Management of Drought in ICRISAT Cereal and Legume Mandate Crops

R. Serraj, F.R. Bidinger, Y.S. Chauhan, N. Seetharama, S.N. Nigam and N.P. Saxena

Abstract

This chapter reviews the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)'s research achievements in the domain of crop drought tolerance and presents future perspectives in the genetic enhancement of crop water use and drought adaptation in the semi-arid tropics. Exploration of crop genetic variability and genotype–environment interactions has contributed significantly to developing suitable screening methods for specific drought-tolerant traits. Genetic sources of drought tolerance were also identified at ICRISAT for all mandate crops, and some of the associated traits have been well characterized. A large spectrum of genotype duration is now available, from long to short and extra-short duration, and matching genotype duration with likely period of soil water availability is the first strategy used against terminal-drought stress. Identification and genetic mapping of quantitative trait loci for specific drought-tolerant traits using molecular markers are currently receiving greater research focus. This approach provides a powerful tool for dissecting the genetic basis of drought tolerance. If validated with accurate phenotyping and properly integrated in marker-assisted breeding programmes, this approach will accelerate the development of drought-tolerant genotypes. Overall, the progress made at ICRISAT during the last three decades proves that it is realistic to develop varieties that have increased yield under drought-prone conditions. Further multidisciplinary research integrating plant breeding, simulation modelling, physiology and molecular genetics will realize the potential of these approaches and increase the efficiency of crop improvement in drought-prone environments.

Introduction

The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)'s mandate crops, i.e. pearl millet (Pennisetum glaucum), sorghum (Sorghum bicolor), chickpea (Cicer arietinum), groundnut (Arachis hypogaea) and pigeonpea (Cajanus cajan), are all known for their relative ability to withstand periods of water-limited conditions and still produce grain and biomass. However, the constant challenge is to reduce yield gaps observed between research plots and farmers’ fields under the rain-fed conditions of semi-arid tropics (SAT), in order to ensure sustained food security for the benefit of resource-poor farmers.

Drought stress is a complex syndrome, involving several climatic, edaphic and...
agronomic factors, and is characterized by three major varying parameters, i.e. timing of occurrence, duration and intensity. The general complexity of drought problems is often aggravated under the SAT conditions, by erratic and unpredictable rainfall and by the occurrence of high temperatures, high levels of solar radiation and poor soil characteristics of the target environments. The high variability in the nature of drought and the insufficient understanding of its complexity have made it generally difficult to characterize the physiological traits required for improved crop performance under drought, consequently limiting plant-breeding efforts to enhance the drought tolerance of crops.

In the agricultural context of SAT and global water challenges, it is critical that both agronomic and genetic management strategies focus on the maximum extraction of available soil moisture and its efficient use in crop establishment, growth, maximum biomass and seed yield. Recent research breakthroughs have revived interest in targeted drought-resistant breeding and the use of new genomics tools to enhance crop water productivity. However, with the fast progress in genomics, a better understanding of the gene functions and drought tolerance physiological mechanisms will also be essential for the progress of genetic enhancement of crop drought tolerance.

It is now well accepted that the complexity of the drought syndrome can only be tackled with a holistic approach, integrating physiological dissection of the resistance traits and molecular genetic tools, together with agronomic practices that lead to better conservation and utilization of soil moisture and matching crop genotypes with the environment.

This chapter reviews the recent progress made at ICRISAT in deciphering the complexity of crop responses to water deficits and developing drought-tolerant varieties of the five mandate crops. The management options for increasing productivity and conserving natural resources adopted by ICRISAT for integrated watershed management are reviewed in a companion chapter (Wani et al., Chapter 12, this volume).

Drought as the Main Challenge for Agriculture in the SAT

The target environments for ICRISAT mandate crops

The agroclimatic and production-system environments of the SAT regions are very diverse and the inherent water constraints that limit crop production are variable. However, it is feasible to broadly characterize the drought patterns of a given environment using long-term water-balance modelling and geographic information system (GIS) tools (Chauhan et al., 2000; Bastiaanssen et al., Chapter 18, this volume). The assessment of the moisture-availability patterns of the target environments is critical for developing genotypes adapted to target environments and to identify environments with similar drought patterns.

