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REVIEW ARTICLE

Molecular Mapping for Salinity Tolerance in Rice (Oryza sativa): Accomplishments and Future Prospects

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Abstract

Rice (*Oryza sativa* L.) is the main source of staple food for the human population. Salinity is the major problem for agricultural production and it affects rice production globally. Different approaches have been developed and exploited to ameliorate the harmful effects of salinity on crop production. Development of salt-tolerant cultivars is the best option which ensures sustainable crop production. Molecular mapping approaches have greatly helped in the identification of genomic regions involved in salinity tolerance in different crop plants, including rice. Identified genomic regions associated with salinity tolerance accelerated molecular breeding efforts to develop salt-tolerant rice cultivars. Molecular mapping techniques (both linkage and association mapping) are the main components of genomics and these helped in the identification of genomic regions associated with salt-tolerance in rice. In this review, a detailed description of molecular mapping techniques, and major findings made by these techniques is presented. Prospects of these techniques are also discussed.

KEYWORDS
Genomic, Cultivars, Molecular Breeding, Salinity

1 | INTRODUCTION

Rice (*Oryza sativa* L.) belongs to family Poaceae and genus *Oryza*. Its genome size is approximately 430 Mb contained in 12 chromosomes. Large part of human population depends on it for staple food. Rice is a salt-susceptible crop. One third of world agricultural land is salt affected (Rengasamy 2006). Salinity, both soil and water, has negative effect on rice production (Ren et al. 2005). Elevated Na^+ levels in agricultural lands are increasingly becoming a serious threat to the world agriculture. Plants suffer osmotic and ionic stress under high salinity due to the salts accumulated at the outside of roots and those accumulated at the inside of the plant cells, respectively (Razzaq et al., 2020).

Projected increase in human population demands a proportional increase in the food supply. This demand of increased food supply can be fulfilled only if we utilize all available land resources to their full potential. An associated phenomenon with the increase in human population is the decrease in world agricultural land area due to its use for human settlements. Due to these constraints, even marginal cultivable lands cannot be neglected. This urges that saline soils should be exploited to their full production potential (Zafar et al., 2022). For good crop production on saline areas, different practices such as reclamation, agronomic adjustments, and biological amendments are used in combination. Considering sustainable crop production on these areas, the use of salt-tolerant crop cultivars seems to be most suitable option (Shannon et al. 1998; Saeed et al. 2012; Singh et al. 2016). For development of salt-tolerant cultivars, genetic diversity with respect to salt tolerance in crops has to be evaluated (Zafar et al. 2023; Zafar et al. 2024). For genetic diversity assessment and identification of genomic regions associated with salt tolerance, molecular mapping approaches have made considerable contribution in different crop plants (Veldboom et al. 1994; Mano & Takeda 1997; Yano & Sasaki 1997; Barakat et al. 2013; Lohwasser et al. 2013; Chai et al. 2014; Khan et al. 2015, 2016; Kaur et al. 2016). With the use of molecular mapping approaches, it has become possible to identify the chromosomal regions (quantitative trait loci, QTLs) associated with traits related to salt tolerance in rice. This review tries to cover effects of salinity on rice plant's growth and development, types of molecular mapping approaches, methodology involved in these approaches, and the achievements made through these approaches in salinity tolerance in rice to-date. It also highlights the future prospects of molecular mapping approaches. Thus, it will be a valuable resource for designing future research endeavours aiming at to genetically characterize salt tolerance mechanisms and develop salt-tolerant rice cultivars. It will also facilitate molecular breeding efforts for screening rice germplasm for salinity tolerance.

Effects of Salinity on Rice Plant Growth and Development

Salinity affects different morphological, biochemical, and physiological attributes of rice. Salinity has negative effect on percent relative-plant height, total tillers, root dry weight, shoot dry weight, and total dry matter (Razzaque et al. 2010). Biochemical attributes of rice, affected by salinity, include chlorophyll content, proline content, hydrogen peroxide content, peroxidase (POX) activity, anthocyanins, Na^+ content, K^+ content, Ca^{++} content, total cations content (Khan et al. 2015; Chunthaburee et al. 2016). Physiological attributes of rice, which are affected by salinity, include relative growth rate, osmotic potential, transpiration use efficiency, senescence, Na^+ uptake, K^+ uptake, Ca^{++} uptake, total cations uptake, Na^+/K^+ uptake, Na^+ uptake ratio, K^+ uptake ratio, Ca^{++} uptake ratio, Na^+/K^+ uptake ratio, and total cations uptake ratio (Khan et al. 2015; Chunthaburee et al. 2016; Negrão et al. 2017).

