

Breeding for salt tolerance in cereal and legumes: Status and prospects

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Introduction

Soil salinity is an important limiting factor for crop yield improvement, which affects 5-10% of arable lands - approximately 75-100 million ha worldwide, depending on estimates (Szabolcs, 1994; Munns, 2002). Most crops are sensitive to salt stress at all stages of plant development, from seed germination through vegetative and reproductive growth. Salt originates from marine geological sediments or from accumulation over time because of excessive irrigation. For the last reason, salinity affected areas are increasing (Ghassemi et al., 1995), and proper irrigation management could curb this increase. However, this often contradicts with the immediate economic choices of concerned farmers, thus crop improvement for salt tolerance appears to be the only alternative.

There are broadly two types of “salinity”: (i) an excess Na in soil where pH remains within an optimal range for crop growth, which refers to coastal or dry land salinity (Munns et al., 2002), and is called “*salinity*”; and (ii) an excess Na in soil where pH is above 8.5-9.0, which refers to transient salinity, and is called “*sodicity*”, (Rengasamy, 2002). In sodic soils, the high pH decreases the availability of micronutrients, and undermines the soil structure and porosity, causing water logging (Rengasamy, 2002). In both types, Na saturation causes similar effects. The work at ICRISAT focuses on salinity.

Despite the importance of salinity on the crop production worldwide, and the abundance of knowledge gathered on genes/mechanisms involved in salinity tolerance, there has been surprisingly little effort to breed for improved salinity tolerance (Flowers, 2004), except for wheat (Munns et al., 1999, 2002; Munns and Rawson, 1999) rice (Gregorio et al., 1993, 2002), barley (Ellis et al., 1997), or soybean (Owen et al., 1994). Developing tolerant crop varieties is critical because: (i) increased water scarcity will boost the use of salt-loaded residual waters or waters more likely to be saline in deeper bore-wells; and (ii) crop production needs to increase and potential target areas for that purpose are those transiently affected by salinity during the post-rainy season, such as rice fallows of saline coastal areas.

The purpose of this position paper is to review the level of advances in research towards breeding for salinity tolerance in ICRISAT’s mandate crops. In a first part, we report on our approach to salt stress and the protocols and traits targeted for salinity tolerance screening. In the second part, we review the progress and stage of advance toward molecular breeding in each of ICRISAT’s mandate crops.

Approach, method, and mechanisms for salt stress response

Approach, method and measurements

Although the genetic basis for salinity tolerance and evidence of genetic diversity between and within species appears to be well established (Epstein et al., 1985), the difficulty remains as how to assess salinity tolerance and whether to approach salt stress research from the field or from the lab. **(i)** Controlled environment evaluation

of salinity tolerance uses artificial conditions, often using much higher salt levels than in natural saline conditions, does not evaluate salt tolerance based on harvestable yield (grain or fodder), and exposes plants to light and vapor pressure deficit (VPD) levels usually lower than those in the field. A plethora of work has evaluated salinity tolerance at germination or very early stages. Although it is fast and easy, its applicability is questionable (seedlings germinate in wet soil, when salinity levels would be at the lowest levels), and studies have shown a poor relation between the performance at germination or early stages under salinity to that at later stages (e.g., Munns and James 2003, Flowers, 2004, Krishnamurthy et al., 2007;). However, controlled conditions ensure that salt treatment is homogenous, and that a non-saline control is used. **(ii)** Field evaluation of salinity tolerance results in large experimental errors because of heterogeneity of salinity in the field, requires large plots to get reliable estimates of yield under field conditions, which limits the number of genotypes that can be assessed, often cannot use a control non-saline field. An obvious advantage of field evaluation is that it assesses directly what a farmer would eventually need: yield under salinity. A combination of both controlled environment and field-testing is then needed. Highlight of ICRISAT's work on this are:

- A facility has been set up that allows both a rigorous control on salt treatment and yield evaluation. This facility is located outdoors, is equipped with moveable rainout shelters, uses large pots filled with natural soil. Salt application is made on a per unit soil basis dissolved in irrigation water to ensure uniform distribution, at a rate previously determined on a crop basis. Adequate watering maintains salinity levels constant throughout the experimental period.
- Yield evaluation showed little relation to vegetative stage evaluation for salinity tolerance, across crops, which prompted our decision to screen for yield.
- An optimized protocol gives us very good data reliability across crop species (low coefficient of variation and a good genotypic discrimination).
- Seed yield under salinity was in many cases related to the yield potential under control conditions. Salinity tolerance *per se* accounts only for the part of the variation in the yield under salinity that is not explained by the yield potential. Therefore, there is a strict need to evaluate plants under salinity along with a non-saline control.