Most of the ICRISAT experimental research on drought is accomplished at its centre at Patancheru in peninsular India, characterized by a relatively short growing season in a generally dry semi-arid climate, with high average temperatures and potential evaporation rates (Fig. 8.1). Soils are mainly Alfisols and Vertisols, with low to moderate levels of plant-available water content. In addition, the dry season at this location is generally rain-free, with a high mean air temperature and vapour-pressure deficits, which provide an ideal screening environment to expose plants to controlled drought-stress treatments by managing the timing of irrigation (Bidinger et al., 1987).

The main target environment for ICRISAT work on drought in pearl millet in India is the growing area of the north-western states of Rajasthan, Gujarat and Harayana, where postflowering stress, either alone or in combination with preflowering stress, is a very common feature of the environment (van Oosterom et al., 1996). The focus of pearl-millet research has thus been on terminal drought as it is also the most damaging to grain yield (Mahalakshmi et al., 1987).

Sorghum is one of the most extensively adapted crops; it is grown from 35°S to 45°N of the equator, and the elevation ranges
from sea level to nearly 2000 m a.s.l. The rainfall during the crop season could vary from 300 up to 2000 mm. Terminal-drought stress is most limiting for sorghum production worldwide. In sub-Saharan Africa, drought at both seedling establishment and grain-filling stages is also very common. In India, sorghum is grown during the rainy and the post-rainy seasons. The variable-moisture environment during the rainy season can have a severe impact on grain and biomass yield, affecting both preflowering and postflowering stages.

Characterizing drought in post-rainy-season crops, such as rabi sorghum and chickpea, is simpler, compared with the intermittent drought experienced by rainy-season crops. This is because much of the rainfall is received before the planting of the crop, which is therefore grown almost entirely on stored soil moisture and exposed mostly to progressively increasing (terminal) water deficits. Therefore, the factors governing crop growth and water use in the post-rainy season, i.e. radiation, temperature, vapour pressure and potential evaporation, are relatively stable and predictable, so that simulation modelling of both crop growth and the effects of various crop traits is quite feasible.

Groundnut is an important rainy-season crop in most of the production systems in south Asia and sub-Saharan Africa, where it is grown under varying agroecologies, either as a sole crop or intercropped with sorghum and pigeonpea. Groundnut yields are generally low and unstable under rain-fed conditions, due to unreliable rainfall patterns, with frequent droughts, and to a lack of high-yielding adapted cultivars.

Pigeonpea is grown mainly by resource-poor farmers in India and, to a varying extent, throughout the tropics, usually under rain-fed conditions. Traditionally, medium-to
long-duration landraces have been cultivated, with a crop duration of 150–300 days. Pigeonpea can be exposed to intermittent drought stress during dry periods of the rainy season and to terminal-drought stress in the post-rainy season. However, over the last two decades, shorter-duration pigeonpea (SDP) genotypes have been developed, with some genotypes capable of reaching maturity within 90 days (Nam et al., 1993). The introduction of such genotypes has enlarged the scope of pigeonpea cultivation in various, non-traditional cropping systems. However, the developed short-duration genotypes are usually sensitive to intermittent drought.

**The Yield Gap of Rain-fed Agriculture in the SAT**

Yield losses due to drought are highly variable, depending on timing, intensity and duration, coupled with other location-specific environmental stress factors, such as high irradiance and temperature. Global yield losses due to drought have been estimated to be around 6.7 million t of groundnut, 3.7 million t of chickpea and around 1.8 million t of pigeonpea (Subbarao et al., 1995). It has also been shown that a large proportion of these yield losses can be potentially recovered through efforts in crop improvement (Subbarao et al., 1995).

Drought may cause complete crop failure or a varying amount of reduction in biomass and grain yield. In addition to the direct effect of drought on the yield, the potential beneficial effects of improved crop-management practices, such as fertilizer application or intercropping, are not fully realized in terms of increased production. Drought reduces carbon assimilation through photosynthesis, due to limited gas exchange, and adversely affects symbiotic nitrogen-fixation processes in leguminous crops (Serraj et al., 1999a), resulting in significant reductions in crop yields and soil fertility. Furthermore, the problem of drought is often compounded by related stress factors, such as the infection of roots and stalks, and rot-causing fungi that cause premature death and severe lodging, all of which result in significant yield losses.

