

Development of Drought-Resistant and Water-Stress Tolerant Crops through Traditional Breeding

Rodomiro Ortiz¹, I.J. Ekanayake¹, V. Mahalakshmi², A. Kamara¹,
A. Menkir¹, S.N. Nigam², B.B. Singh¹ and N.P. Saxena²

Introduction

Abiotic stresses may account for 71% of yield reduction in crops (Boyer, 1982). In this regard, access to and control of water resources are among the most important issues of the 21st century. On-going climate change also influences the water supply by affecting rainfall and evapo-transpiration. Presently, 450 million people are subjected to severe water shortage and in 2025 this number may increase to about 2.7 billion (or 1/3 of the world population). Statistics show that in the USA, insurance indemnities are paid more for crop losses due to drought than for any other kind of loss.

Some are advocating an increase of farm water use by 15 to 20% for sustaining food security and alleviating rural poverty. Environmentalists claim, however, that water resources should drop by 10% in the coming 25 years to be able to protect natural water resources (in rivers, lakes and wetlands). Furthermore, 10 to 20 million km² of continental land have experienced desertification owing to inappropriate agricultural and water engineering practices. The annual rate of desert expansion lies between 0.5 to 0.7%, i.e. about 80,000 km² are undergoing desertification every year at a 0.5% rate. If the trend continues, about 1 billion people in the semi-arid and arid tropics will be affected.

There are distinct options for managing water resources; irrigation (or modifying the environment) was the traditional approach for dealing with water shortages but now that water resources are scarce other solutions are being sought. For example, plant breeders are conducting research for the development of crops better adapted to drought-prone environments or for plants with high water use efficiency. Research suggests that relatively high productivity could be achieved even in unfavorable environments if selection for adaptation to these environments could occur in targeted crops. Nevertheless, selection for tolerance in stress environments often leads to low-yielding genotypes when grown in non-stress environments.

Drought tolerance in plants

Mechanisms for plants to become better adapted to water-scarce environments are widely reported but most of them have not yet been elucidated (Table 1). The most important include root architecture, leaf morphology, physiological characters such as osmotic adjustment or proline accumulation, partitioning of total biomass (determined by dry matter or harvest index), timing of plant development (e.g. earliness), or others associated with the plant reproductive biology. Some of these characteristics are specific while others are common for many species. Some reports indicate a significant association between crop tolerance to heat and respective adaptation to drought-prone environments in the warm tropics.

¹ International Institute of Tropical Agriculture (IITA), Nigeria c/o L.W. Lambourn and Co., Carolyn House, 26 Dingwall Road, Croydon, CR9 3EE, UK

² International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, 502 324 AP, India

The physiology of drought tolerance in crops has remained controversial (Blum, 1988) because new knowledge on the subject keeps emerging though significant gains were obtained in the last decade. Plants need to maximize photosynthesis under stress at the tissue level, and growth must be maintained when the evapo-transpiration demand will be at minimum levels. An appropriate crop canopy that increases the capture of limiting radiation and enhances water use efficiency can achieve this objective. Regarding crop production itself, two-stage process affects the plant under water stress: first the plant maintains its ability for gas exchange and therefore acquires carbon, and secondly, the plant only survives while losing carbon due to respiratory losses.

Drought tolerance is a complex trait because several mechanisms are involved. Drought escape, dehydration avoidance and dehydration tolerance are the most frequently reported plant mechanisms to deal with drought. Short growth duration seems to be the best option for drought escape, e.g. through an appropriate flowering date and grain filling period in the growing season. Dehydration avoidance was defined as the plant's capacity to retain a high level of "hydration" (or leaf water potential) under soil or atmospheric water stress, e.g. maintenance of leaf water potential under soil moisture stress. Dehydration tolerance (i.e., cells lose turgor and become dehydrated when plants are not protected from dehydration by the avoidance mechanism could be unwieldy for breeding because the control of the plant tissue-water status or turgor appears to be difficult as a selection tool since it will depend on cellular processes.