Rice shows different levels of salt tolerance at leaf and whole plant level (Yeo et al. 1985; Sytar et al. 2017). Similarly, behavior of rice plants towards salt stress may be different at vegetative and reproductive phases and this may not correlate with their mean level of relative resistance (Lutts et al. 1995). It is important to know the specific salt susceptible phase of a rice variety to have a better comparison of performance among varieties under salinity stress.

Vegetative and reproductive growth potential of plant depends upon the process of photosynthesis. Increased sodium concentration in the leaf tissue negatively affects net photosynthesis and essential cellular metabolism (Yeo et al. 1985; Horie et al. 2012). Chlorophyll content is important in photosynthesis. Reports suggest that there is no correlation between the chlorophyll content and photosynthesis under salinity stress. Net photosynthesis was reduced by a sodium concentration which did not affect chlorophyll content (Yeo et al. 1985). It implicates the disturbance by salinity stress of other cellular processes involved in photosynthesis. Sodium accumulation in the leaf also affects stomatal aperture and carbon dioxide fixation simultaneously (Yeo et al. 1985) and thus it may be one of the reasons for reduced photosynthesis due to sodium accumulation. The most salt-susceptible cultivars had lowest K^+/Na^+ ratio in the leaves and exhibited strongest yield reductions (Asch et al. 2000). Rice plant evolved different mechanisms to cope salinity stress conditions. One of these mechanisms is compartmenting salts within the plant body (Yeo & Flowers 1983).

Molecular Mapping Approaches: Types and Methodology

Types of Molecular Mapping Approaches

Molecular mapping approaches are of two types, linkage mapping and association mapping, on the basis of mapping population used.

Linkage Mapping

In linkage mapping, bi-parental segregating populations are used. Mapping populations used in linkage mapping include backcross populations, doubled haploid (DH) lines, F_2 populations, introgression lines (ILs), near isogenic lines (NILs) and recombinant inbred lines (RILs). JoinMap (Van Ooijen & Voorrips 2001), MapMaker (Lander et al. 1987) or QTL IciMapping (Meng et al. 2015) soft-wares are used for the construction of genetic linkage maps. WinQTLCartographer (Basten et al. 2001), QTL IciMapping (Meng et al. 2015), and QTLNetwork (Yang et al. 2005) programs are used for the identification of QTLs. Detailed information about input file requirements, statistical parameters thresholds, and the procedure to run the software are provided in the user manuals of these softwares.

Association Mapping

Association mapping uses natural populations for mapping purposes. In this technique, commercial crop cultivars can be employed for the assessment of QTLs. First reported in humans, association mapping is now widely used in plant sciences. Assessment of marker-trait associations is facilitated by controlling underlying population structure in the used plant material for mapping purposes (Zhao et al. 2007). STRUCTURE software is used for identifying sub-populations in the used plant germplasm (Pritchard & Wen 2004). TASSEL software is used for the identification of QTLs in this case (Bradbury et al. 2007).

DNA Markers used in Molecular Mapping Approaches

In molecular mapping approaches, different types of DNA markers are used to identify QTLs. Amplified fragment length polymorphism (AFLP), restriction fragment length polymorphism (RFLP), simple sequence repeats (SSRS), sequence tagged sites (STS), simple sequence length polymorphism (SSLP), and single nucleotide polymorphism (SNP) (Hongxuan et al. 1998; Koyama et al. 2001; Yao et al. 2005;

Bimpong et al. 2013; Khan et al. 2016a) are different types of DNA markers which are employed for genotyping in molecular mapping studies.

Achievements made through Molecular Mapping Approaches with Respect to Salinity Tolerance in Rice

By using linkage and association mapping approaches, a number of QTLs linked to salinity tolerance in rice, have been identified. Detail of identified QTLs is given below.

Linkage Mapping

Linkage mapping has been very successful in the identification of QTLs linked to salinity tolerance in rice. A number of significant QTLs associated with salinity tolerance in rice were identified through linkage mapping approach (Table 1). In these studies, the mapping populations used were F_2 population, F_3 population, $F_{2:4}$ population, near-isogenic lines (NILs), recombinant inbred lines, doubled haploid population, backcross-inbred lines, BC_3F_5 lines, BC_2F_8 advanced backcross introgression lines, and reciprocal introgression lines. Marker systems used in these studies included SSR, RFLP, SSLP, SSR AFLP, and SNPs.