**Integrated Drought-management Options**

Given the increasing scarcity and competition for water resources, irrigation is generally not a possible option for alleviating drought problems in the SAT. For increasing biomass and seed yield, therefore, drought-management strategies, whether agronomic or genetic, need to focus on maximum extraction of available soil moisture and its most efficient use in both crop establishment and maximum crop growth.

The following steps are essential for planning improvement programmes for crop yields for a given target drought-prone area:

- Characterize the major patterns of drought stress and their frequency of occurrence in the target environment.
- Evaluate crop response to the major drought patterns (simulation modelling).
- Match crop phenology (growth period, sowing, flowering, seed filling) with the most favourable period of soil moisture and climatic regimes.
- Develop a strategy for the optimal use of supplementary irrigation, when available.
- Increase the soil water available to crops through agronomic management practices.
- Identify plant traits that would maximize: (i) the use of available soil moisture in transpiration; (ii) the production of biomass per unit water transpired; and (iii) partitioning into seed, thereby conferring enhanced crop water productivity.

Agronomic and genetic options that do not involve the external input of irrigation can only partially alleviate drought effects, because yield is always lower than what can be achieved with irrigation. For example, under drought-prone conditions at ICRISAT, India, chickpea yields higher than 3 t ha\(^{-1}\) were obtained in 110 days of crop duration with irrigation in large-plot field trials (ICRISAT, 1982), compared with the average yield at this location of around 1.0 t ha\(^{-1}\) in rain-fed conditions in 85 days of crop duration.
**Scope for Genetic Enhancement of Yield under Drought**

**Crop yield and water use**

The response of plants to soil-water deficit can be generally described as the sequence of three successive stages of soil dehydration (Fig. 8.2). Stage I occurs at high soil moisture, when water is still freely available from the soil and both stomatal conductance and water-vapour loss are maximal. The transpiration rate during this stage is therefore determined by environmental conditions around the leaves. Stage II starts when the rate of water uptake from the soil cannot match the potential transpiration rate. Stomatal conductance declines, so that keeping the transpiration rate similar to the rate of uptake of soil water results in the maintenance of the water balance of the plant. Finally, stage III begins when the ability of the stomata to adjust to the declining rate of water uptake from the soil has been exhausted and stomatal conductance is at a minimum.

Virtually all major processes contributing to the crop yield, including leaf photosynthetic rate, leaf expansion and growth, are inhibited late in stage I or in stage II of soil drying (Serraj et al., 1999b). At the end of stage II, these growth-supporting processes reach zero and no further growth occurs in the plants. The focus of stage III is survival, and water conservation is essential to allow the plant to endure these severe conditions. Plant survival is a critical trait in natural dryland ecosystems but, for most agricultural situations, stage III has little relevance to questions about increasing crop yield and water productivity, especially in the case of intermittent droughts. Consequently, the amount of water extracted up to the end of stage II determines the cumulative growth by the plants on a particular soil-water reservoir. Not surprisingly, research on soil-water use in crop growth going back more than 100 years has consistently shown an intimate and stable relationship between plant growth and transpirational water use after correcting for variation in atmospheric humidity (Sinclair et al., 1984). Therefore,

![Fig. 8.2. Typical plot of normalized leaf transpiration (NTR) against the fraction of transpirable soil water (FTSW). From data of Sinclair and Ludlow (1986).](image-url)
options to enhance crop survival do not usually mean an increase in crop yield under drought conditions. Increased crop yields and water productivity require the optimization of the physiological processes involved in the critical stages (mainly stage II) of plant response to soil dehydration.

**Genetic-enhancement approaches**

Four genetic-enhancement approaches have been implemented at ICRISAT to improve the adaptation of the mandate crops to drought-prone environments. These were:

- the development of short-duration genotypes that can escape terminal drought;
- the development of genotypes with superior yield performance in drought-prone regions following a conventional breeding approach;
- the development of drought-resistant genotypes following the physiological breeding approach;
- the identification of quantitative trait loci (QTL) for drought tolerance and their use in marker-assisted breeding.

A large germplasm collection of the five mandate crops, available in the ICRISAT gene bank, provides the base material for implementing the above four approaches of genetic enhancement in drought resistance.

**Development of Short-duration Genotypes**

The appropriate crop duration is a compromise of various factors, including the length of the season, the yield potential and the timing of the occurrence of drought stress.

