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### Improving Salinity Tolerance in Cereals

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# Improving Salinity Tolerance in Cereals

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Cereals are grown in almost every region of the world and are exposed to a variety of environmental stresses that severely affect their growth and grain yield. Of various abiotic stresses, salinity is one of the more significant threats to cereal crops. To ensure food security, there is a need to adopt strategies to overcome this specific threat. Undoubtedly, plant scientists have been exploiting a variety of approaches to achieve enhanced crop productivity on salt affected soils. Of the various biotic approaches, conventional breeding, marker-assisted selection and genetic engineering to develop salt-tolerant lines/cultivars of cereals all seem plausible. Some success stories have been reported for improvement in salt tolerance of wheat and rice, but are scarce for other cereals. A number of barriers to the development of salt-tolerant cultivars/lines have been identified and include a lack of knowledge about the genetics of crops, their physiological and biochemical behavior, wide variation in environmental conditions, and the complex polygenic nature of the salt tolerance character. This review focuses on how improvements have been made in salt tolerance in cereals through different biotic means, such as conventional breeding, marker assisted selection and genetic engineering.

**Keywords** cereals, marker-assisted selection, conventional breeding, transgenic approaches, salt tolerance

## I. INTRODUCTION

Cereals are the grain-producing crops that provide more than 50 percent of human energy and protein needs (Stoskopf, 1985). They are grown on more than two-thirds of all cultivated land. Cereals are considered to be the earliest cultivated crops and have been the staple food for most human societies for over 10,000 years due to specific features such as ease of growth, storage and transport (Calderini and Slafer, 1998). They are grown in many regions of the world and comprise of numerous species and varieties adapted to different climatic conditions. For example, the temperate climate of Northern Europe, some parts of Asia and North America is ideal for wheat and barley while a hotter climate is best for maize (MacNeish and Eubanks, 2000), so it is widely cultivated in tropical regions. Rice is a crop of the wet tropics while sorghum can survive in very hot and dry conditions. All of these crops have a number of adaptations which enable them to survive and grow well in the particular environmental conditions. These adaptations are either structural or physiological (Calderini and Slafer, 1998; Conway and Toenniessen, 1999)

Increasing human population and reduction in land available for cultivation are two threats for agricultural sustainability (Cassman, 2003). The accumulation of soluble salts is the most important reason for reduction in cultivated land area. High concentrations of sodium ( $\text{Na}^+$ ), chloride ( $\text{Cl}^-$ ), magnesium ( $\text{Mg}^{2+}$ ), calcium ( $\text{Ca}^{2+}$ ), sulphate ( $\text{SO}_4^{2-}$ ) and bicarbonate ( $\text{HCO}_3^-$ ) in soil disturb plant growth and development, ultimately leading to loss in yield (Shahbaz and Ashraf, 2007; Shahbaz *et al.*, 2011; Shahbaz *et al.*, 2012). Although scientists have succeeded to some extent in improving stress tolerance

of cereals (Slafer *et al.*, 1999; Araus *et al.*, 2002), there is still great potential to enhance this character in cereals through biotic means. Of the various biotic approaches, conventional breeding, marker-assisted selection and transgenic approaches are the most viable ones. The need for enhanced cereal production and salt-tolerant crops has been felt due to many reasons: i) cereal production has not been increased at the pace registered from the 1950s to the 1990s (Calderini and Slafer, 1998; Conway and Toenniessen, 1999); ii) use of cereals is increasing due to their nutritional value, but salinity stress directly affects their production and quality (Khush, 1999); iii) production of first-generation biofuels from cereal starches has increased demand; iv) harsh environmental factors such as increased temperature, high evapotranspiration rate and low precipitation have been the major factors for land leaving cultivation due to salinity (The World Bank, 2007; Rijsberman, 2006; Lobell *et al.*, 2008).

A number of strategies to overcome the salinity problem have been explicitly discussed in several comprehensive reviews (Ashraf, 1994; 1999; 2009; Ashraf and Foolad, 2007; Munns and Tester, 2008; Ashraf *et al.*, 2008; Ashraf and Akram, 2009; Shahbaz *et al.*, 2012). These include the reclamation of salt-affected soils, exogenous application of various inorganic/organic compounds and plant growth regulator. The best alternative is the use of biotic approaches, such as the use or production of highly salt-tolerant plants. Growing halophytes on saline soils is an effective way to use saline land, but since most of the halophytes are used for fodder purposes, so just growing halophytes on saline soils is not enough to fulfill the demand in terms of food supply. The main focus of this review is progress to date in salt tolerance of the cereal crops wheat, rice, oat, barley, maize, sorghum and millet through biotic approaches (conventional breeding, marker assisted selection and genetic engineering for salt tolerance).

## II. WHEAT (*Triticum aestivum* L.)

### A. Genetics and Evolution of Wheat

Common wheat (*Triticum aestivum* L.) is the main staple food world-over (Kawaura *et al.*, 2008). It is hexaploid ( $2n = 6x = 42$ ), having three genomes designated as A, B, and D. The whole genome of hexaploid wheat (see Figure 1) is contributed by three diploid species: *T. urartu* Thun. (A genome source), *Aegilops speltoides* (Tausch) Gren. or a closely related species (B genome source), and *A. tauschii* Coss. (D genome source). The size of the wheat genome is large (17 Gbp) (Bennett and Leitch, 1995) due to a high content of repeated sequences. For this reason, complete sequencing of wheat is very difficult (Kawaura *et al.*, 2008), although there has now been significant progress using comparative genomics to identify over 88,000 genes and assign many to the component genomes (Edwards and Batley, 2010). Bread wheat genetic maps with molecular markers, and some cytological maps derived from deletion mutants of chromosome segments have been available for some time (Qi *et al.*, 2004; Xue *et al.*, 2008). Inferences on *T. aestivum* genome organization and

