

## **Molecular breeding for drought tolerance: Progresses, issues, orientations**

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### **Introduction**

Water deficit, often referred to as “drought”, is the most prominent abiotic stress, severely limiting crop yields and opportunities to improve livelihoods of poor farmers in the semi-arid tropics. For example, it is estimated that annually, drought causes US\$ 520 M losses in groundnut alone (Subbarao et al., 1995). One of the major research objectives at ICRISAT is to exploit modern science techniques to develop crops that are more resilient to low and erratic rainfall patterns.

Conventional breeding of early maturing varieties, capable to escape drought and mature before water deficit becomes too severe, has been a common approach in most mandate crops of ICRISAT. However, substantial variation for drought tolerance, beyond earliness has not been identified nor utilized extensively. However, conventional, yield-based selection for drought tolerance is difficult due to the large genotype by environment (GxE) interactions for yield under stress. In view of this, the application of molecular biology technologies holds great promise not only to improve, but also speed up the breeding of drought tolerant genotypes (Ribaut et al., 1996).

In this position paper, we report the progress and success in the use of marker-assisted selection (MAS) in pearl millet and sorghum, and describe the rationale, status and future needs of a trait-based approach to increase drought tolerance. Finally, we highlight the close links between this research and other position papers on the development of genomic tool (RK Varshney et al), the exploration of diversity (HD Upadhyaya et al), the use of wild relatives (N Mallikarjuna et al), and the use of transgenics (KK Sharma et al), links without which biotechnology and trait-based approaches would be imprecise and ineffective.

### **Successes in marker assisted breeding for terminal drought tolerance**

*This part relates to another paper on the use of MAS breeding (CT Hash et al)*

Research on drought tolerance in cereals has focused on post-flowering (terminal) stress as this is the most damaging stress to grain yield, as a determinate cereal has less opportunity to recover from a reproductive stage stress than an indeterminate legume.

Pearl millet: Research on genetic variation in grain yield under post-flowering stress indicated that as much as half of the variation in yield of pearl millet under terminal drought is explained by two non-stress related parameters: yield potential and phenology. Therefore, a drought response index (DRI) was calculated to quantify the remaining part of the variation, associated with tolerance/susceptibility (Bidinger et al 1987) and to identify traits linked to tolerance. Panicle harvest index (PNHI) was found to be closely related to the DRI, and was evaluated as a phenotypic selection criterion and as a target trait for QTL identification. Highlights are:

- Yield gains of 5+% per cycle of selection under terminal stress were achieved in both population breeding and hybrid parental line selection using PNHI as a selection criterion (Bidinger et al., 2000)

- A major QTL, which accounts for significant variation in grain yield and PNHI under terminal drought on linkage group 2 was identified in two mapping populations (Yadav et al 2002, 2004, Bidinger et al., 2007).
- MABC transfer of the tolerant allele at this QTL into the background of terminal drought sensitive H77/833-2 and 841B, produced introgression lines with superior terminal drought tolerance under the same environment in which the QTL was identified (Serraj et al., 2005, Hash et al., 2005).

Current efforts are now on pyramiding the drought tolerance QTL on LG2 with downy mildew resistance in elite hybrid parent backgrounds. Recent work on selected QTL introgression lines suggested that more profuse rooting in deeper soil layer might be a major underlying factor to that QTL (Vadez et al., 2005). Efforts are on going to further characterize the role of roots in that QTL.

Sorghum: The focus has been on reduced leaf senescence, the “stay-green” trait, which prolongs photosynthesis under declining soil moisture (Borell and Hammer 2000). We have used published information (Crasta et al., 1999; Haussman et al., 2002) to add QTLs *stg1*, *stg2*, *stg3*, *stg4*, *stgA* and *stgB*, from the donor parent B35 to a number of senescent lines in a MABC program. Highlights are:

- An evaluation of BC 1 and BC 2 lines confirmed: (i) the expression of the trait in post rainy season line R 16, (ii) an improvement of stover quality, (iii) a modest improvement in grain filling and grain yield under terminal stress.
- On going evaluation of BC 3 and BC 4 backcross progenies from the same recurrent parent with several stay green QTL. Initial data indicate that some of these are much better agronomically than the BC1 s and significantly less senescent than R 16.
- A number of markers have been added in the vicinity of QTL *Stg3*, which will help in background selection to more quickly recover the recurrent parent phenotype.