**Pearl millet**

Drought escape is a major mechanism in pearl millet, determining relative cultivar performance in individual stress environments (Bidinger et al., 1987), and is often a major cause of genotype-by-environment (G × E) interaction in multi-environmental trials (van Oosterom et al., 1996). For example, in the case of the rains ending early, a 1-week difference in time to flowering between two cultivars is equivalent to about 30% of the grain-filling period, which would escape stress in the early-flowering cultivar, but which would be affected by stress in the later-flowering one (Mahalakshmi et al., 1988).

The effects of the timing of the occurrence of single periods of stress before and after flowering provide quantification of the effects of drought escape. For example, an early genotype that flowered 20 days after the onset of terminal-drought stress had about one-quarter of the yield reduction (−12% vs. −51%) of a later-flowering genotype that flowered only 10 days before the onset of the same stress (Mahalakshmi et al., 1987). However, despite the strong effects of drought escape in pearl millet, the scope for using this mechanism in crop improvement under drought conditions still depends upon the predictability of the occurrence of stress (Mahalakshmi et al., 1987).

**Sorghum**

Breeding for earliness has been a tremendous success, especially for increasing the yield of rainy-season sorghums in India (Seetharama et al., 1982). Such sorghums are also more suited for intercropping with other species. However, this approach also has some disadvantages. For example, reduced vegetative growth of early sorghums results in lower stover yield, which is critical to most resource-poor farmers. Earliness also increases susceptibility to grain moulds, as the grain matures during the end of the season, when it may rain frequently in some years. Earliness is more advantageous during the post-rainy season, although a crop maturing earlier than 3 months may not achieve high yields (Seetharama et al., 1982). In West Africa, phenotypic plasticity derived from photoperiod sensitivity is also an important adaptive trait, useful for matching the crop growth and development with the water-availability period.
Chickpea

Short-duration varieties that mature before the onset of severe terminal drought have proved successful in increasing yield under drought-prone conditions in chickpea (Kumar et al., 1996). However, since seed yield is generally correlated with the length of crop duration under favourable crop-growing conditions, any reduction of crop duration below the optimum would have a penalty in yield (Saxena, 1987). Depending upon the water availability, optimum crop duration for maximum yield would vary. Thus the selection of varieties needs to be matched with the maximum length of the growing period (LGP). Significant progress has been made in developing improved chickpea varieties of short duration that mature in 70–90 days in mild-winter chickpea-growing conditions, as prevailing in peninsular India (Kumar et al., 1996). Even extra-short-duration chickpea varieties, termed super-early, have now been developed (Kumar and van Rheenen, 2000). The development of these new varieties has expanded options to include chickpea as a crop in many prevailing and evolving new production systems, such as rice fallows.

Groundnut

In most of the SAT groundnut-growing regions, the rainfall distribution is erratic and the season length is less than 100 days (Virmani and Singh, 1986). ICRISAT has made considerable progress in shortening the crop duration of groundnut without substantially decreasing the realized yield (Vasudeva Rao et al., 1992). The short-duration varieties developed at ICRISAT have shown 23–411% superior pod yield over local control varieties in the seventh series of international trials across several countries (ICRISAT, unpublished data). However, the early-maturing genotypes usually have shallow root systems, which could make them more susceptible to intermittent dry spells if grown as a rainy-season crop and also result in a reduction of the yield potential. However, genotypic differences in rooting depth have been observed in groundnut (Wright et al., 1991; Nageswara Rao et al., 1993), suggesting scope for combining early maturity with an efficient root system.

Pigeonpea

Traditional long- and medium-duration pigeonpea landraces have evolved under and have apparently adapted to terminal-drought-stress conditions. However, studies in which irrigation has been supplied during the reproductive phase indicate that terminal drought usually reduces grain yield of landraces growing in their typical environment (Chauhan et al., 1992). This is more apparent in the shorter-duration environments closer to the equator, where evapotranspiration is high during the post-rainy season. Thus, in terms of maximizing grain yield, the duration of these landraces seems too long for the common period of soil-moisture availability. However, a large spectrum of genotype duration is now available (Gupta et al., 1989), and matching genotype duration with likely period of soil-water availability is the first line of defence against terminal-drought stress. Further, opting for an SDP cultivar rather than for those traditionally used in a region does not necessarily mean a sacrifice in yield potential, as even extra-short-duration pigeonpea (ESDP) varieties can produce yields above 2.5 t ha\(^{-1}\) (Nam et al., 1993).