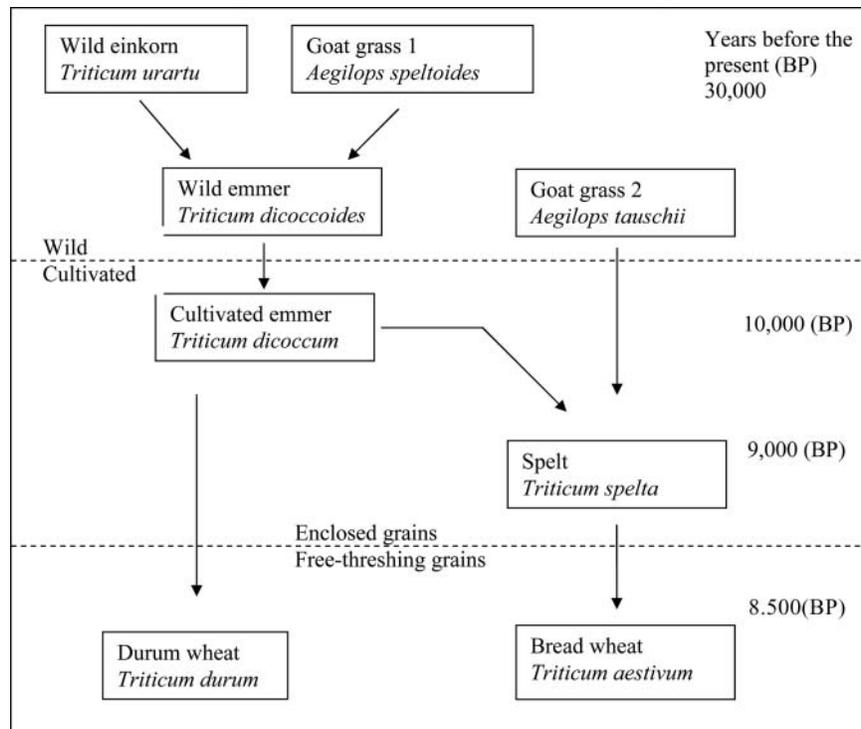


FIG. 1. Evolution of bread wheat (reproduced from <http://www.newhallmill.org.uk/wht-evol.htm> with permission).

evolution are directly applicable to diploid relatives of wheat (Kawaura *et al.*, 2008).

The evolution of wheat was thought to have been triggered by allopolyploidization in two ways: 1) revolutionary changes—allopolyploidization caused a sharp genome change by the rapid generation of a variety of cardinal genetic and epigenetic alterations; and 2) evolutionary changes—allopolyploidy facilitated periodic changes in the genome during the life of a species that are not attainable at the diploid level (Feldman and Levy, 2005; Bento *et al.*, 2011; Zhao *et al.*, 2011). These revolutionary and evolutionary changes can further be defined by various points (Feldman and Levy, 2005). The revolutionary changes consist of: a) coding and non-coding regions of DNA sequences are eliminated through non-random means, b) epigenetic changes in coding and non-coding regions of DNA, c) activation of genes which affect the expression of adjacent genes. All these changes occur in the first generation(s) of the nascent allopolyploids (Feldman and Levy, 2005). These changes could be categorized into two phases: firstly in the formation of allotetraploid wheat (about 0.5 million years ago) and secondly in the formation of hexaploid wheat (about 10,000 years ago) (Feldman and Levy, 2005). The second types of changes were evolutionary: a) horizontal intergenomic transfer of chromosome segments between the constituent genomes, b) production of recombinant genomes, and c) mutations. All the above changes caused a wide adaptability in wheat to grow well under various environmental conditions (Feldman and Levy, 2005; Bento *et al.*, 2011; Zhao *et al.*, 2011).

## B. Biotic Approaches to Improve Salt Tolerance

Wheat yield losses on moderately saline soils are considerable (Quayyum and Malik, 1988; Shahbaz *et al.*, 2011, 2012) and growth is severely affected (Perveen *et al.*, 2011; 2012a; 2012b). The consequences of biotic approaches to increased productivity are as follows.

### 1. Conventional Breeding

Although wheat is a very important cereal crop, progress in breeding for salt tolerance has been slow with most progress being made in India, Pakistan and Australia (Table 1). Of various successful releases of salt-tolerant lines are Indian KRL1–4 and KRL 19, from the Central Soil Salinity Research Institute (CSSRI) at Karnal, whereas in Pakistan LU26S and SARC-1 were released by the Saline Agriculture Research Centre (SARC) at University of Agriculture, Faisalabad and in Egypt Sakha 8, from the Agricultural Research Centre at Giza. In India, almost all salt-tolerant lines have been derived from Kharchia 65. This line was developed by Indian farmers through selection on sodic-saline soils of the Kharchi-Pali area of Rajasthan (Rana, 1986). KRL1–4 was developed from a cross of Kharchia 65 with another wheat cultivar WL711. It performed well on the saline soils of northern India, but it was not successful in Pakistan because of water logging and soil texture (Hollington, 2000). A double haploid wheat line (KTDH 19) was developed in the UK by Quarrie and Mahmood by crossing Kharchia 65 with TW161 (a line identified with exceptional  $\text{Na}^+$  exclusion). However, this derivative of Kharchia showed good performance

TABLE 1  
Improvement in salt tolerance of cereal crops using conventional breeding approach

