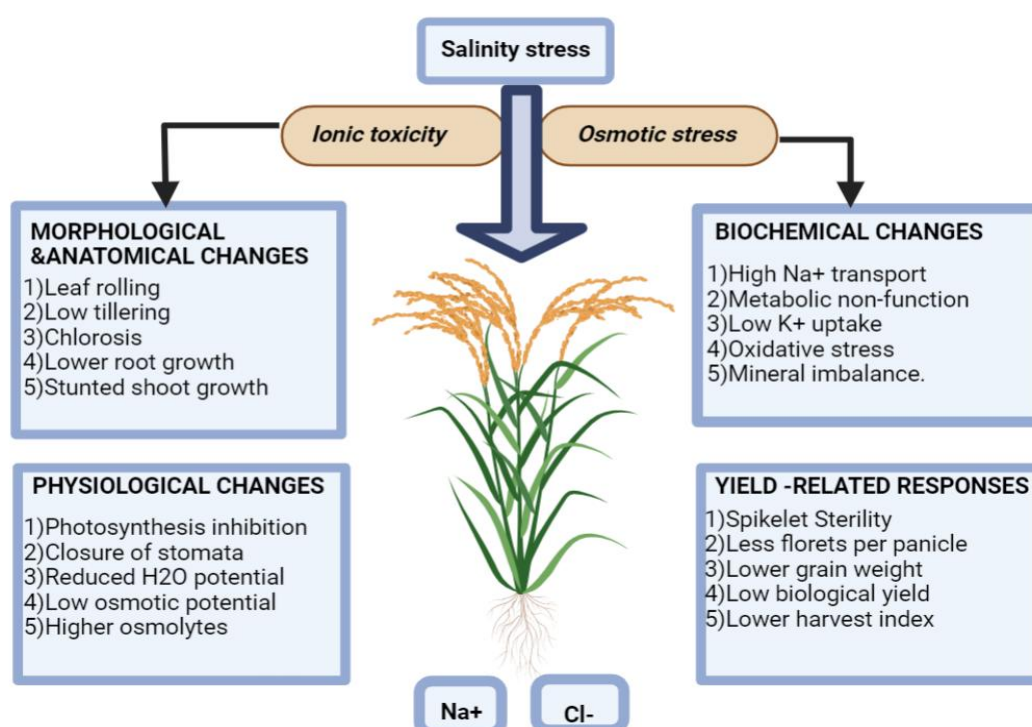


Fig. 1. Schematic representation showing morphological, anatomical, physiological, biological and yield related responses of salt sensitive cereals under salinity

Source: [6]

### 3. $\text{Na}^+$ AND $\text{K}^+$ CONTENT IN SHOOT AND ROOT OF RICE VARIETIES

Ionic concentrations of  $\text{Na}^+$  and  $\text{K}^+$  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  $\text{Na}^+$  concentration in shoots and roots among NIL's substantially less than RP (recurrent parent), but similar to DP (donor parent). Nevertheless, concentration of  $\text{K}^+$  in shoots and roots of NIL's is compellingly higher than recurrent parent but similar to donor parent. So, root and shoot  $\text{Na}^+/\text{K}^+$  ratio of NIL's was significantly lower than PB1509 but comparable and similar to FL478 [83]. 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  $\text{Na}^+$  in the foliage and lower levels of accumulated  $\text{Na}^+$  in the root region. Less  $\text{Na}^+$  concentration in the shoot is used as a criterion for choice when breeding salinity resilience varieties in cereals [60].

### 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

[39]. *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  $\text{Na}^+/\text{K}^+$  ratio and salt endurance at the sprouting of seed or seedling stage are the two primary effects of the *Saltol* QTL [22 and 4] and also observed that under salt stress, rice seedlings have less  $\text{Na}^+$  and higher  $\text{K}^+$  engrossment, and lower  $\text{Na}^+/\text{K}^+$  ratio [21]. For FL478 a (RIL) Recombinant Inbred Line, pokkali is the source for positive alleles [4]. Rather the *saltol* region in FL478 was donated by IR29 [79]. 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 [71].