Screening Tools and Breeding for Drought Tolerance

Screening and selection methodologies

In order to identify sources of drought tolerance, it is necessary to develop screening methods that are simple and reproducible under the target environmental conditions. Therefore, managing drought-screening nurseries requires a careful analysis of likely sources of non-genetic variation among plots, replications and repeated experiments and establishment of procedures for minimizing these factors (Bidinger, 2002).
Several field- and laboratory-screening methods have been used at ICRISAT to screen the mandate crops for drought tolerance, including line-source-sprinkler irrigation, rain-out shelters and measurement of the drought-susceptibility index (DSI).

The line-source-sprinkler irrigation method was first developed by Hanks et al. (1976) and further standardized at ICRISAT (Nageswara Rao et al., 1985). This system creates a gradient of drought stress and allows the evaluation of large numbers of genotypes at varying intensities of drought in a given environment. It proved to be useful for screening pearl millet (Mahalakshmi et al., 1990), chickpea (Johansen et al., 1994), groundnut (Nageswara Rao et al., 1985) and pigeonpea (Chauhan et al., 1998). However, where response to applied water is linear, simpler stress/no-stress techniques provide a more efficient means of conducting preliminary evaluations (Mahalakshmi et al., 1990).

When the yield level obtained under stress was not related to the number of days until 50% flowering occurred, the DSI, as proposed by Fisher and Maurer (1978), was calculated from yield under rain-fed conditions and the potential yield under irrigation. The lower the DSI, the greater the drought tolerance of the line. The DSI method was modified by Bidinger et al. (1987) to include cases in which yield under stress was related to drought escape and yield potential; it was thus used for screening pearl millet and identifying tolerant genetic material.

Both line-source and DSI methods have been found to be very effective in identifying sources of tolerance to terminal drought in chickpea. Sources of drought tolerance identified by the first method (Saxena, 1987) were further validated by the second (Johansen et al., 1994). More than 1500 chickpea germplasm and released varieties were screened for drought tolerance and evaluated in replicated trials at ICRISAT. Promising drought-tolerant germplasm, such as the line ICC 4958, was used in the drought-improvement programme (ICRISAT, 1992; Saxena et al., 1993).

ICRISAT adopted a holistic approach in screening and selecting groundnut genotypes with superior performance under mid-season and end-of-season drought conditions. To avoid confounding effects of drought incidence with phenology of the crop, the varietal comparisons for drought sensitivity were made within a given taxonomic group. Genotypes resistant to drought have been identified by assessing total dry-matter production and pod yield under a range of drought intensities imposed at critical phases, using a line-source-sprinkler technique. Their ability to recover from mid-season drought has also shown significant genotypic variation (Harris et al., 1988).

The line-source-sprinkler technique was also used to identify several drought-tolerant pigeonpea lines during the rainy seasons of 1986 and 1987. In both seasons, long breaks in rains occurred around the reproductive stage, which facilitated the imposition of drought treatments. Thirty SDP and ESDP advanced breeding lines in the first year and 40 in the second year were sown across a gradient of moisture. Among the pigeonpea hybrids tested, ICPH 8 and ICPH 9 were the most drought-tolerant; a fact which was further confirmed in multilocation trials (Chauhan et al., 1998).

The creation of the rain-out shelter facility at ICRISAT has also significantly improved the precision of drought screening. Thirty-two pigeonpea lines were screened for flowering-stage drought and substantial differences were recorded using the DSI. The line ICPL 88039 showed greater drought tolerance in this screening (Chauhan et al., 1998). Drought screening under the rain-out shelter, though reliable, has limitations of space, and pigeonpea cannot be grown year after year at the same place. To overcome the latter problem, rain-out shelters that can be moved to different places have been designed (Chauhan et al., 1997).