More markers in the vicinity of QTLs that are tightly linked to undesirable characters would be highly needed to speed up and precise that process. We also hypothesized that the staygreen trait, i.e. the maintenance of functional green leaves late into the maturation cycle, would necessarily require drought avoidance mechanisms (increased water uptake, or water saving strategies). We found that under water deficit roots of staygreen materials are about 60 cm deeper than in senescent materials (Vadez et al., 2005). In parallel, we have started evaluating transpiration efficiency of lines contrasting for stay green.

#### **A trait-based approach based on the yield architecture ( $Y = T \times TE \times HI$ )**

Research is on going to exploit the genetic differences in drought avoidance mechanisms, i.e. better water capture (T) or transpiration efficiency (TE). These are two components of a simple model defined by Passioura (1977) where yield (Y) is defined as  $T \times TE \times HI$ , where HI (harvest index) represents how biomass is converted into grain. Beside the rationale, these component traits may have a higher heritability than yield, easing the identification of QTL. The trait-based approach has indeed yielded good success for some abiotic stresses (Hall, 1992; Condon et al., 2002; Sinclair et al., 2000).

#### Roots.

Work on chickpea has spear headed research activities on roots at ICRISAT during the past 15 years. Chickpea is exclusively grown during the post-rainy season, and almost exclusively depends on stored moisture, thereby, facing terminal drought conditions. It has been found that besides earliness, deep and more profuse rooting was a direct contributor

to the seed yield under terminal drought (Kashiwagi et al., 2006a). Breeding for root traits is therefore ongoing. Highlights of this research are:

- A dramatic improvement in the methods used to assess root traits (Kashiwagi et al., 2005, 2006), i.e. in 1.2 m long and 18 cm diameter PVC cylinders, where the data agrees well with those from the field (Kashiwagi, 2006b).
- Larger variation for root traits than previously reported has been found, particularly in genotypes with deeper and more profuse roots than “icon” ICC4958.
- One QTL accounting for over 30 % of the variation in root length density has been identified (Chandra et al., 2004) from a population developed between variety Annigeri (shallow roots) and ICC4958 (deep and profuse roots).
- New segregating populations have been developed between parents showing more contrast for root traits than Annigeri and ICC4958.

The phenotyping and genotyping of two new populations is under way (ICC1882 x ICC4958 and ICC283 x ICC8261) and there is good scope to find more, and hopefully more significant QTLs for root traits. Next step toward MAS breeding in chickpea is to initiate the introgression of these QTLs into locally adapted varieties.

We are currently expanding the work on roots to the other crops of ICRISAT. As mentioned above, roots may play a potential part in terminal drought QTL of pearl millet and staygreen QTL in sorghum. Preliminary experiments confirm previous statements (Ketring et al., 1984) that root have large range of variation in groundnut. Hence, we are planning to set up a large facility for studies on roots. Root washing remains a time-consuming activity even by using the new method in cylinders. We hope to achieve a needed quantum leap in root research, in particular by assessing root traits by lysimetric measurements of transpiration and/or canopy temperature.

#### Transpiration efficiency (TE)

Groundnut has led the work on TE during the past 15 years at ICRISAT. This crop is usually grown under rain fed conditions, and is often exposed to erratic rainfall patterns, thereby exposing the crop to intermittent drought spells at every stage of crop development. Current research has focused on developing varieties capable of efficiently using erratic rainfalls, having high TE. Genetic variability for TE has been found in groundnut (Wright et al., 1994). Highlights are:

- The identification of surrogate traits of TE (which is difficult to measure)
- The development of segregating populations for TE
- The recent development of markers to map QTLs
- The identification of drought tolerant varieties that could help understand better the mechanisms involved in TE

However, a breeding approach to increase yield under drought using surrogates has not been superior to a conventional approach (Nigam et al., 2005), in part due to a negative relation between TE and high HI (Wright et al., 1991). Recent work shows that care should be taken in the use of surrogates of TE (Krishnamurthy et al., in prep.). Efforts are then needed to ease and speed up the phenotyping of TE itself. Also, recent data show a 4-fold range of variation for TE in a large and representative set of groundnut germplasm, much higher than the range previously used for breeding for TE, thereby warranting the use of that diversity. Such variation for TE should also be widely explored in crops where drought avoidance is a must, such as in sorghum and millet.