Time could be saved in these facilities by using drip irrigation for the control treatments. A network of locations for field-testing of most promising materials is getting developed.

Physiological and biochemical mechanisms of salt tolerance.

The mechanisms by which plants tolerate salt are well described in the literature. These mechanisms target: **(i)** minimizing the entry of sodium into the plant; **(ii)** increasing the Na efflux from the root; **(iii)** avoiding Na loading into the xylem; **(iv)** storage of Na in stem tissues; **(v)** storage in non-vital cell compartments (vacuoles, apoplast); **(vi)** storage in old leaf blades; and **(vii)** cellular protection of key enzymes by specialized metabolites. Mechanisms, (i), (ii), (v) and (vii) are those receiving the most attention, in particular for the molecular studies, with a number of cell membrane and tonoplast transporters involved in Na extrusion or compartmentation, and a number of metabolites involved in cell protection. We believe that mechanisms (i) and (ii) have probably received too much attention, part of the

reason being the conditions used to assess plant materials (overwhelming salt treatments whereby mechanisms (i) and (ii) are “unavoidable”). The relevance of mechanisms (v) and (vii) may also be questionable if plants are not exposed to exaggerated salt level. We believe that under the salt level that crops would face in natural and still potentially productive saline fields, mechanisms (iii) and (iv) may best explain differences in salinity tolerance. The mechanisms highlighted above (i-vii) also overlook the effects of salt stress on reproduction. Thus, we now focus our research efforts on how crops avoid Na loading into the xylem (iii) and/or store Na in stem tissues (iv), and how tolerant genotypes manage to have a successful reproduction under salt stress.

Advances towards molecular breeding in ICRISAT’s mandate crops

Sorghum

Sorghum [*Sorghum bicolor* (L.) Moench] is known to be relatively more tolerant to salinity than other crops such as maize or legumes, and has the potential to replace maize in saline soils (Igartua et al. 1994). Many studies in sorghum have assessed salinity tolerance at the germination stage (Gill et al., 2003; Ismail, 2003; Malibari et al., 1993; Marambe and Ando 1995), although little relation was found with tolerance assessed at later stages (Munns et al., 2003; Krishnamurthy et al. 2003a). At ICRISAT, a range of improved hybrid parental lines, hybrids, germplasm lines, and parents of mapping populations have been screened under saline conditions in our facility. Highlights of that research are:

- A salt treatment of 21.06 g/9kg Alfisol is optimal to reliably screen salinity tolerance.
- Large contrast for salinity tolerance as assessed by the seed yield under salinity or the ratio of seed yield salinity / seed yield control exists.
- Significant positive relation between the seed yields in saline and non-saline conditions ($r^2 > 0.50$).
- Among the lines identified as tolerant, several have been successfully tested in farmers’ fields of coastal saline areas of Orissa, India.
- Hybrids do not have superior salinity tolerance *per se* over inbreds, although the seed yield of hybrids under saline conditions was higher than inbreds.
- The parents of two existing RIL populations of sorghum have a large contrast for salinity tolerance, creating the possibility to identify salinity tolerance QTLs.
- No relation between the seed yield or seed yield ratio and the biomass or biomass ratio at vegetative stages, showing that assessment for salinity tolerance needs to be made at maturity and that salt effects on reproductive stages were the major explanation for genotypic difference in seed yield under saline conditions.

Forthcoming efforts on salt stress at ICRISAT will focus on: **(i)** screening a large representative set of sorghum genotypes for salinity tolerance (mini-core initially, then a subset of 300 representative genotypes based on SSR markers), **(ii)** identifying the traits involved in salinity tolerance, using outputs from (i); **(iii)** investigating the reasons for the sensitivity of reproductive stages to salt stress; and **(iv)** developing RIL populations and using existing mapping populations showing parental contrasts for initial salinity tolerance QTL identification **(v)** Test promising lines in multi location trials.