Crop-improvement strategies

Since a strong relationship between the yield potential and the sensitivity of genotypes to end-of-season drought was observed for all ICRISAT mandate crops, a first approach to minimizing yield losses due to terminal...
drought has been to breed for earliness. But in the case of mid-season drought such a relationship does not hold, as this requires specific genetic-enhancement programmes for drought resistance. Both conventional and trait-based approaches have been used at ICRISAT in the breeding programmes for drought. The empirical breeding approach is based on the selection for yield and its components under a given drought environment. While such an approach has been partly successful, huge investments in land, labour and capital are required to screen a large number of progenies. In addition, there is evidence of increasingly marginal returns from conventional breeding (Fehr, 1984), suggesting a need to seek more efficient methods for genetic enhancement of drought resistance. On the other hand, associating drought responses with the expression of specific physiological mechanisms can help greatly in establishing screening protocols, which allow better management of G × E interactions. However, it has been argued that a focus on very basic mechanisms is likely to be at the cost of the linkages to final grain yield and increased measurement costs, thereby complicating conventional and molecular breeding for tolerance (Bidinger, 2001).

For pearl millet, it was assumed that grain yield can be improved under water-limited environments if specific traits and responses associated with drought tolerance can be identified and incorporated into elite high-yielding genotypes of appropriate crop duration (Bidinger et al., 2000; Yadav et al., 2002). The QTL-mapping approach is ideal to meet such objectives as it can both identify individual genetic factors associated with a specific response and monitor the incorporation of the identified factors into the breeding programmes. The objective of using mapping-population progenies, based on commercially important hybrid parents, is to improve the drought tolerance of the parents so that the popular hybrids produced by them will have greater tolerance to drought (Yadav et al., 2002).

An ideotype approach was followed for genetic improvement of drought tolerance in chickpea (Saxena and Johansen, 1990). Using ICC 4958 (drought-tolerant parent), Annigeri (a high-yielding parent) and ICC 12237 (a wilt- and root-rot-resistant parent), a three-way cross was made. Following a diversified bulk method of breeding, generations were advanced and nine yield- and root-trait-based selections were made. Yield-based selections were effective in producing varieties with high yield and trait-based selections in producing varieties with a greater degree of drought tolerance (Saxena, 2003). Promising drought-tolerant, Fusarium-wilt-resistant lines with high yields are ICCVs 94916–4, 94916–8, 94920–3, 94924–2 and 94924–3 (Saxena, 2003). A backcross programme was also initiated at ICRISAT, with the objective of incorporating drought-tolerant traits in elite cultivars and of combining drought-tolerant traits. Seven varieties that combine the traits of large roots and fewer pinnules were developed (ICCV 98901 to ICCV 98907). A few of these recombinants showed a greater degree of drought tolerance than and a yield similar to that of the high-yielding parent (Saxena, 2003).

The approach followed at ICRISAT for enhancing drought resistance in groundnut has been previously described in detail (Nageswara Rao and Nigam, 2003). An empirical approach was first followed for selection among segregating populations and for evaluation of advanced breeding lines for their sensitivity to mid-season and end-of-season droughts, based on pod and seed yields. While the empirical approach was partly successful, it was concluded that a more efficient breeding approach required the selection of traits associated with drought resistance. There has been significant progress in understanding the physiological basis of genotypic variability of drought response in groundnut, suggesting scope for selecting genotypes with traits contributing to superior performance under water-limited conditions. For instance, substantial genetic variation has been observed in partitioning of dry matter to pods (Nageswara Rao et al., 1993).

Significant genotypic variation in total amount of water transpired (T) and transpi-
ration efficiency (TE) has been shown under field conditions (Wright et al., 1994). Further studies have confirmed large cultivar differences in TE in groundnuts grown in glasshouse and field conditions (Hubick et al., 1988; Wright et al., 1994). These studies made it possible to analyse the yield variation under drought conditions, using the physiological framework proposed by Passioura (1977), where:

\[ \text{pod yield} = T \times \text{TE} \times \text{harvest index (HI)} \]

Research has also shown that TE and carbon isotope discrimination in leaves (\(\Delta\)) are well correlated in groundnut (Wright et al., 1988, 1994), suggesting the possibility of using \(\Delta\) as a rapid, non-destructive tool for selection of TE in groundnut. However, further research has shown that specific leaf area (SLA, cm\(^2\) g\(^{-1}\)) is well correlated with \(\Delta\) and TE in groundnut (Wright et al., 1994). Further studies are currently in progress to compare the efficiency of the trait-based selection approach vis-à-vis the empirical approach.