Table 1 Examples of plant mechanisms for drought tolerance or water-use efficiency in crops

Crop	Plant characteristics or mechanisms
<i>Cereals</i>	
Barley	Earliness, harvest index, low transpiration efficiency, proline accumulation, short grain filling period, tillering
Maize	Anthesis-silk interval, fertile ear number, grain number per fertile ear, great partitioning of biomass to the ear (or high harvest index)
Pearl millet	Panicle harvest index or ratio of grain mass to total panicle mass
Rice	High harvest index, intermediate plant height, leaf rolling, high leaf water potential, osmotic adjustment, root length density, root penetration ability, root pulling resistance, small total dry matter content
Sorghum	High water extraction efficiency, few nodal roots per plant, few higher late metaxylem, small leaf area, stay-green owing to delayed senescence
Wheat	Abscisic acid (ABA) accumulation, leaf water potential, proline content, transpiration efficiency
<i>Legumes</i>	
Bean	Ability to avoid flower abscission and sustain pod formation
Chickpea	Deep roots, earliness, rapid root development and water extraction, rapid rate of large seed development, small leaf area due to few pinnules
Cowpea	Delayed leaf senescence and slow growth or stop growth for conserving plant tissue moisture, thereby staying alive
Groudnut	Harvest index, specific leaf area, total amount of water transpired and transpiration efficiency
Lentil	Early flowering, osmotic adjustment, pod set, transpiration efficiency
Lupin	High number and large seeds per pod owing to fast seed growth
Pigeonpea	Osmotic adjustment, seedling establishment and early growth vigor
Soybean	Root size, ability to degrade ureides, leaf Mn ⁺² concentration, transpiration efficiency
<i>Starchy crops</i>	
Cassava	Growth index, leaf retention, photosynthetic rate, root length density, stomatal conductance
Musa	Leaf stomatal conductance, photosynthetic rate, stomatal morphology, transpiration
Potato	Low water potential, root pulling resistance, stomatal conductance
Sweetpotato	Leaf water potential, root pulling resistance, root systems

Breeding for drought tolerance

Plant breeding provides a means for closing the gap between actual and potential yield in stressed environments (i.e. marginal dry areas) through genetic manipulations (Acevedo and Ferreres, 1993). Crops or cultivars within each crop are replaced with others showing a higher fitness in an environmental gradient arising from physical limiting uncontrolled factors. Therefore, farmers and breeders attempt to identify crop tolerance in these gradients arising from the specific abiotic stress. For example, in West Asia and Near East, bread wheat grows in areas well endowed with water, while farmers prefer barley in more drought-prone areas. Breeders know well that cultivars with a high yield potential are not able to outyield stress-resistant cultivars (i.e. a crossover interaction) in the respective stressful environments. These high-yielding cultivars may even perform poorly in stressful environments. Researchers, farmers and policy makers should also keep in mind the plant breeding paradigm that economic phenotype performance (P) is influenced by many factors and their interactions as indicated in the equation below:

$$P = \text{Genotype} \times \text{Environment} \times \text{Crop Management} \times \text{Policy (affecting both people and markets)} \times \text{Institutional Arrangements} \times \text{Social Demographics}$$

Two approaches are advocated for breeding under stress environments: (a) increasing yield of broadly adapted genotypes (Rajaram *et al.*, 1997) or (b) exploiting genotype adaptation (particularly of landraces as at least one parental source) and fit cultivars to the specific targeted environment (Ceccarelli, 1997). The two approaches may stem from a distinct perspective in understanding adaptability and adaptation that could affect the preservation of genetic variation in respective crop breeding pools. Adaptability, which depends on the available genetic diversity within each population, refers to the capacity for genetic response to selection that results in adaptation. However, when cultivars are highly adapted to a specific environment, there will be less adaptability for evolutionary change, which appears to be essential for sustained crop improvement by both farmers and professional plant breeders. Decentralized (through networking) and participatory plant breeding with local partners may provide a means for compromising both approaches while breeding in marginal, low input, stressful environments. Decentralization of plant breeding requires refining target areas, targeting local research partners for crop improvement and shifting responsibility from a central breeding station to local undertakings (which may not only include germplasm testing but also new material generation through specific crosses with landraces for further selection). In this way, individual breeding programs (irrespective of their size) will maintain deliberately genetic diversity across locations.

Germplasm screening for tolerance to drought under naturally occurring drought stress does not seem to be reliable. Lack of uniform drought stress in the field will render screening for drought tolerance ineffective and thus limit progress from selection. Greenhouse methods are also available for screening germplasm at early stages of plant development. Selection must occur under controlled environments, where drought will be reliably induced to distinguish between tolerant and susceptible genotypes, particularly at flowering or grain filling stages in seed crops.