In addition to these in the *saltol* region "OSAP1" zinc finger proteins and transcription factors like "HBP1b" gives salinity inducible genes [39 and 40]. 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 [25]. MAS was used in the introduction of *Saltol* QTL from IR61920 (DP) to Novator (RP) by microsatellite markers [77].

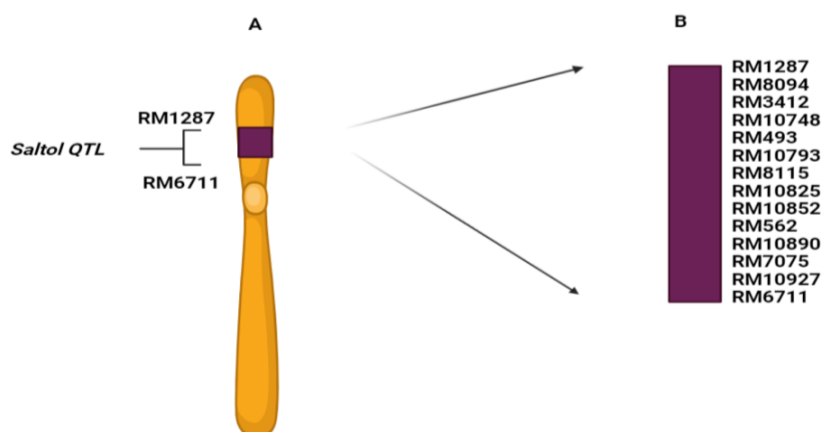


Fig. 2. Chromosome 1 in which *Saltol* QTL (purple colour) is present on short arm, bound by simple sequence repeats (SSR) like RM1287 and RM6711. Central circle portion is Centromere.

A) 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

Source: [81]

## 5. SALT TOLERANCE MECHANISMS IN RICE

### a) Regulation of ionic balance

More concentration of  $\text{Na}^+$  and  $\text{Cl}^-$  causes salinity stress in the soil [33 and 55]. The ions are imported into the crop plants by various transporters at organ and cellular levels [11].  $\text{Na}^+$  and  $\text{K}^+$  are entranced by same transporters in the cell but compete with each other for space [20].  $\text{K}^+$  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  $\text{Na}^+/\text{K}^+$  homeostasis which helps in growing of plants in salt stress conditions [48,16, 2 and 15]. Moreover, mechanisms like decrease in cytosolic  $\text{Na}^+$  intake, assortment of  $\text{Na}^+$  into the vacuole and increment in  $\text{Na}^+$  outflow, and also salt inducible enzymes, anti-transporter like OsSOS1 helps in carrying away cytoplasmic  $\text{Na}^+$  ions into the apoplast and outflow of  $\text{Na}^+$  from shoot respectively by increasing salinity tolerance [84 and 13]. The  $\text{H}^+$  ion translocating enzyme (OsVP1) in vacuole transport  $\text{H}^+$  from cytoplasmic fluid into vacuoles by increase in inducible  $\text{H}^+$  gradient potential between them and promotes  $\text{Na}^+/\text{H}^+$  exchange which enhance saline tolerance in rice [47]. When plants are exposed to high levels of salt, their molecular

signalling mechanisms are triggered, which activate both drought-induced and sodium-specific pathways [74].

In rice  $\text{Na}^+/\text{H}^+$  anti-transporter (OsSOS1) situated in cell membrane helpful in lowering the  $\text{Na}^+/\text{K}^+$  ratio at tissue level whereas the vacuole  $\text{Na}^+/\text{H}^+$  anti-transporters (OsNHX1, OsNHX2, OsNHX3, OsNHX4, OsNHX5 and OsARP/OsCTP) has a role of compartmentalization of  $\text{Na}^+/\text{K}^+$  to determine and development of saline tolerance in rice crop [13,50,47,17 and 76].

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  $\text{Na}^+$  accumulation [34 and 35] and vascular  $\text{Na}^+/\text{H}^+$  anti-transporters like TNHx1, TNHx2, and TVP1 are helpful in growth and development of seedlings in wheat through Na sequestration and PH balance [6].

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.