Breeding programmes on pigeonpea in recent years have focused on developing SDP types of 90–150 days of maturity (Gupta et al., 1989). This has made it possible to match phenology with periods of soil-moisture availability, a proven way of combating terminal drought (Chauhan et al., 1998). Nevertheless, there is a considerable yield gap, which is largely due to the adverse effect of intermittent droughts in different environments (Nam et al., 1993). The SDP and ESDP cultivars are generally shallow-rooted (Chauhan, 1993), and what they gain by being able to escape drought stress they lose by their inability to extract water from the deeper soil layer. Indeed, it is observed that these genotypes extract water from shallower (<75 cm) layers, compared with unstressed controls (Nam et al., 2001). In addition, large gaps within the rainy-season rainfall are not unusual in the semi-arid regions, when ESDP and SDP may be forced to grow with limited ability to extract water, owing to their shallow root system. Therefore, more work is needed on screening and selecting pigeonpea cultivars for intermittent-drought tolerance.

Characterization of drought-resistance traits

Identification of simple-to-observe morphological and phenological traits reflective of mechanisms and processes that confer drought tolerance has been a high-priority activity in drought research at ICRISAT. An appropriate screening trait for drought-stress tolerance should fulfill the following criteria: (i) a strong link with higher or more stable grain yield in the target stress environment; (ii) a high level of heritability; and (iii) an easily measurable expression of tolerance, with adequate replication.

The traits associated with some promising drought-tolerant sources for ICRISAT cereal and legume mandate crops are listed in Table 8.1. Most of these characteristics that appear to enhance crop drought resistance are the manifestation of perhaps several individual mechanisms and are most probably under complex genetic control.

The panicle harvest index (PNHI), i.e. the ratio of grain to total panicle weight, has been evaluated as a selection criterion for terminal-stress tolerance in pearl millet in both variety and hybrid-parent breeding (Bidinger et al., 2000). It is also currently used as one of the traits for which QTL are being identified, from a mapping population made from parents that differ in the ability to maintain PNHI under stress. PNHI, however, is readily and inexpensively measured in field experiments and can be readily used as a direct selection criterion. The main potential benefit in identifying a QTL for PNHI would be to allow marker-assisted backcross transfer of improved tolerance of terminal stress to elite lines and varieties, without the requirement for extensive field screening.

In sorghum, delayed senescence or stay-green is considered as a useful trait for plant adaptation to postflowering drought stress, particularly in environments in which the crop depends largely on stored soil moisture for grain filling. To identify superior sources of stay-green, sorghum genotypes have been recently evaluated for patterns of postflowering leaf senescence in replicated field experiments during the 1998/99 and 1999/2000 post-rainy seasons at ICRISAT.
Table 8.1. Examples of early-maturing genotypes, putative drought-tolerance traits and genetic sources for the ICRISAT mandate crops.

<table>
<thead>
<tr>
<th>Crops</th>
<th>Trait</th>
<th>Source</th>
<th>Yield advantage under drought</th>
<th>Reference</th>
</tr>
</thead>
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<tr>
<td>Pearl millet</td>
<td>Phenology: early maturing</td>
<td>ICTP 8203, ICMV 88908</td>
<td>Yes</td>
<td>Rai et al., 1990</td>
</tr>
<tr>
<td></td>
<td>Phenology: early maturing</td>
<td>ICMV 88904</td>
<td>Yes</td>
<td>Witcombe et al., 1995</td>
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<td>Sorghum</td>
<td>Phenology: early maturing</td>
<td>IS 22380, S 35,</td>
<td>Yes</td>
<td>Rao, 1983</td>
</tr>
<tr>
<td></td>
<td>Stay-green</td>
<td>QL 27, QL 10</td>
<td>NDa</td>
<td>Mahalaksmi and Bidinger, 2002</td>
</tr>
<tr>
<td>Chickpea</td>
<td>Phenology: extra-short duration</td>
<td>ICC 2</td>
<td>Yes</td>
<td>Kumar and van Rheenen, 2000</td>
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<td></td>
<td>Large root system</td>
<td>ICC 4958</td>
<td>Yes</td>
<td>Saxena et al., 1993</td>
</tr>
<tr>
<td></td>
<td>Fewer pinnules</td>
<td>ICC 5680</td>
<td>Yes</td>
<td>Saxena and Johansen, 1990</td>
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<td></td>
<td>Small pinnules</td>
<td>ICC 10480</td>
<td>Yes</td>
<td>Saxena and Johansen, 1990</td>
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<tr>
<td>Groundnut</td>
<td>Phenology: short duration</td>
<td>ICGV 92029</td>
<td>Yes</td>
<td>ICRISAT (unpublished)</td>
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<td></td>
<td>Transpiration efficiency</td>
<td>ICGS 76</td>
<td>Yes</td>
<td>Wright and Nageswara Rao, 1994</td>
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<td></td>
<td>Specific leaf area</td>
<td>Tifton 8</td>
<td>Yes</td>
<td>Wright et al., 1994</td>
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<tr>
<td>Pigeonpea</td>
<td>Phenology: extra-short duration</td>
<td>ICPL 87, 83015</td>
<td>Yes</td>
<td>Nam et al., 1993</td>
</tr>
<tr>
<td></td>
<td>Leaf-area maintenance</td>
<td>ICPL 87</td>
<td>Yes</td>
<td>Lopez et al., 1997</td>
</tr>
<tr>
<td></td>
<td>Root and shoot biomass accumulation</td>
<td>ICPH 8, ICPH 9</td>
<td>Yes</td>
<td>Chauhan et al., 1998</td>
</tr>
<tr>
<td></td>
<td>Drought-susceptibility index</td>
<td>ICPL 88039</td>
<td>Yes</td>
<td>Chauhan et al., 1998</td>
</tr>
</tbody>
</table>