Cereal crop	Genotype/line/cultivar released	Releasing source	Good performance	Reference
Wheat	Indian KRL1-4 and KRL 19,	Central Soil Salinity Research Institute (CSSRI) at Karnal, India	Saline soils of northern India	Hollington, 2000
	LU26S and SARC-1	Saline Agriculture Research Centre (SARC) at University of Agriculture, Faisalabad-Pakistan	All saline soils	Munns <i>et al.</i> , 2006
	Egyptian Sakha 8	Agricultural Research Centre, Giza, Egypt	All saline soils	Munns <i>et al.</i> , 2006
	Kharchia 65	Indian farmers through selection on sodic-saline soils	Kharchi-Pali area of Rajasthan, India	Rana, 1980.
	Line KTDH 19	Quarrie and Mahmood	Performed well in Spain only	Hollington <i>et al.</i> , 1994
	S-24	Department of Botany, University of Agriculture, Faisalabad-Pakistan	On all saline soils	Ashraf, 2002
Rice	CSR 10	Central Variety Release Committee (CVRC) of India	High salt levels	Singh <i>et al.</i> , 2004; Sankar <i>et al.</i> , 2011
	CSR 13, CSR 27, Narendra Usar 2 and Narendra Usar 3	Central Variety Release Committee (CVRC) of India	Moderate to high salt levels	Singh <i>et al.</i> , 2004; Sankar <i>et al.</i> , 2011
	Basmati CSR 30	Central Variety Release Committee (CVRC) of India	Moderate salt stress	Singh <i>et al.</i> , 2004; Sankar <i>et al.</i> , 2011
	SR 26 B, CSR 1, CSR 2, CSR 3, Panvel 1, Panvel 2, Panvel 3, Pokkali (in Kerala only), Vytilla 1 and Vytilla 2	The Central Soil Salinity Research Institute (CSSRI), Karnal, India	The coastal saline soil	Mishra <i>et al.</i> , 2003
	CSR 22, CSR 23, CSR 26, CSR 27 and CSR 30	The Central Soil Salinity Research Institute (CSSRI), Karnal, India	Sodic soil	Mishra <i>et al.</i> , 2003
	Pokkali, Vytilla 1, Vytilla 2, Vytilla 3, Vytilla 4 and Vytilla 5	Kerala Agricultural University, India	Coastal regions	Sankar <i>et al.</i> , 2011
	SR 26 B, Kalarata, Bhurarata, Panvel 1, Panvel 2, and Panvel 3 and BTS 24	International Rice Research Institute, Philippines	Coastal regions	Sankar <i>et al.</i> , 2011
	Savitri, Ponni, Swarnadhan, Mansarovar, Salivahan and Pavizham	International Rice Research Institute, Philippines	Shallow water salinity conditions	Ali <i>et al.</i> , 1999; Sankar <i>et al.</i> , 2011
	BR 10, Patnai 23, SR 26 B, PVR 1, PY 1, CSR 1, CSR 4, Co 43, AD 85002, IET 8113, TRY 1 and TRY 2	International Rice Research Institute, Philippines	Saline area of Tamal Nadu	Sankar <i>et al.</i> , 2011
	Sorghum	Hybrids		Salt tolerant at all saline soils

in Spain (Hollington *et al.*, 1994) but a low yield in India and Pakistan, mainly due to maturing two weeks later as compared to local genotypes (Hollington, 2000). To solve this problem, mutation breeding has been employed to reduce its time to maturity by three weeks without adverse effects on yield at 150 mM NaCl

(Mahar *et al.*, 2003). This early maturity along with its Na<sup>+</sup> exclusion characteristic makes it a good line for Pakistan and India (Hollington, 2000). In Pakistan, line LU26S performed well on saline soils (Qureshi *et al.*, 1980), but is highly susceptible to rust and not adapted to dense saline-sodic soils where there is

the possibility of water logging (P. A. Hollington, personal communication). Later LU26S was crossed with Kharchia-65 and two salt-tolerant genotypes, S24 and S36, were selected from F<sub>3</sub> populations at salinity levels of 24 and 36 dS m<sup>-1</sup>, respectively (Ashraf and O'Leary, 1996). Genotype S-24 proved to be highly salt tolerant, compared to its parents Kharchia, LU26S and SARC-1, and the possible mechanism for its high salt tolerance was reported to be due to its low accumulation of Na<sup>+</sup> in leaves (Ashraf, 2002). The yield of S-24 was higher than that of many other wheat cultivars (Ashraf, 1994, 2002; Arfan *et al.*, 2007; Shahbaz *et al.*, 2008; Perveen *et al.*, 2010, 2011, 2012).

## 2. Transgenic Approaches

Transgenic plants, developed using a variety of genetic engineering tools, have been proposed as an accelerated solution for developing crops with resistance against adverse environmental condition. Although reports on the success of stress resistant transgenic plants in natural fields are very few (Flower, 2004; Ashraf and Akram, 2009), scientists are making progress in this field (Ashraf and Akram, 2009). Salinity tolerance is a complex trait that is controlled by a number of minor genes. To improve wheat salt tolerance, scientists have made efforts to transfer a single gene to develop tolerant transgenic cultivars/lines. For example, some genes for ion transport have been introduced to improve salt tolerance. Overexpression of the vacuolar Na<sup>+</sup>/H<sup>+</sup> antiporter gene *AtNHX1* (from *Arabidopsis*) in wheat has improved growth attributes such as germination rate, plant biomass and yield (Xue *et al.*, 2004). This line showed reduced leaf Na<sup>+</sup>, enhanced leaf K<sup>+</sup> accumulation and had 68% higher shoot dry weight, as well as 26% higher root dry weight under saline conditions in comparison those of the wild type (Xue *et al.*, 2004).