Morphological parameters are supposed to be indicators of salt tolerance. There were various reports in which QTLs related to morphological traits under salt stress were identified (Hongxuan et al. 1998; Prasad et al. 2000; Takehisa et al. 2004; Yao et al. 2005; Lee et al. 2007; Lang et al. 2008; Zang et al. 2008; Kim et al. 2009; Wang et al. 2012a, b; Bimpong et al. 2013; Khan et al. 2016a). In these mapping studies, the plant material was phenotyped at the seedling, tillering, or the maturity stage. Data for different morphological traits were recorded in these studies. These traits included seed germination (%), seedling survival days, seedling vigour, seedling root length, shoot length, fresh shoot weight, dry shoot weight, dry root weight, reduction rate of dry weight, reduction rate of fresh weight, reduction rate of leaf area, reduction rate of seedling height, tiller number, salt tolerance rating, score of salt toxicity of leaves, plant height, and grain yield-related traits. A number of significant QTLs were identified in these studies. These identified QTLs included a QTL for seedling survival days (Hongxuan et al. 1998); a QTL for root length flanked by restriction fragment length polymorphism (RFLP) markers RG162-RG653 (Prasad et al. 2000); QTLs with heritability values up to 53.3% (Yao et al. 2005); two significant QTLs, *qST1 and qST3*, for salt tolerance at seedling stage with 35.5–36.9% phenotypic variance explained values, respectively (Lee et al. 2007); same QTLs conferring salt tolerance at both seedling and tillering stages (Zang et al. 2008), SSR marker RM223 associated with salt tolerance in rice (Lang et al. 2008), and a major QTL for straw yield , *qSY-3* (Khan et al. 2016a). These studies also suggested that it is possible to combine favorable alleles associated with salt tolerance in a single cultivar through marker-assisted selection (MAS) of main effect QTLs (M-QTLs; Wang et al. 2012a). Similarly, pleiotropic effects were found for some QTLs which were found associated with both drought and salt tolerance (Wang et al. 2012b).

There are also a number of reports of QTLs identified for different physio-biochemical traits through linkage mapping (Koyama et al. 2001; Bonilla et al. 2003; Lin et al. 2004; Haq et al. 2010; Thomson et al. 2010; Ahmadi & Fotokian 2011; Cheng et al. 2012; Wang et al. 2012c; Ghomi et al. 2013; Hossain et al. 2015; Khan et al. 2015). Traits which were studied in these reports were shoot Na^+ concentration; shoot K^+ concentration; leaf Na^+ concentration; leaf K^+ concentration; Na^+ uptake; K^+ uptake; Na^+ absorption; K^+ adsorption; Na^+/K^+ absorption ratio; K^+/Na^+ ratio; ratio of leaf Na^+ to sheath Na^+ concentrations; sodium (Na^+) and potassium (K^+) in roots; Na^+ concentration and Na/K ratio in the flag leaf; and sodium (Na^+), potassium (K^+), and calcium (Ca^{++}) accumulation traits. Major discoveries in these studies included a major QTL (*QKr1.2*) identified for K^+ content in the root on chromosome 1 explaining 30% of the total variation (Ahmadi & Fotokian 2011); pollen fertility, Na^+ concentration and Na/K ratio in the flag leaf were found as the most important attributes for salt tolerance at the reproductive stage in rice (Hossain et al. 2015), QTLs for sodium and potassium uptake were identified on different linkage groups (chromosomes) (Koyama et al. 2001) suggesting that different pathways are involved in Na^+ and K^+ uptake; and a major locus controlling Na^+ uptake (*QTLsur-7*) was identified on chromosome 7, with R^2 value of 72.57 % (Khan et al. 2015).