The most common breeding method consists of screening under controlled drought stress the offspring derived from populations, followed by the assessment of selected genotypes at a location where drought occurs frequently, and testing the most promising genotypes for yield potential and yield stability at multiple sites representing the target ecology. An alternative knowledge-led breeding method may include (a) defining an ideotype that possesses the main characteristics associated with stress tolerance and high productivity in a drought-prone environment, (b) screen the assembled genetic resources (landraces and breeding materials) in a water stress gradient in targeted environment, and (c) correlate putative drought tolerance traits with others that can be easily recorded and show a high heritability, which will allow effective indirect selection.

Genetic analysis in some crops suggests that a few genes control each of the independent plant mechanisms of drought tolerance. Development of recombinant inbred lines between contrasting parents, divergent selection starting with their F₂ generation, and testing derived F₅ or F₆ lines in opposing environments allow genetic analysis, trait identification and breeding *per se* for drought tolerance in seed crops.

Examples: maize for cereals, cowpea for legumes, groundnut for oil crops

Breeding for tolerance to drought in maize in West and Central Africa

Drought is considered to be one of the major abiotic constraints in the Guinea savanna belt of West and Central Africa. The risk of drought stress is particularly high in the Sudan savanna zone because rainfall in much of this area is unpredictable in quantity and distribution. Even in those lowland locations with adequate precipitation for maize production, periodic droughts can occur at the most drought-sensitive stages of the crop such as flowering and grain filling. Drought stress coinciding with flowering and grain filling stages of maize had been reported to reduce yields by 50% and 21%, respectively, and 12% annual yield loss of maize grain had resulted from drought stress in West and Central Africa. Consequently, breeding for tolerance to drought can help farmers better cope with the risks imposed by erratic rainfall. Until recently, the maize breeding program at the International Institute of Tropical Agriculture (IITA, Ibadan, Nigeria) screened germplasm for tolerance to drought under naturally occurring drought stress at a location in the Sudan savanna. However due to the lack of uniform drought stress in the field, screening for drought tolerance was ineffective and thus limited progress from selection was achieved. To effectively differentiate between tolerant and susceptible genotypes, selection needs to be made under controlled conditions where drought stress is reliably induced. Consequently, IITA has been screening various accessions of maize germplasm under drought stress at a location carefully controlled to coincide with the flowering and grain filling stages of the crop since 1997.

Developing a source population with a high frequency of desirable alleles can play an important role in determining the rate of gain from selection. In an attempt to form a broad-based late maturing adapted population with tolerance to drought, we evaluated five drought-tolerant populations from the Centro Internacional de Maíz y Trigo (CIMMYT): Pool 26 Sequia C3, Pool 16 Sequia C4, Pool 18 Sequia C4, Laposta Sequia C4, Tuxepeno Sequia C8, and a cross between DTP1 C7 and an adapted population from IITA (DT-SR 3) under controlled drought stress from 23 days before anthesis until harvest in the 1998 dry season. More than 200 promising S₁ plants with a high level of tolerance to drought were derived from these populations. These S₁ lines were crossed to tester inbred lines to form 225 late maturing testcrosses, which were included in a trial planted at Niore (Senegal), Vallée de Kou (Burkina Faso) and Ikenne (Nigeria) in the 1999 dry season. This trial was subjected to drought stress by withdrawing water for a period of at least 25 days starting from two weeks before flowering. The combined analyses of variance showed that testcross x location interaction mean squares were significant for grain yield and other traits. Differences among testcrosses were highly significant ($P < 0.01$) for all the traits. We used an index that combined high grain yield under drought stress and non-stress conditions with short anthesis-silking interval, increased number of ears per plant as well as desirable changes in other agronomic traits to select the best testcrosses. Outstanding testcrosses selected from this trial gave as high an average grain yield as a commercial hybrid (OBA SUPER I) with and without drought stress. These testcrosses were similar to the hybrid for other agronomic traits. The top 25 selected testcrosses gave 32% higher mean yield under drought stress than the mean of all the testcrosses with favorable changes in other traits including increased yield under non-stress conditions. Remnant seeds from the S₁ lines of the selected 25 testcrosses were inter-crossed in 2000 to form a broadly based late