Accumulation of free proline under saline conditions is also a unique feature of salt-tolerant plants. Overproduction of proline in plants may improve salt tolerance of plants. In wheat,  $\Delta^1$ -pyrroline-5-carboxylate synthetase (*P5CS*) enhanced salt tolerance of wheat by accumulating 2.5-fold higher proline compared to the non-transformed control (Sawahel and Hassan, 2002). Transgenic wheat plants remained almost unaffected up to 200 mM NaCl and showed a slight reduction at 250 mM NaCl, in comparison with wild type plants which died or showed low growth at 100 mM NaCl (Table 2).

## III. RICE (*Oryza sativa* L.)

### A. Genetics and Evolution of Rice

The size of euchromatic portion of the rice genome is estimated as 430 Mb—smallest of the cereal crops (Arumuganathan and Earle, 1991; Eckardt, 2001; Sasaki and Burr, 2000). If we compare it with that of *Arabidopsis thaliana*, it is 3.7 times larger (Martienssen and McCombie, 2001; Bevan *et al.*, 2001). Rice is favorite for studying a variety of physiological, developmental, genetic and evolutionary attributes of plants due to well-defined

protocols for genetic transformation, widely distributed high-density genetic and physical maps (Tao *et al.*, 1994; Umehara *et al.*, 1995), and high degrees of synteny among cereal genomes (Wang *et al.*, 1995; Gale and Devos, 1998; Messing and Llaca, 1998; Bevan and Murphy, 1999; Goff, 1999). *Arabidopsis* is known as a model plant for dicots and rice for monocots. It is estimated that about 190 Mb of long terminal repeat retrotransposon sequences were lost from the rice genome during the last eight million years (Ma *et al.*, 2004).

Rice (*Oryza sativa*) evolved from the Asian A-genome group of species of the genus *Oryza* (Chang 1976; Oka 1988; Wang *et al.*, 1992; Khush, 1999; Ge *et al.*, 1999). There is presently a debate as to whether the species *O. nivara* or *O. rufipogon* are the direct wild progenitors of currently cultivated rice or whether it evolved under cultivation, once or multiple times, from other unknown wild species. The characteristics of both extant wild relatives of domesticated rice differ. *O. nivara* was established for those populations which were annual, photoperiod insensitive, predominantly self-fertilized, and well adapted to dry habitats. *O. rufipogon* was meant for populations which were perennial, photoperiod sensitive, mostly cross-fertilized, and well adapted to wet habitats (Sharma *et al.* 2000). Two major rice cultivars, recognized as *O. sativa* subspecies *indica* and subspecies *japonica*, are not only divergent morphologically and physiologically, they are also partially isolated by a post-zygotic barrier (Li *et al.*, 1997; Chang, 2003). Further study of restriction fragment length polymorphism (RFLP) markers with 93 accessions of 21 *Oryza* species, revealed that the *indica* and *japonica* cultivars were more closely related to wild species than to each other (Wang *et al.*, 1992).

The genomes of the two major subspecies (*indica* and *japonica*) have also been completely sequenced (Londo *et al.*, 2006). Comprehensive studies show that *japonica* emerged first, followed by *indica* (Garris *et al.*, 2005).

### B. Biotic Approaches to Improve Salt Tolerance

The increase in productivity rate of rice during the past few decades has been stagnant. Several biotic and abiotic factors, and the narrow genetic diversity of modern rice cultivars have been the main barriers to continued enhancement of rice yield. In rice, several genes with polygenic nature (*qST1*, *qST3*) have been reported to be involved in abiotic stress tolerance, including salinity tolerance (Causse *et al.*, 1994; Jena and Mackill, 2008). Polygenic traits are sometimes difficult to incorporate through conventional breeding approaches, but such difficulties can be overcome through molecular and biotechnological approaches (Jena and Mackill, 2008).

#### 1. Conventional Breeding

To lessen the effect of salinity, development of salt-tolerant varieties is an important way forward. Development of salt-tolerant varieties through conventional breeding seems to be feasible, cost-effective and socially acceptable. According to Singh *et al.* (2004), in India six rice varieties developed through

TABLE 2  
Improvement in salt tolerance of cereal crops using transgenic/genetic engineering approach

Cereal crop	Gene engineered	Source organism	Trait improved	Growth improved	Reference
Wheat	vacuolar Na <sup>+</sup> /H <sup>+</sup> antiporter gene <i>AtNHX1</i>	<i>Arabidopsis</i>	Germination rate, plant biomass and yield. Low leaf Na <sup>+</sup> and high leaf K <sup>+</sup>	Increase in shoot dry weight was 68% and root dry weight 26%	Xue <i>et al.</i> , 2004
	Δ <sup>1</sup> -pyrroline-5-carboxylate synthetase ( <i>P5CS</i> )	Moth bean ( <i>Vigna aconitifolia</i> )	Accumulated 2.5-fold more proline as compared to that in wild type	Transgenic plants remained unaffected up to 200 mM and showed slight reduction at 250 mM, while respective wild plants died at 100 mM	Sawahel and Hassan, 2002
Rice	Vacuolar Na <sup>+</sup> /H <sup>+</sup> antiporter <i>AgNHX1</i>	<i>Atriplex gmelini</i>	Activity of these antiporters was 8-fold high	Seedling survival increased from 51% or 81–100%.	Ohta <i>et al.</i> , 2002
	Vacuolar Na <sup>+</sup> /H <sup>+</sup> antiporter gene <i>PgNHX1</i>	<i>Pennisetum glaucum</i> (L.) R. Br.	Well developed root system	About 81% higher shoot and root lengths.	Verma <i>et al.</i> , 2007
	Vacuolar Na <sup>+</sup> /H <sup>+</sup> antiporter gene <i>OsNHX1</i>	Wild rice ( <i>Oryza sativa</i> L.)	High accumulation of Na <sup>+</sup> and low K <sup>+</sup>	Tolerate salinity level up to 0.2 M where wild plants died	Fukuda <i>et al.</i> , 2004
	Δ <sup>1</sup> -pyrroline-5-carboxylate synthetase ( <i>P5CS</i> )	Moth bean ( <i>Vigna aconitifolia</i> )	Transgenic plants accumulated more proline under both saline and non-saline conditions	Shoot fresh weight was increased from 30–93% and root fresh weight 37–74% under 200 mM NaCl as compared to those in wild type	Su and Wu, 2004
	Na <sup>+</sup> /H <sup>+</sup> antiporter <i>SOD2</i>	Yeast	Transgenic plants accumulated higher K <sup>+</sup> , Ca <sup>2+</sup> , Mg <sup>2+</sup> and lower Na <sup>+</sup> in their shoots as compared to respective non-transformed controls	Transgenic plants showed good performance under saline conditions	Zhao <i>et al.</i> , 2006
	<i>OPBP1</i> gene	Tobacco	Transgenic plants showed high resistance against salt and disease		Chen and Guo, 2008
Maize	Vacuolar Na <sup>+</sup> /H <sup>+</sup> antiporter <i>AtNHX1</i>	<i>Arabidopsis thaliana</i>	Germination percentage	Germination capacity of transgenic plants was 80% while those of wild type 13–57% at 0.5% NaCl	Xiao-Yan <i>et al.</i> , 2004
	Na <sup>+</sup> /H <sup>+</sup> antiporter gene <i>OsNHX1</i>	<i>Oryza sativa</i>	Yield was improved	Showed higher biomass and yield even at 200 mM NaCl	Chen <i>et al.</i> , 2007