Association Mapping

In recent years, association mapping is widely used to identify QTLs in plants. Association mapping approach is relatively new arrival in plant genetics. There are some reports of association mapping for salt tolerance in rice (Ahmadi et al. 2011; Negrão et al. 2013; Emon et al. 2015; Kumar et al. 2015; Zheng et al. 2015; Khan et al. 2016b; Krishnamurthy et al. 2016). Main findings of these association studies are presented in Table 2. In these studies, rice mapping populations used consisted of European Rice Core collection (ERCC) containing 180 *japonica* accessions (Ahmadi et al. 2011), 96 rice germplasm accessions including Nona Bokra (Emon et al. 2015), 220 rice accessions (Kumar et al. 2015), three hundred and forty-one japonica rice accessions (Zheng et al. 2015), 94 rice genotypes (Krishnamurthy et al. 2016), and 24 indica rice genotypes (Khan et al. 2016b). Traits for which data were recorded in these studies included Na^+/K^+ ratio, survival days of seedlings,

Table 1: QTLs identified through linkage mapping studies.

Trait	Plant Material used	Marker System used	Reference
Seedling survival days	RILs population	RFLP	Hongxuan et al. (1998)
Seed germination (%); Seedling root length; Seedling dry matter; Seedling vigour	Doubled haploid (DH) population	RFLP	Prasad et al. (2000)
Shoot length; Tiller number; Shoot fresh weight	Backcross inbred lines	RFLP	Takehisa et al. (2004)
Salt tolerance rating; Na^+/K^+ ratio in roots; Dry matter weight of shoots	F_2 population	SSR	Yao et al. (2005)
Survival days of seedlings; Score of salt toxicity of leaves; Shoot K^+ concentration; Shoot Na^+ concentration; Fresh weight of shoots; Tiller number per plant; Plant height at the tillering stage	BC_2F_8 introgression lines (IL)	SSR	Zang et al. (2008)
Plant height; Panicle length; Tillers per hill; Spikelets per panicle; Grain yield	RILs population	SSR	Lang et al. (2008)
Reduction rate of dry weight; Reduction rate of fresh weight; Reduction rate of leaf area; Reduction rate of seedling height	Introgression lines	SSR	Kim et al. (2009)
Seedling height; Dry shoot weight; Dry root weight; Na/K ratios in roots	RILs, $F_{2:9}$	SSR	Wang et al. (2012a)
Days to seedlings survival; Score on salt toxicity symptoms on leaves; Shoot K^+ concentration; Shoot Na^+ concentration at seedling stage	BC2F8 advanced backcross introgression lines (ILs)	SSR	Wang et al. (2012b)
Plant height; Root length; Shoot dry weight; Shoot fresh weight	RILs	SNP	Bimpong et al. (2013)
Morphological and yield-related traits	F_2 population	SSR	Khan et al. (2016)
Sodium and potassium uptake	RILs	AFLP, RFLP, SSR	Koyama et al. (2001)
Salt tolerance traits	RILs	RFLP, SSLP	Bonilla et al. (2003)
Salt tolerance traits	F_2 and F_3 populations	RFLP	Lin et al. (2004)
-	140 RILs	SSR	Thomson et al. (2010)
Leaf Na^+ concentration; K^+/Na^+ ratio; K^+ concentrations; ratio of leaf Na^+ to sheath Na^+ concentrations	RILs	RFLP, SSR	Haq et al. (2010)
Sodium (Na^+) and Potassium (K^+) in roots and shoots; Na^+/K^+ ratio in roots and shoots	Advanced backcross-inbred lines (BILs)	SSR	Ahmadi & Fotokian (2011)
Na^+ and K^+ concentrations in the roots and shoots	RILs, $F_{2:9}$	SSR	Wang et al. (2012c)
Physiological traits	$F_{2:4}$ population	SSR, AFLP	Ghomi et al. (2013)
Pollen fertility; Na^+ concentration and Na/K ratio in the flag leaf	F_2 population	SSR	Hossain et al. (2015)
Sodium (Na^+), potassium (K^+), and calcium (Ca^{++}) accumulation traits	F_2 population	SSR	Khan et al. (2015)