maturing population. A second trial consisting of 160 early maturing testcrosses of S1 lines from TZE COMP3 C2 with a reciprocal tester composite, TZE COMP4 C2, was planted at the same three locations during the 1999 dry season. This trial was exposed to drought stress by withdrawing water for a period of at least 25 days starting from two weeks before flowering. The mean squares for testcross x location interactions were significant for grain yield and other traits. Differences among testcrosses were highly significant ($P < 0.01$) for all the traits. The 24 best testcrosses selected from this trial, using an index described above, produced higher grain yields than a cultivar from the previous cycle of selection (TZE COMP3 C2) with and without drought stress. These testcrosses were either similar to or better than this cultivar for other agronomic features. The selected testcrosses gave a 30% higher mean grain yield than the mean of all the testcrosses under drought stress with favorable changes in other traits including increased yield under non-stress conditions. The parental S1 lines of the selected 24 testcrosses were intercrossed in 2000 to form an early maturing drought-tolerant population. The resulting late and early maturing broad-based populations will be improved for drought tolerance using recurrent selection schemes.

Farmers' landraces collected from marginal growing environments including drought conditions could be used as sources of new desirable traits to enhance the performance of adapted germplasm under drought stress. Two trials composed of 25 early maturing local landraces from Senegal and 23 late maturing local landraces from Burkina Faso along with improved cultivars as checks were evaluated at Ikenne under drought stress by withdrawing water from 16 days before anthesis until harvest in the dry season. Some improved cultivars were also included in each of these trials. We used a base index that integrated days to tassel, ear aspect, anthesis-silking interval, number of ears per plant and leaf death score as an indicator of resistance or susceptibility of the genotype to drought stress. As shown in Figs. 1 and 2, the index scores accounted for 64 to 92 % of the total variation in grain yield under drought stress. The early maturing improved open-

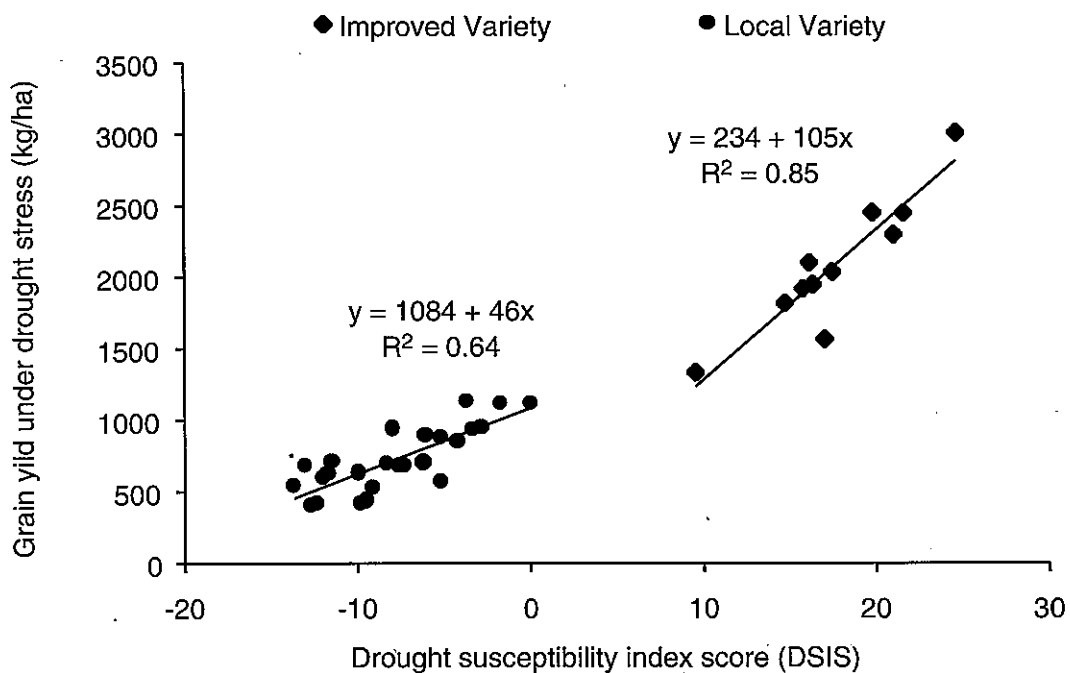


Fig. 1 Regression of grain yield on drought susceptibility index score of early maturing improved and local varieties evaluated at Ikenne under drought stress in 2000. $DSIS = (-0.5 \times \text{Days to tassel}) + (-2 \times \text{Ear aspect}) + (-2 \times \text{anthesis-silking interval}) + (2 \times \text{ears per plant}) + (-2 \times \text{leaf death score})$

pollinated cultivars were separated from the local landraces in terms of grain yield under drought stress and drought susceptibility scores (Fig. 1). Marked differences were detected among the local and improved early maturing cultivars for grain yield under drought stress and drought susceptibility index scores. Substantial differences were also detected among the late maturing local landraces in grain yield under drought stress and in the drought susceptibility index score (Fig. 2). Some of these were selected for further evaluation to confirm their reaction to drought stress.