conventional breeding were released as salt tolerant through the Central Variety Release Committee (CVRC) for cultivation on salt-affected soils with varying salinity levels. For example, CSR 10 for high salt levels, CSR 13, CSR 27, Narendra Usar 2 and

Narendra Usar 3 for moderate to high salinity and a basmati CSR 30 rice for only moderate salt stress (Sankar *et al.*, 2011). These varieties have even been used in land reclamation programs in Uttar Pradesh of India (Sankar *et al.*, 2011). Many further rice

varieties have been developed through conventional breeding for various inland and coastal saline and alkaline soils with fragile habitats (Mishra *et al.*, 2003). The Central Soil Salinity Research Institute (CSSRI) India developed 32 salt-tolerant rice varieties, of which, CSR 10 was the first salt-tolerant variety which was dwarf, high yielding, and early maturing. The coastal saline soil adapted varieties are SR 26 B, CSR 1, CSR 2, CSR 3, CSR 13, Panvel 1, Panvel 2, Panvel 3, Pokkali Vytilla 1 and Vytilla 2, CSR 22, CSR 23, CSR 26, CSR 27 and CSR 30 (Mishra *et al.*, 2003). These varieties proved to be suitable particularly for sodic soils (Table 1). Furthermore, to overcome the salinity problem of coastal regions, salt-tolerant rice varieties like Pokkali, Vytilla 1, Vytilla 2, Vytilla 3, Vytilla 4 and Vytilla 5 were developed by Kerala Agricultural University. Some other varieties, such as SR 26 B from Orissa, Kalarata, Bhurarata, Panvel 1, Panvel 2, and Panvel 3 from Maharashtra and BTS 24 from Andaman and Nicobar Islands, have also been developed to minimize the salinity problems (IRRI). Similarly, other high yielding varieties such as Savitri, Ponni, Swarnadhan, Mansarovar, Salivahan and Pavizham were recognized as tolerant to shallow water salinity conditions. In the Tamal Nadu area, BR 10, Patnai 23, SR 26 B, PVR 1, PY 1, CSR 1, CSR 4, Co 43, AD 85002, IET 8113, TRY 1 and TRY 2 varieties are recommended as salt tolerant (Sankar *et al.*, 2011). Thus, a good number of salt-tolerant rice cultivars/lines have been developed employing conventional selection and breeding.

## 2. Marker Assisted Selection

Rice is reported to be sensitive to saline conditions during both the vegetative and reproductive stages (Naheed *et al.*, 2008; Shahbaz and Zia, 2011). However, it seems that growth stage based salinity tolerance is controlled by independent genes. For example, in salt-tolerant cultivar Pokkali, a major QTL (*Saltol*) was identified which is located on chromosome 1 and involved in salinity tolerance at the vegetative stage (Bonilla *et al.*, 2002). This QTL caused 64 to 80% of the phenotypic variation under saline conditions and has also been confirmed in other varieties of rice (Takehisa *et al.*, 2004). Similarly, in cv. Nona Bokra, a gene for salt tolerance at the vegetative stage has been identified at the same position on chromosome 1 (Ren *et al.*, 2005; Jena and Mackill, 2008). The mechanisms of the QTL and the gene are similar. A QTL (chromosome 1) *SKC1* for salt tolerance, is involved in maintaining  $K^+$  homeostasis, especially in the salt-tolerant cultivars under salt stress, while the gene *SKC1* encodes a member of HKT-type transporters (Ren *et al.*, 2005). However, QTLs for salt tolerance at the reproductive stage are not reported in the literature.

## 3. Transgenic Approaches

Some salt-tolerant rice varieties have also been developed through genetic engineering (Table 2). In most of the studies, scientists have incorporated the genes for vacuolar  $Na^+/H^+$  transporters from various sources into rice and observed improvement in salinity tolerance (Ohta *et al.*, 2002; Zhao *et al.*, 2006;

Verma *et al.*, 2007). For example, incorporation of vacuolar  $Na^+/H^+$  antiporter *AgNHX1* gene from *Atriplex gmelini* showed an eight-fold higher activity of the vacuolar-type  $Na^+/H^+$  antiporter, thereby enhancing survival of rice seedlings from 50% or 81% to 100% under saline conditions (Ohta *et al.*, 2002). Another vacuolar  $Na^+/H^+$  antiporter gene, *PgNHX1* from *Penisetum glaucum* (L.) R. Br., caused an extensive root system in transgenic rice plants and showed about 81% higher shoot and root lengths than did the non-transformed control plants (Verma *et al.*, 2007). In another study, transgenic rice plant expressing the yeast  $Na^+/H^+$  antiporter *SOD2* gene performed well under saline conditions (Zhao *et al.*, 2006). The transgenic plants accumulated higher  $K^+$ ,  $Ca^{2+}$ ,  $Mg^{2+}$  and lower  $Na^+$  in their shoots compared with those of non-transformed controls.