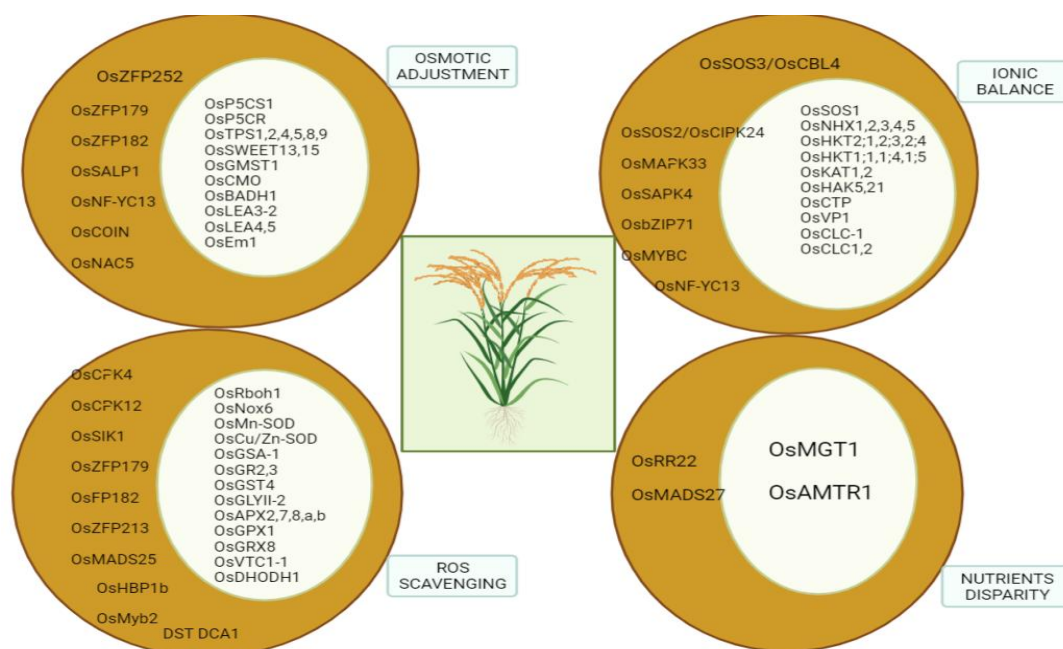


Fig. 3. Genes involved in control of saline resilience in rice

Source: [46]



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 [46].

#### **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 [48]. 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 [24]. As a physiological indication of salinity tolerance, proline levels are employed [45]. 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 [72 and 73]. 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 [51]. In wheat betaine helps in inhibit the Na<sup>+</sup> & Cl<sup>-</sup> from roots and promotes K<sup>+</sup> transport to enhance salinity tolerance [8]. Plant specific membrane protein which encodes gene OsSALP1 develops salt stress tolerance by enhancing OsP5CS and proline synthesis in amply to salt stress [86].

#### **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<sub>2</sub>, O<sub>2</sub><sup>-</sup>, H<sub>2</sub>O<sub>2</sub> and OH<sup>-</sup> [52 and 61]. 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 [1 and 52]. Crop plants use antioxidants to mollify ROS stress which is two types of mainly a) enzymatic b) Non-

enzymatic [85]. 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) [84,58,53 and 75]. Non-enzymatic antioxidants include glutathione (GSH), ascorbic acid (ASH), phenolic compounds, tocopherol, carotenoids, glutathione (GSH), flavonoids and alkaloids [19 and 5]. CAT and APX enzymes help in removing of H<sub>2</sub>O<sub>2</sub> for crop tolerance [2]. 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 [42]. 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 [64]. Magnesium ion transport in root zone increases OsHKT1;5 that limits Na<sup>+</sup> cumulation in shoots which leads to enhance in saline tolerance [7]. In rice aminotransferase and cytokinin type -B response regulator control stress associated proteins and Zn-transporter genes respectively which maintains salinity tolerance [18].

#### **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 [78]. 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 [67].

## **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<sup>+</sup> and K<sup>+</sup> plays important role in control of abiotic or salt stress. As Na<sup>+</sup> 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.

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## COMPETING INTERESTS

Authors have declared that no competing interests exist.

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