Pearl millet

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is often grown in saline lands and, as sorghum, is known to be relatively more tolerant to salinity than other crop plants, particularly maize and legumes (Dua 1989; Ashraf and McNeilly 1987). There are relatively few studies on the effect of salinity on pearl millet. Pearl millet responses to salinity have been evaluated at germination stages (Ashraf and Mcneilly, 1992; Varma and Poonia, 1979), although poor relation was found with later evaluation (Krishnamurthy et al., 2003b). As in sorghum, a range of improved hybrid parental lines, hybrids, germplasm lines, and parents of mapping populations have been screened under saline conditions in our facility. Highlights of that research are:

- A salt treatment of 21.06 g/9kg Alfisol is optimal to reliably screen salinity tolerance
- Several pairs of parents of existing RIL populations have been identified with a large contrast for salinity tolerance based on repeated trials. The contrast is sufficiently large to justify the search of QTLs for salinity tolerance using these RIL populations.
- Among the lines identified as tolerant, several have been successfully tested in farmers' fields of coastal saline areas of Orissa, India.
- Little relation between the yield or yield ratio and biomass or biomass ratio at booting stage, showing that genotypic differences for salinity tolerance were explained by differences in the sensitivity of the reproductive stages to salt stress.
- Significant positive relation between seed yield under saline and control conditions.

Future work is very similar to that in sorghum: **(i)** evaluate a large and representative set of germplasm to fully explore the salinity tolerance variability in pearl millet; **(ii)** investigate the mechanisms of tolerance to salt stress in pearl millet. Tolerant pearl millet also had high shoot $[Na^+]$, mechanism **(v)** also may be relevant **(iii)** study the sensitivity of reproductive stages to salt stress; and **(iv)** use existing RIL populations where parental contrast for salt stress was found for the purpose of salinity tolerance QTL identification and develop new RIL populations. **(v)** Test promising lines in multi location trials.

Chickpea

Saline soils are very common in West and Central Asia and Australia, where chickpea is widely grown. It has been earlier stated that chickpea was fairly susceptible to salinity, and that there was not enough genetic variation to warrant breeding for that trait (Saxena, 1984, Johansen et al., 1990). However, Dua (1992) found fairly large variation in sodicity tolerance, and several tolerant sources were identified in India (Singh and Singh 1980, Dua, 1992 Dua and Sharma, 1995). A salinity tolerant *desi* chickpea variety (CSG 8962) was released in India for salt affected soils. Work at ICRISAT has re-assessed the previous statements by Saxena (1984) and explored a large range of genotypes, including the mini-core. Highlights are (Vadez et al., 2006, 2007):

- A treatment of 8.88 g/7.5 kg Vertisol is optimal to reliably screen salinity tolerance.
- A 5-6-fold range of variation for seed yield under saline conditions exists across chickpea germplasm, with 10 genotypes yielding 10-20% better than CSG 8962.
- Saline yield was well correlated with control yield.

- Little relation between the yield or yield ratio and biomass or biomass ratio at vegetative stages under salinity.
- Salinity tolerance *per se* was well correlated to the ratio of seed number, indicating that tolerant genotypes were those able to maintain a large number of viable reproductive structures and that genotypic differences in salinity tolerance were explained by differences in the sensitivity at the reproductive stages.
- Na accumulation in shoots was low (0.1 – 0.6%) and not related to salinity tolerance.
- Desi types were more salt tolerant than kabuli.
- Three crosses between tolerant and sensitive genotypes have been made to develop mapping populations.

Forthcoming work in chickpea will concentrate on the following aspects: **(i)** phenotype and identify QTL for salinity tolerance, first using the existing RIL where parents ICCV 2 and JG 62 contrast for salinity tolerance, and then using the new crosses developed for that purpose; **(ii)** investigate why and what processes during reproduction are affected by salinity that later lead to genotypic differences in salinity tolerance; and **(iii)** test the most contrasting lines in saline fields.

Groundnut

Very little work has been done on the effect of salinity on groundnut. Interest is increasing in countries like India where groundnut production needs to increase and salt-affected areas are potential targets for such increase in the groundnut production area. However, there has been no clear trait identified related to salinity tolerance. We have set up a protocol where suitable salt stress could be applied and salinity tolerance assessed in a large range of genotypes, including the mini-core collection. Research highlights are (Srivastava et al., 2007a&b):

- A salt treatment of 10.53 g/9kg Alfisol is optimal to reliably screen for salinity tolerance (Vadez et al., 2005).
- A five fold range of variation was found for pod yield among the genotypes tested
- No relation was found between seed yield under saline and non-saline conditions.
- A poor relation was found between the biomass at maturity and seed yield under saline condition (Srivastava, 2007b)