Transformation to yield increased levels of compatible solutes is another strategy that has been used. Over-accumulation of proline is also considered an important selection criterion for salt tolerance. Over-expression of  $\Delta^1$ -pyrroline-5-carboxylate synthetase (*P5CS*) actively converts glutamate to  $\Delta^1$ -pyrroline-5-carboxylate leading to a reduction in proline. The gene *P5CS* obtained from moth bean (*Vigna aconitifolia*) has been over-expressed in rice (Su and Wu, 2004) and the transgenic rice so produced accumulated many-fold higher proline in comparison to their wild types under both non-saline and saline conditions. Over-accumulation of trehalose is also an important characteristic of salt-tolerant cultivars. Transgenic rice with the trehalose gene (*TPSI*) from yeast showed not only enhanced salt tolerance but also enhanced tolerance to drought and cold stress (Garg *et al.*, 2002). Similarly, in another transgenic rice line with the chimeric gene *Ubi1::TPSP*, high amounts of trehalose accumulated thereby providing high salt tolerance (Jang *et al.*, 2003). Over-expression of chloroplast glutamine synthetase gene enhanced the salt tolerance of transgenic rice (Hoshida *et al.*, 2000). Transgenic rice plants transformed with *mtlD* and *gutD* genes also showed high tolerance to salt stress by accumulating high amounts of mannitol and sorbitol (Wang *et al.*, 2000). Transgenic rice plants accumulated much more mannitol and sorbitol and showed high salt tolerance as compared to their respective control. Engineering of *OPBPI* gene from tobacco into rice also enhanced both salt and disease resistance in transgenic rice plants by lowering the adverse effects of salinity and enhancing the ability of plants to resist against the pathogen attack by producing toxic secondary metabolites (Chen and Guo, 2008).

## IV. BARLEY (*Hordeum vulgare* L.)

### A. Genetics and Evolution of Barley

The genome map and mapping-based analysis system of barley is excellent (Costa *et al.*, 2003) due to the fact that its chromosomes are homoeologous to cultivated wheat and rye (Hori *et al.*, 2003). It is used as a model species for both physiological and genetic studies in cereals (Koornneef *et al.*, 1997). It is a diploid ( $2n = 2x = 14$ ), self-pollinated species. The seven

chromosomes have been labeled on the basis of size (chromosomes 1 – 5) and other characteristics (presence of satellites, chromosomes 6, 7) (Burnham and Hagberg, 1956; Kleinhofs and Han, 2002). Barley is among the important founder crops of Old World agriculture. Archaeological data indicate that it was domesticated about 8000 B.C. (Zohary and Hopf, 1993; Diamond, 1998; Nesbitt and Samuel, 1996). Its wild relative, *Hordeum spontaneum* C. Koch., was traditionally considered in a separate taxon (Nevo, 1992), while modern classification considers *H. vulgare* L., *H. spontaneum* C. Koch, and *H. agriocrithon* as subspecies of *H. vulgare* (Bothmer and Jacobsen, 1985). *H. spontaneum* and *H. vulgare* have similar morphological characteristics (Zohary 1969). The wild progenitor *H. spontaneum* is still found in its primary habitats in the Fertile Crescent from Israel and Jordan to southern Turkey, Iraqi Kurdistan, and southwestern Iran (Harlan and Zohary, 1966; Nevo, 1992). In addition, Bothmer *et al.* (1995) also reported *H. spontaneum* in Greece, Egypt, southwestern Asia, and eastward as far as southern Tajikistan and the Himalayas.

## B. Biotic Approaches to Improve Salt Tolerance

There are few reports of the application of biotic approaches to increase salt tolerance in barley. One possible reason could be that barley is a naturally salt-tolerant crop (Ayers *et al.*, 1952; Hassan *et al.*, 1970).

## V. MAIZE (*Zea mays* L.)

### A. Genetics and Evolution of Maize

Contribution of maize to food is substantial. Many forms of maize and especially maize products are used in the human diet (oil, starches) and as animal feed. These forms are sometimes classified into various types based on the availability of starch, e.g., flour corn (*Zea mays* var. *amylacea*), popcorn (*Zea mays* var. *evarta*), dentcorn (*Zea mays* var. *indentata*) and flint corn (*Zea mays* var. *indurata*). The number of chromosomes in maize is 10 and its genome size is reasonably large; 2400 Mb (Rayburn *et al.*, 1993).

Initially Mangelsdorf and Reeves (1939) proposed that maize arose from a now extinct wild maize. This was known as “tripartite hypothesis,” but has now been superseded by the “teosinte hypothesis” (Beadle, 1939) which proposes that maize arose from teosinte, a wild ancestor. In the 1990s the teosinte hypothesis was challenged by another proposal known as the “tripsacum-diploperennis hypothesis” (Eubanks, 1995). According to this, maize arose from a cross between a species of teosinte (*Zea diploperennis*) and a grass (*Tripsacum*). As evidence, a putative hybrid between *Tripsacum* and *Z. diploperennis* was used in conjunction with archaeological evidence (Eubanks, 1995, 1997; MacNeish and Eubanks, 2000).