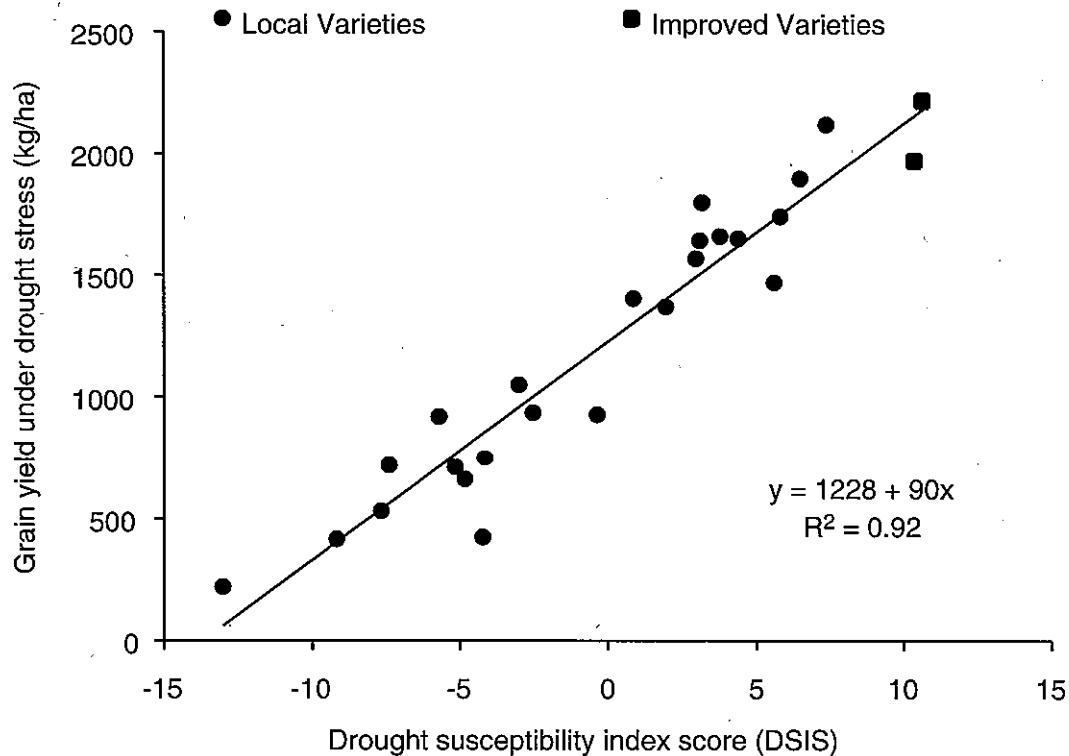


Fig. 2 Regression of grain yield on drought susceptibility index score of late maturing local varieties evaluated at Ikenne under drought stress in 2000. $DSIS = (-0.5 \times \text{days to tassel}) + (-2 \times \text{ear aspect}) + (-2 \times \text{anthesis-silking interval}) + (2 \times \text{ears per plant}) + (-2 \times \text{leaf death score})$

Breeding for drought-tolerant cowpea for the African dry savanna

Farmers grow cowpea widely in the semi-arid tropics of Africa and Asia, where drought remains a major constraint. Although cowpea appears to be the most drought-tolerant species among the popular legume crops of the dry savanna of Africa (Singh *et al.*, 1999b), it may still be affected by frequent drought in the Sahel, where rainfall can be irregular and scanty. Japan International Research Center for Agricultural Sciences (JIRCAS) and IITA have collaborated in the development of cowpea cultivars with better adaptation to drought-prone environments. A simple screening method was developed to accurately discriminate between tolerant and susceptible genotypes (Singh *et al.*, 1999a). Wooden boxes (130 cm length x 65 cm width x 15 cm depth) made of 2.5 cm planks were lined with polyethylene sheets, filled with a 12 cm layer of soil and sand mixture (1:1) and kept on the table top in a greenhouse. Testing materials were planted in these boxes (10 cm between rows and 5 cm between plants within rows) and watered daily until the partial emergence of the first trifoliolate, after which watering was discontinued. Percentage of permanent wilting was recorded at various intervals for each testing line until the plants of a known susceptible cultivar died. Watering then resumed

and the percentage of recovery was recorded. Days to permanent wilting and percentage of recovery were the two characteristics used to discriminate genotypes in this early drought screening method. Field and pot testing confirmed the correspondence between drought tolerance at this seedling stage and reproductive stage. Seedlings selected after this early screening in the wooden boxes may be transplanted to the field for further progeny testing and selection.