#### Toward improving HI under drought

From Passioura’s model,  $Y = T \times TE \times HI$  (1977), virtually no effort has been made to improve the HI under water deficit. It is well known that reproduction is extremely

sensitive to any abiotic stress, in particular drought (see lifetime work by JS Boyer, e.g. Boyer and Westgate, 2004). In the end, the success of agriculture is tightly bound to the success of reproduction. Preliminary work indicates that genotypic variation exists for the sensitivity of reproduction to water deficit in groundnut and chickpea. A thorough assessment of that variation is really needed. Also, we need to investigate how roots and TE, the other two components of the model, interact with HI. For instance, we found a positive relation between HI and profuse rooting in deep layer under severe drought (Kashiwagi et al., 2006a). Therefore, research is needed to address T, TE, and HI in a comprehensive way rather than in a piece-meal fashion, and investigate how these traits interact with each other.

### **Exploitation of the diversity and molecular tools**

#### Germplasm diversity

One key to efficiently use molecular breeding for traits conferring drought tolerance is to develop segregating populations from parents having maximum contrast for these traits. For this, it is important to assess a large range of representative germplasm for these traits. The difficulty to assess large number of germplasm lays in the choice of entries to test: Collections containing often more than 15,000 accessions are difficult to deal with. A major highlights of the work on genetic resources of ICRISAT, has been to study the patterns of diversity in these collections and to establish representative core and mini core collections (10% of entire collection) to enhance the use of germplasm in improvement programs (CCER paper by HD Upadhyaya et al). Highlights are:

- Development of core and mini core collection in several mandates crops
- The range of genetic variation for drought related trait in the mini core of chickpea (Kashiwagi et al 2006b) and groundnut (Upadhyaya, 2005).

These core and mini-core collections (Upadhyaya and Ortiz, 2001) were established using data on geographic origin and phenotypic traits. Work is on going to develop composite collections representing global crop diversity, including core or mini core collections, and to genotype them using 20-50 SSR markers. The purpose is to determine population structure and identify a most diverse set of 300 germplasm accessions for each crop for extensive phenotyping for various traits including drought. We plan to use these diverse sets for establishing putative association between marker and trait via linkage disequilibrium (LD)-based association mapping. This approach involves the screening of the diverse germplasm collection either with a larger number of molecular markers (that scan the whole genome) or candidate genes associated with the QTLs for the trait.

#### Wide hybridization

Wild relative of cultigens are a precious resource for rare alleles having putative roles in drought tolerance (and many other traits) (CCER document by Mallikarjuna et al). This is where a trait-based approach can find interesting characteristics in the wild relative. So far, little effort have been put on trying to introgress characteristics from wild relative into the cultivated for drought tolerance purpose. This may be in part because the traits contributing to “drought tolerance” are not clearly established. Further work is needed to clearly determine whether and which trait from the wild could potentially improve the overall drought tolerance of the cultigens.

Another interest of the wild relative is to “re-introduce” polymorphism at the genetic level and favor all sorts of recombinations with the DNA from cultivated species. In recalcitrant crop from the point of view of polymorphism, such as groundnut, introgression of alleles from the wild species is currently being attended. Groundnut is one such crop that probably results from a single event of hybridization between two wild ancestors,

which has created a genetic bottleneck and limits exploitable genetic polymorphism between most of the cultivated germplasm. In collaboration with EMBRAPA (Brasil), a re-synthesis of groundnut from its wild progenitors is on going. These synthetic, from which we can expect interesting recombinants, would be explored for component traits of drought tolerance.