Of these three hypotheses, the teosinte hypothesis is most acceptable since the biological evidence is overwhelmingly in its favour.

## B. Biotic Approaches to Improve Salt Tolerance

Various biotic approaches have been used to improve salt tolerance in maize. Maize breeding generally aims towards broadly adaptable germplasm, and examples of screening cultivars derived from classical breeding techniques for salt tolerance includes Ashraf and McNeilly (1990) and Banziger and Araus (2007) who have shown that seedling salt tolerance in maize can be developed successfully through conventional breeding.

Marker-assisted selection for salt tolerance has not been successful for reasons that could include the complex genetic basis of salt tolerance in this crop and influence of genetic background, developmental stage and environment on QTL effects (Tuberosa *et al.*, 2002), limitations in precise phenotyping of component traits, time and cost considerations in fine mapping of QTLs, and gene-by-gene effects (Campos *et al.*, 2004).

Genetic engineering has been employed successfully (Table 2). For example, Xiao-Yan *et al.* (2004) introduced the vacuolar Na<sup>+</sup>/H<sup>+</sup> antiporter *AtNHX1* gene from *Arabidopsis thaliana* into *Zea mays* and the transgenic plants showed remarkably higher germination capacity (80%) compared to parental wild type plants (13–57%) under saline conditions (0.5% NaCl). A further advance in *AtNHX1* transgenic maize was obtained by Li *et al.* (2010) who reported that elimination of *als* genes in *AtNHX1* transgenic maize (marker-free transgenic maize) showed remarkable high salt tolerance which was manifested from high grain yield and improved some key physiological attributes in comparison to their respective control parental plants. In an earlier study, Chen *et al.* (2007) also made a successful effort to develop salt-tolerant maize by introducing the rice Na<sup>+</sup>/H<sup>+</sup> antiporter gene (*OsNHX1*) into maize. The transgenic line showed higher biomass at 200 mM salt level when compared with non-engineered plants.

## VI. SORGHUM [*Sorghum bicolor* (L.) Moench.]

### A. Genetics and Evolution of Sorghum

Sorghum is an important major grain crop. Of the species of sorghum, *Sorghum bicolor* (L.) Moench. is considered the fourth most important cereal crop after wheat, rice, and maize, and is grown throughout the arid and semi-arid tropics (Smith and Frederiksen, 2000). The wild species of sorghum provide a potential source to breeding programs aimed at improving the sorghum crop. The genus “*Sorghum*” comprises 25 recognized species which are taxonomically categorized into five subgenera *Eusorghum*, *Chaetosorghum*, *Heterosorghum*, *Parasorghum* and *Stiposorghum* (Garber, 1950). The species have differing numbers of chromosomes ( $2n = 10, 20, 30, \text{ or } 40$ ; Garber, 1950; Lazarides *et al.*, 1991). Of the subgenera, *Eusorghum* includes cultivated sorghum, *S. bicolor* and its subspecies *drummondii* and *arundinaceum*, and the wild species *S. alnum* Parodi, *S. propinquum* (Kunth) Hitch. and *S. halepense* (L.) Pers. (deWet, 1978). These species are throughout Africa and southern Asia (deWet, 1978; Duvall and

Doebley, 1990). *S. bicolor* and *S. propinquum* have the same number of chromosomes ( $2n = 20$ ). However, there is variation in sorghum hybrids due to ploidy level. Hybrids of *S. bicolor* and *S. propinquum* are meiotically regular with 10 bivalents observed at meiotic metaphase I (Doggett, 1988). On the other hand, *Sorghum halepense* ( $2n = 40$ ) is polyploid and meiotic analysis of *S. bicolor* and *S. halepense* hybrids showed that *S. halepense* possesses two types of genome. One is similar to *S. bicolor*, while the other is a divergent or rearranged genome, which suggests that *S. halepense* is a disomic polyploid (Duara and Stebbins, 1952; Endrizzi, 1957; Tang and Liang, 1988).

Anthropological evidence indicates that hunter-gatherers consumed sorghum as early as 8000 BC (Smith and Frederiksen, 2000). Sorghum was domesticated in Ethiopia and surrounding countries, commencing about 4000–3000 BC. Various varieties of sorghum were created in the process of selection depending on a specific character (Doggett, 1970). As a result, a balance was created by farmer selection for cultivated traits and natural selection for wild characteristics. Both these criteria produced a variety of improved sorghum types, wild types and intermediate types (Doggett, 1970). The improved sorghum generated through the efforts of farmers, was spread through the movement of people and trade routes into various regions of Africa, India (approx. 1500–1000 BC), the Middle East (approx. 900–700 BC), and eventually into the Far East (approx. AD 400). Its introduction to America occurred in the late 1800s to early 1900s.

### B. Biotic Approaches to Improve Salt Tolerance

Sorghum is considered to be more salt tolerant than maize and many other crops (Igartua *et al.*, 1994). Substantial genetic variation for salt tolerance during development has been reported in sorghum (Igartua *et al.*, 1994; de la Ibarra and Maiti, 1994; Maiti *et al.*, 1994; Peng *et al.*, 1994; de la Ibarra and Maiti, 1995; Krishnamurthy *et al.*, 2003) since regulation of the salt tolerance trait is very complex mainly due to dominant gene effects (Igartua *et al.*, 1994).