Two mechanisms of drought tolerance were observed in the cowpea germplasm developed in this IITA-JIRCAS project (Mai-Kodomi *et al.*, 1999a): (a) under drought stress some genotypes stopped growing and retained the moisture in all their plant tissues to stay alive for over two weeks, when gradually the entire plant parts dried together (Type 1), and (b) in other genotypes slow growth of the trifoliates continued, whereas the unifoliates of these genotypes under continued moisture stress showed early senescence and dropped off while their growing tips remained turgid and alive over a long period of time (Type 2). Such behavior suggests that moisture was mobilized from the unifoliates to the growing tips. Genetic analysis of segregation patterns revealed that drought tolerance for each type was controlled by a single dominant gene (*Rds 1* and *Rsd 2*, respectively), though Type 1 could be dominant over Type 2, as demonstrated by the test of allelism (Mai-Kodomi *et al.*, 1999b). Hence, these two genes for tolerance to drought stress in cowpea may be located at the same locus or tightly linked, which may preclude the incorporation of both mechanisms into the same cowpea cultivar.

Improving groundnut for water-stressed environments

Groundnut, an annual legume, is grown primarily for the high quality of edible oil and easily digestible protein in seeds. It is grown on 23.8 million ha with a total production of 34.5 million ton in shell and an average productivity of 1.4 t pods ha⁻¹. More than 80% of the world groundnut production is derived from rainfed agriculture. Drought is a major abiotic stress factor affecting yield and quality of rainfed groundnut worldwide. Yield losses due to drought are highly variable in nature depending on the timing, intensity, and duration coupled with other location-specific environmental stress factors such as irradiance and temperature. Furthermore, in the presence of drought, the beneficial effects of improved crop management practices in terms of increased production are not fully realized: calcium uptake by pods and N₂ fixation processes are adversely affected. Photosynthesis is reduced due to limited gas exchange. End-of-season drought conditions are conducive to aflatoxin contamination. An annual estimated loss in groundnut production equivalent to US \$ 520 million (at the prevailing price of 1994) is caused by drought. Almost half of it (US \$ 208 million) can be recovered through genetic improvement for drought resistance with a benefit: cost ratio of 5.2. Even under irrigated conditions, water shortage is now being felt in many areas. Water use-efficient genotypes are presently required to sustain crop productivity. Most of the drought resistance breeding at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT, Patancheru, India) is conducted in the postrainy season (November - April) when interference from the rains is the lowest. However, the evaluation of advanced breeding lines is carried out in both rainy (June - October) and postrainy seasons. Using the line-source sprinkler system of irrigation (Fig. 3), germplasm lines are screened for early season, mid-season, end-of-season, and intermittent drought in the field. Based on the harvest index (HI) and biomass production, germplasm lines are selected for resistance to different kinds of drought. Several lines with superior performance under different kinds of drought are now available for use in breeding programs.



Fig. 3 Field screening of groundnut using line-source sprinkler system of irrigation