Table 2: QTLs identified through association mapping studies

Trait	Plant Material used	Marker System used	Reference
Salinity tolerance	180 *japonica* accessions	SNPs, SSR	Ahmadi et al. (2011)
Na^+/K^+ ratio equilibrium; signalling cascade; stress protection	392 rice accessions	SNPs	Negrão et al. (2013)
Salinity tolerance	96 germplasm accessions	SSR	Emon et al. (2015)
Stress-responsive genes	220 rice accessions	SNPs	Kumar et al. (2015)
Survival days of seedlings and shoot K^+/Na^+ ratio	341 japonica rice accessions	SSR	Zheng et al. (2015)
Seedling stage salt tolerance	94 rice genotypes	SSR	Krishnamurthy et al. (2016)

shoot K^+/Na^+ ratio, Na^+ uptake, Ca^{++} uptake, total cations uptake, Ca^{++} uptake ratio, K^+ uptake ratio, Na^+/K^+ uptake and salinity tolerance scoring. Major findings made in these studies included an observation that distribution of favorable alleles associated with salt tolerance was random in ERCC (Ahmadi et al. 2011); forty new allelic variants found in coding sequences of five salt-related genes (Negrão et al. 2013); STS marker, RM22418, for *SKC1*, on Chr. 8 was found associated with salinity tolerance (Emon et al. 2015); region containing *Saltol* was found associated with Na^+/K^+ ratio (Kumar et al. 2015); marker RM3412 was found associated to salinity tolerance at seedling stage due to its close linkage to *SKC* gene (Krishnamurthy et al. 2016); and the report that other QTLs, in addition to *Saltol*, might be involved in salinity tolerance (Krishnamurthy et al. 2016). These reports highlighted that in rice germplasm there might be other genomic regions involved in salt tolerance. These genomic regions need to be characterized in future to add a wealth of information in the present rice genetics knowledge pool. Random distribution in the rice germplasm of favorable alleles associated with salt tolerance is a worthwhile finding which should be considered while exploring and selecting crossing parents in breeding programmes.

Future Prospects and Conclusions

Climate change has affected world agriculture a lot. The most pronounced effects of climate change are the heat stress and periodic drought conditions in major rice producing countries of the world (Zafar et al. 2023). Due to periodic drought conditions, the already existing problem of high amounts of salts in the upper surface soil has intensified. So, there is a dire need to opt for a coordinated approach to address the problem of salinity stress for rice production. Genomics has great potential to assist in this coordinated programme. With the help of molecular mapping approaches, a number of major and minor QTLs associated with salinity tolerance in rice have been identified in recent years and there are further accelerated research efforts underway in this direction. The identified QTLs are a valuable resource for marker-assisted selection (MAS) to develop elite salt tolerant rice cultivars. Great task is needed to be done in this regard so that marker-assisted breeding (MAB) approach can be implemented successfully in routine breeding programmes. In future, efforts should be directed to develop climate-smart rice cultivars which can perform stably under diverse environmental conditions. Identified QTLs and rice germplasm found tolerant to salinity stress can be exploited in three major ways: a) to understand the molecular genetics of salt tolerance in rice; b) salinity stress tolerant rice germplasm might be incorporated into salt-tolerant rice cultivars development molecular breeding programmes; c) identified QTLs incorporated into MAS for screening rice germplasm against salinity stress. New genes involved in salt tolerance will be identified by this approach. Genome sequence of rice, both indica and japonica subspecies, is available now. In the next phase of annotation of the rice genome, molecular mapping results can be of help in combination with the comparative genomics approach (Razzaq et al., 2020).

Lot of work related to molecular mapping for salinity tolerance in rice is to be performed yet. The main cautious point is the plant phenotyping for salt stress tolerance. Accuracy in the phenotyping work is the key in the authentic identification of QTLs related to salt tolerance. Hydroponics should be tried for this purpose. Under salinity stress conditions, phenotyping at germination, seedling, tillering, and reproductive phases require different strategies and care. In case of quantitative traits, such as salinity stress tolerance, there is pronounced effect of environment. Efforts should be made to design a judicious phenotyping plan which can minimize effect of environment. In case of plant genotyping work, robust marker systems with high resolution power such as SNPs should be preferred over other marker systems. Genotyping-by-sequencing (GBS) is another option.

Previous research efforts have pointed out that the distribution of favorable alleles, associated with salt-tolerance, is random among the rice germplasm (Ahmadi et al. 2011). So, it is possible to pyramid favorable alleles of salt-tolerance in an elite rice genotype through well-planned crossing programme. This elite rice cultivar will have great potential with regard to salt tolerance. In view of inland intrusion of the seas, we have to concentrate on the coastal areas to fully exploit their agricultural production potential. This is also imperative in view of alarming increase in human population and to feed this population we have to exploit every available land for agricultural production. It is hoped that genomics approaches will play a greater part in this exploitation of land by providing salt tolerant crop cultivars.

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