Reports on conventional breeding to further enhance salinity tolerance in sorghum are limited (Table 1). This might be due to the problem of providing the optimum selection environment (Igartua, 1995). For example, a strong genotype  $\times$  salinity level interaction was observed while evaluating salt tolerance of sorghum (Azhar and McNeilly, 1987; Krishnamurthy *et al.*, 2003). In such a situation, a breeder has to determine whether the improvement in trait is for the whole target environment (breeding for wide adaptation), or for a specific homogeneous sub-environment (breeding for specific adaptation) (Igartua, 1995). To date, information on breeding for a specific area does not exist, so breeders have to follow the approach by which tolerant sorghum genotypes/lines for multiple habitats can be developed (Igartua 1995). Field trials of a few genotypes of sorghum showed that hybrids have better salt tolerance than their respective parents (Peng *et al.*, 1994; Azhar *et al.*, 1998). Overall, progress on improvement of salt tolerance in sorghum through conventional breeding programs has been limited.

Little progress has also been made on marker-assisted selection for salinity tolerance in sorghum, although some scientists have reported some molecular markers (Rao *et al.*, 2007). Similarly, there is little information available in the literature on improving salt tolerance in sorghum through genetic engineering, in part due to slow progress in developing transformation protocols.

## VII. PEARL MILLET [*Pennisetum glaucum* (L.) R. Br.]

### A. Genetics and Evolution of Millet

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is diploid ( $2n = 2x = 14$ ) and is a cross-pollinated plant (Martel *et al.*, 1997). It is grown for grain or fodder purposes, especially in eastern Africa and Asia (Kapila *et al.*, 2008). It is an important cereal that was domesticated in Africa, in the sub-Saharan area from Senegal to Sudan. The wild progenitor of pearl millet is *Pennisetum glaucum* ssp. *monodii* (Harlan, 1975; Brunken, 1977). However, there is some controversy concerning its origin and domestication. An alternative hypothesis is that present day pearl millet resulted from multiple domestications, as shown by the variation in key characteristics (Harlan, 1975; Porteres, 1976; Marchais and Tostain, 1993), while another proposal is that domestication occurred once (Marchais and Tostain, 1993). Selection of pearl millet as a domesticated crop has been due to some characteristic features like it is an annual (Wilson *et al.*, 1990) and highly tolerant to adverse environmental conditions such as drought and poor soil fertility (Rachie and Majumdar, 1980). The most important reason for its domestication was the high nutritional value of its grain (Goswami *et al.*, 1969; Sawaya *et al.*, 1984; Khairwal *et al.*, 1999). Phenotypically, pearl millet has considerable variation in terms of flowering time, panicle length, grain and stover characteristics (Bhattacharjee *et al.*, 2007).

### B. Biotic Approaches to Improve Salt Tolerance

There are no reports on biotic approaches to increase salt tolerance in millet.

## VIII. CHALLENGES AND FUTURE PROSPECTS

Cereals are an important source of human diet. The history of cereals shows that their adoption as domesticated crops is very interesting and many of the current forms are found due to the requirements of humans, the most important being for foods with maximum nutritional value and availability. Environmental factors, including salt stress, are the great threats to cereal crop production. Of various strategies to improve productivity, biotic approaches to generate salt-tolerant cultivars have received much attention during the last few decades. Tremendous success has been achieved in terms of developing salt-tolerant lines of many crops, including tomato and potato, but progress with respect to cereal crops has not been quite so successful. The literature documents only few reports for wheat, rice and maize of

efforts to generate salt-tolerant crops using conventional breeding, marker-assisted selection or genetic engineering for salt tolerance, whereas there are no reports for oats, barley, sorghum, and pearl millet. In wheat, most of the work related to conventional breeding for salt tolerance has been performed in India and Pakistan.

In rice, although a large number of salt-tolerant varieties have been developed through conventional breeding, these varieties are specific only for a particular region due to the complex nature of climatic conditions and soil composition. Only six varieties, CSR 10, CSR 13, CSR 27, Narendra Usar 2, Narendra Usar 3, and basmati CSR 30, were found to be tolerant over a variety of environments (Mishra *et al.*, 2003). Marker-assisted selection for salt tolerance in rice has been useful. However, these QTLs were stage specific and one type of QTL may not be effective in maintaining salt tolerance at various growth stages. The transgenic approach has been reported to be very effective for rice, with several genes involved in salt tolerance having been successfully incorporated into rice (Verma *et al.*, 2007).

In maize, transgenic approaches have been employed to some extent for improving the salt tolerance trait. Such reports for oat, barley, sorghum, and pearl millet are scarce in the literature.

Scientists have tried to develop salt-tolerant lines/cultivars of cereal crops through biotic approaches but the success to this end has been limited. Certainly problems, such as variation in environmental conditions, particularly in soil texture, temperature, precipitation rate, variable salinity levels at various places and other related conditions, have been strong barriers to development of varieties using biotic approaches. Although many cereal crops may grow under one type of climatic condition, their performance in other locations with different climatic conditions is often poor.

The other major problem in developing salt-tolerant cereals is the considerable variation in salt tolerance at different developmental phases as well as the complex nature of the salt tolerance trait that involves many genes. Salt sensitivity of most crops is not uniform at different growth stages, although the possibility of identifying genotypes that are tolerant at more than one stage exists in some cereal crops. Salt tolerance that has evolved naturally is controlled by multiple of genes. There are a number of studies in which transfer of a single gene is considered to have improved salt tolerance of a particular crop. In most of the cases dealing with salt stress, NaCl has been used to induce salt stress, while many other salts are also involved in causing salinity in soils, such as sulfate ions. Transgenic plants having high tolerance to NaCl salt stress may not perform well under sulfate-induced salt stress (Yamaguchi and Blumwald, 2005; Munns and Tester, 2008).

When we critically examine the literature, it is clear that most of the transformation studies are related to model plants, such as *Arabidopsis* and tobacco. The progress in terms of improved salt tolerance is high in these plants but now there is a demand to introduce these genes to other crop plants, including cereals. However, still there is the question as to whether or not these

genes will be effective to ameliorate the adverse effects of salt stress on plants.

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