Because of the paucity of work in the past on salinity stress in groundnut, research orientation at the moment focuses on: **(i)** confirming the contrast for salinity tolerance in a large set of genotypes, including the mini-core collection; **(ii)** developing RIL populations for QTL mapping based on contrasting genotypes identified in (i); **(iii)** assessing putative traits using contrasting genotypes to better understand the mechanisms of tolerance in groundnut; **(iv)** assessing the sensitivity to salt stress of reproductive and seed filling stages in groundnut since it appears that salinity tolerance is related to both the ability to maintain and fill a large number of viable pods under saline conditions; and **(iv)** identifying suitable research locations to screen the most contrasting lines in saline fields.

Pigeonpea

It is not clear under what experimental basis it has been asserted that pigeonpea was relatively tolerant to salinity (Sharma and Lavanya, 2002). Rather, pigeonpea appears to be among the most sensitive legume species to salinity, as previously

reported (Keating and Fischer 1985). There appears to be appreciable genotypic differences in tolerance to salinity, although these differences were considered insufficient to undertake a breeding program. It has been reported that wild relatives of pigeonpea, especially *C. plathycarpus* and *C. sericeus* and *C. albicans* have more tolerance than cultivated types. Although F1 hybrids between these wild and cultivated germplasm were indeed more tolerant than the cultivated pigeonpea (Subbarao et al., 1990a&b), the work has not been taken any further, likely due to a lack of funds.

We have recently screened the mini-core pigeonpea collection (Upadhyaya et al 2006), along with a set of genotypes from 10 species of wild relatives of pigeonpea (Srivastava et al., 2007c). It appears that given the high sensitivity of pigeonpea to salinity, there is a high rate of mortality in the trials, although many accessions do produce high amounts of biomass. Therefore, we have considered in this particular case that a biomass evaluation at a sufficiently advanced stage would be sufficient to screen tolerant materials. Highlights of the work are (Srivastava et al., 2006):

- A salt treatment of 5.26 g/9kg Alfisol is optimal to reliably screen salinity tolerance.
- A large range of variation for biomass and biomass ratio exists.
- Range and degree of salinity tolerance was greater in the mini core accessions than in the germplasm from salinity areas.
- A number of *C. plathycarpus*, *C. sericeus* and *C. scaraboides* accessions were tolerant, whereas the other species tested were mostly sensitive.

Given the extremely high sensitivity of pigeonpea to salt stress and the relative tolerance found in the wild relative, we believe that wide hybridization is the most promising avenue. Further work should: (i) confirm the contrast in materials screened so far and develop inter-specific segregating populations; and (ii) study the mechanisms of tolerance, in particular Na loading in the xylem, using outputs from (i).

Conclusions and future plans

From our results so far, we can conclude that ICRISAT's mandate crops vary in their level of salinity tolerance, roughly in the following order: Sorghum = Pearl millet > Groundnut > Chickpea >>> Pigeonpea. Within each species, we have shown that a large genotypic variability exists (sometimes including variability of wild relatives), which fully justifies an investment in breeding to exploit these differences. Given the complexity of phenotyping for salt tolerance, MAS breeding would eventually be the mean of introgressing salt tolerance characteristics in farmer-preferred crops. Efforts are underway in all crops, at various stages of advance, to progress toward that goal.

Our strengths and orientations in salinity research are three-fold:

(i) We have established a facility to screen and phenotype for salinity tolerance that gives reliable results, allows the evaluation of a large number of accessions, and combines the advantages of all screening methods used thus far, in particular it allows yield evaluation under salt stress. We will exploit this facility to further confirm the contrast between lines, to phenotype RIL population. Then we plan to develop a network of field locations to test the most contrasting accessions within each specie.

(ii) By following a systematic approach for assessing salinity tolerance in large sets of representative germplasm, we have identified large variations for salinity tolerance in all the mandate crops of ICRISAT. These valuable sources will be used

for breeding, to understand the key mechanisms involved in salinity tolerance, and to develop mapping populations;

(iii) We have a few excellent research hypotheses in relation to the mechanisms involved in salinity tolerance. The effect of salt stress on reproduction, which has been little studied previously appears to be a crucial factor explaining genotypic differences for salinity tolerance. This is an area where ICRISAT is having cutting edge approaches and will invest significantly more time.

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