Breeding approaches vary with the patterns of drought. Once the crop is established, early season drought in groundnut is not serious. Actually, the exposure to a 20 to 25-day moisture stress early in the season and subsequent release by applying irrigation are recommended to induce heavy and uniform flowering leading to the increase of productivity in groundnut. Genotypic yield accounts for 90% of the variation in pod yield sensitivity to water deficit during the seed filling stage. Therefore, matching of phenological development of a cultivar with the period of soil moisture availability is an effective strategy to minimize the impact of drought on crop production. Using soil moisture balance models in association with crop-weather modeling and geographic information service (GIS) technology, a judicious matching of genotype duration with the most probable soil moisture pattern can be achieved. ICRISAT has made considerable progress in shortening the crop duration of groundnut without unduly sacrificing yield. However, it is still necessary to screen genotypes in a given maturity group for resistance to end-of-season drought for two reasons. Firstly, to identify genotypes with reasonable pod yields and better vegetative growth (since groundnut haulms are a valuable fodder in most of the semi-arid environments) under severe end-of-season droughts. Secondly, end-of-season drought is closely linked with aflatoxin contamination of the produce and screening for end-of-season drought may also enable to identify of genotypes with resistance to *Aspergillus flavus* infection and aflatoxin production. A low relationship between the yield potential (achieved under adequate water availability) and the sensitivity of genotypes to mid-season drought suggested that it may be possible to identify or develop genotypes with a high yield potential and relatively low sensitivity to mid-season drought. For the development of genotypes with a superior yield performance under drought conditions, germplasm and segregating populations are evaluated and selected under simulated drought conditions (Table 2) in the post-rainy season. In addition to simulated drought conditions, the advanced breeding lines are also evaluated under rainfed conditions in the rainy season. Following the above empirical approach, several drought-resistant advanced breeding lines have been developed and distributed to national

programs in the form of international drought resistance groundnut varietal trials.

Table 2 Drought patterns and selection criteria used in drought resistance breeding in groundnut at ICRISAT

Germplasm	Segregating populations	Replicated yield trials
<i>Drought patterns</i>		
Early-season	Mid-season	Mid-season
Mid-season	End-of-season	End-of-season
End-of-season		Under rainfed conditions (only in the rainy season)
Intermittent		Under normal irrigated conditions (Control)
<i>Selection criteria</i>		
Index = HI, Biomass	High pod and seed yield	High pod and seed yield under both normal and drought conditions

However, the empirical approach to drought resistance breeding is resource-extensive and tardy. More efficient breeding methods based on traits that confer yield advantage under drought conditions are required to accelerate the progress. In recent years, there has been a significant improvement in our understanding of the physiological basis of genotypic response to drought in groundnut. The traits contributing to a superior performance under drought conditions in groundnut have been identified and substantial genetic variation observed for them. These include harvest index (HI), and total amount of water transpired (T) and transpiration efficiency (TE, defined as the amount of dry matter produced per unit amount of water transpired). However, some of these physiological traits can not be easily measured under field conditions. Recent studies have identified surrogate traits, carbon isotope discrimination in leaf and specific leaf area (SLA), which are associated with TE in groundnut. The SLA, which is a crude but easily measurable parameter, can be used as a rapid and inexpensive selection criterion for high TE. In earlier studies, TE and HI were found to be negatively correlated. A more comprehensive study indicated that the negative association between TE and HI could be broken and both traits could be improved concurrently.

Linking classical genetic improvement and advances in molecular breeding

Marker-aided genetic analysis confirmed that most of the variation for responses to drought or water use efficiency may be accounted for by a few quantitative trait loci (QTL) (Martin *et al.*, 1989; Mackill *et al.*, 1999; Thomas and Howarth, 2000). It was surprising that such complex traits are controlled by a few loci. Right phenotyping for water stress tolerance was very important for obtaining these results.

In soybeans, the QTL associated with drought tolerance coincided with maturity and determinancy QTL (Specht *et al.*, 2001). This QTL analysis also suggested that drought tolerance and yield responsiveness to water could be mutually exclusive. In this regard, cross-breeding assisted by selection with DNA markers could become a method for a rapid objective selection of new cultivars with enhanced adaptation to water-scarce environments. A reverse transcriptase polymerase chain reaction procedure (or differential display) allowed to identify cDNA corresponding to transcripts affected by water stress in groundnuts or peanuts (Jain *et al.*, 2001). These differentially expressed transcripts are collectively designated as PTRD (peanut transcripts responsive to drought). A total of 43 PTRD have been reported in this crop so far.

The above investigations as well advances in molecular biology in plant (or crop) model systems offer a new means for improving crops in drought-prone environments. For example, cowpea and chickpea (Kumar

and Abbo, 2001) are suitable species to determine the genetic potential of legume crops for drought using QTL analysis and germplasm characterization, whereas soybean and *Medicago* are the available tools among legume species for assessing the whole genome transcriptional response to drought. The characteristics of interest in a drought-tolerant "consensus legume" species include the root architecture, transcriptional pathways, physiological parameters (e.g. osmotic adjustment), plant development (e.g. earliness), and genetic control points. Comparative mapping will enable to identify gene synteny of drought tolerance loci between crop legume genomes. Forward and reverse genetics (in these legume species) may enable to identify key regulators of drought-tolerant genotypes. The outputs of this legume genomic research include genetically defined loci controlling this trait, candidate genes (defined by mapping, mutation and transcriptional investigations) for drought tolerance, and DNA markers for assisted selection or aided introgression and germplasm management regarding the improvement of drought adaptation in these crops.