#### *Marker development and technology*

Breeding of drought tolerance also requires having the necessary tools to breed (CCER paper by RK Varshney et al). This includes the development of sufficient number of markers and/or the development of efficient marker technologies, so that putative molecular marker-phenotypic trait associations can be efficiently pinpointed. Over the past several years we have been able to develop and map a small number (ca. 40) of EST-SSR markers in pearl millet, and establish protocols for doing this on a larger scale in sorghum (where much larger EST resources are available). We have also initiated exploitation of markers detected by conserved intron-spanning primers (Feltus et al., 2006), and are adding these gene-based markers to base maps for both sorghum and pearl millet. Although sorghum enjoys genome wide genetic and physical maps, and soon genome sequence data, other ICRISAT mandated crops lack a reasonable number of molecular markers or good intraspecific genetic maps. Therefore, efforts are being to develop the genomic resources for these crops (see CCER document by Varshney et al.)

#### Transgenics, a form of “functional” diversity

This approach could be very useful to speed up the process of molecular introgression of putatively beneficial genes that offer enhanced tolerance to drought. Several gene transfer approaches have been attempted to improve drought tolerance in different crops (Holmberg and Bulow, 1998; Vinocur and Altman, 2006, Umezawa et al., 2006). However, a “single-gene” transgenic approach may not be suitable for developing drought tolerance since abiotic stress tolerance is a multigenic trait. A wiser approach may be using transcription factor/s, i.e. major “switch” to trigger a cascade of genes in response to a given stress (Chinnusamy et al., 2004). This approach has been undertaken at ICRISAT in groundnut and chickpea by using the drought responsive element (DRE) DREB1A from *Arabidopsis thaliana* driven by the stress-responsive promoter rd29A from *A. thaliana* (Liu et al., 1998; Kasuga et al., 1999). A large number of independently transformed events of groundnut (Bhatnagar-Mathur, 2006) and chickpea (Vani et al., 2006) have been developed. These are undergoing evaluation under laboratory and greenhouse conditions. The highlights are:

- 14 transgenic events of groundnut showed significant differences in the kinetics of transpiration response to soil drying (Bhatnagar-Mathur et al., 2004)
- Several T3 generation transgenics had higher TE than the wild type parent under well watered conditions, and that one event had higher TE than the wild type parent across moisture conditions (Vadez et al., 2005).
- The range of variation for TE in the transgenics was higher than the range of variation for TE in a RIL population of groundnut developed to map TE QTLs.
- The kinetics of transpiration response to soil drying of DREB1A event is similar in chickpea and groundnut.

Current efforts are ongoing to identifying more events with superior TE, testing the effect of DREB1A on the response to drought at reproductive stage, and eventually to have contained trials. Also, these materials showing a large variation for TE are isogenics to JL24, and offer an ideal material to study the physiological basis for the differences in TE.

## Conclusions & Future Plans

Advances toward the use and application of MAS breeding to develop new varieties with drought tolerance are making significant progress, at different stages across crops. Here are the priority research areas that would help pushing MAS breeding forward:

1. Marker and MAS: It is needed in the cereals and in groundnut, either to further saturate the QTL location to speed up and ease the identification of suitable introgression lines, or to simply be able to undertake MAS (groundnut). Where QTL is already identified, such as for root in chickpea, MAS breeding should start.

2. “PPP” (parents, populations, phenotyping) for the trait-based approach: We plan to continue to systematically explore the diversity (representative sets), for traits contributing to drought tolerance, to find the parents of populations, which will eventually be phenotyped for QTL mapping. In the case of groundnut, backcross populations from re-synthesized and cultivated groundnut are also likely to reveal interesting recombinants for drought.

3. Roots: We need to further refine/simplify the phenotyping protocols for root traits, and achieve a quantum leap in root research, by focusing more on what roots “do” rather than what root “are”, and then develop the phenotyping capacities for such alternative traits. These would be used to explain the role of root in sorghum and pearl millet QTLs.

4. An integration of traits in the trait-based approach: Research on the HI component of the trait-based approach is lagging behind. We need to explore genotypic variation for HI under drought conditions, and to investigate the relations, synergies, trade-off between water uptake, TE and HI. In this, transgenic materials presented here will be very useful, in particular because preliminary data indicate that DREB1A also influences the root development, and the success of reproduction under water deficit.

For additional information/clarification, contact Dr Vincent Vadez. [V.vadez@cgiar.org](mailto:V.vadez@cgiar.org)

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