Recent analysis of molecular responses to drought and other abiotic stresses in plants (Shinozaki et al., 1999) suggest that regulation of gene expression and signal transduction in transgenic crops could enhance their adaptation to drought-prone and other stressful environments. However, we must always remember that germplasm improvement and crop management are two complementary approaches for managing water efficiently at drought-stressed locations.

References

- 1) Acevedo, E. and Ferreres, E. (1993): Resistance to abiotic stresses. In Hayward, M.D., Bosemark, N.O. and Romagosa, I. (eds.) *Plant Breeding: Principles and Prospects*. Chapman and Hall, London. pp. 406-421.
- 2) Boyer, J.S. (1982): Plant productivity and environment. *Science* 218, 443-448.
- 3) Ceccarelli, S. (1997): Adaptation to low/high input cultivation. In Tigerstedt, P.M.A. (ed.) *Adaptation in Plant Breeding*. Kluwer Academic Publishers, Dordrecht.
- 4) Jain, A.K., Basha, S.M. and Holbrook, C.C. (2001): Identification of drought-responsive transcripts in peanut (*Arachis hypogea* L.). *Electronic Journal of Biotechnology* 4(2), <http://www.ejb.org/content/vol4/issue2/full/1>
- 5) Shinozaki, K., Yamaguchi-Shinozaki, K., Li, Q., Kasuga, M., Ichimura, K., Mizoguchi, T., Urao, T., Miyata, S., Nakashima, K., Shinwari, Z.K., Abe, H., Sakuma, Y., Ito, T. and Seki, M. (1999): Molecular responses to drought stress in plants: regulation of gene expression and signal transduction. In Smallwood, M.F., Calvert, C.M. and Bowles, D.J. (eds.) *Plant Responses to Environmental Stress*. BIOS Scientific Publishers, Oxford. pp. 133-143.
- 6) Kumar, J. and Abbo, S. (2001): Genetics of flowering time in chickpea and its bearing on productivity in semiarid environments. *Advances in Agronomy* 72, 107-138
- 7) Mai-Kodomi, Y., Singh, B.B., Myers Jr., O., Yopp, J.H., Gibson, P.J. and Terao, T. (1999a): Two mechanisms of drought tolerance in cowpea. *Indian Journal of Genetics* 59, 309-316.
- 8) Mai-Kodomi, Y., Singh, B.B., Terao, T., Myers Jr., O., Yopp, J.H. and Gibson, P.J. (1999b): Inheritance of drought tolerance in cowpea. *Indian Journal of Genetics* 59, 317-323.
- 9) Mackill, D.J., Nguyen, H.T. and Zhang, Jingxian (1999): Use of molecular markers in plant improvement programs for rainfed rice. *Field Crops Research* 64, 177-185.
- 10) Martin, B., Nienhuis, J., King, G. and Schaefer, A. (1989): Restriction fragment length polymorphisms associated with water use efficiency in tomato. *Science* 241, 1725-1728.
- 11) Rajaram, S., Braun, H-J and van Ginkel, M. (1997): CIMMYT's approach to breed for drought tolerance. In Tigerstedt, P.M.A. (ed.) *Adaptation in Plant Breeding*. Kluwer Academic Publishers, Dordrecht. pp. 161-168.
- 12) Singh, B.B., Mai-Kodomi, Y. and Terao, T. (1999a): A simple screening method for drought tolerance in cowpea. *Indian Journal of Genetics* 59, 211-220.

- 13) Singh, B.B., Mai-Kodomi, Y. and Terao, T. (1999b): Relative drought tolerance of major rainfed crops of the semi-arid tropics. *Indian Journal of Genetics* 59, 437-444.
- 14) Spetch, J.E., Chase, K., Macrander, M., Graef, G.L., Chung, J., Markwell, J.P., Germann, M. Orf, J.H. and Lark, K.G. (2001): Soybean response to water: a QTL analysis of drought tolerance. *Crop Science* 41, 493-509.
- 15) Thomas, H. and Howarth, C.J. (2000): Five ways to stay green. *Journal of Experimental Botany* 51, 329-337.