*Not determined.
(Mahalakshmi and Bidinger, 2002). A collection of 72 stay-green lines was clustered into five groups, based on the percentage of green leaf area at 15, 30 and 45 days after flowering in the 2 years. This work identified several tropically adapted sorghum lines (e.g. IS 22380, QL 27, QL 10, E36 x R16 8/1) with stay-green expression levels equivalent to those of the best temperate lines B 35 and KS 19. The stay-green trait is also currently used for QTL identification in sorghum.

Two important drought-avoidance traits have been characterized and widely used for the genetic enhancement of chickpea: the large root system, which appears to be useful in greater extraction of available soil moisture, and the smaller leaf area, which has been shown to reduce transpirational water loss (ICRISAT, 1992). The chickpea line ICC 4958 has multiple traits of large root size, a rapid rate of root development and extraction of water and a rapid rate of seed development related to its large seed size. Lines ICC 5680 and ICC 10480 have a smaller leaf area, due to either narrow pinnules (ICC 10480) or fewer pinnules (ICC 5680). Recombinants with traits of ICC 4958 and ICC 5680 showed a higher midday leaf relative water content compared with the parents in field trials conducted at ICRISAT (Saxena, 2003).

There is large scope for the genetic improvement of the efficiency of crop water use in groundnut (Wright and Nageswara Rao, 1994). Significant genotypic variation in the total amount of water transpired and TE (defined as the amount of dry matter produced per amount of water transpired) have been found in groundnuts grown in glasshouse and field conditions (Wright et al., 1988, 1994). Groundnut lines ICGS 76, ICGS 44, Tifton 8 and Kadiri 3 were identified as having high TE values (Wright et al., 1994).

Important putative drought-resistance traits for pigeonpea include early vigour, leaf-area maintenance, root and shoot growth rate and development plasticity (Johansen, 2003). Early growth vigour is an important factor in drought resistance as it permits the establishment of a root system that is more effective in extracting water during later drought periods. This is considered to be the main reason why pigeonpea hybrids, such as ICPH 8 and ICPH 9, grow and yield better than the varieties from which they are derived, under both drought and well-watered situations. There are considerable differences in early growth vigour of pigeonpea (Johansen, 2003). Early-maturing genotypes generally show more vigour than later-maturing ones, with hybrids showing most vigour, but there are exploitable differences in this trait within maturity groups.

While reduction in leaf area under drought stress would reduce further transpirational losses and thus enhance survival ability, leaf-area maintenance seems to be an important consideration for pigeonpea under drought (Subbarao et al., 1995). Leaf-area maintenance under intermittent drought stress would involve an integration of several lower-level traits, such as a root system effective in water extraction, dehydration tolerance, leaf movements, etc. Leaf-area maintenance is an easily observable trait, amenable for use in screening segregants of a breeding programme. Pigeonpea shows large genotypic differences for this trait (Lopez et al., 1997). The SDP genotype ICPL 87 performs better than a sister genotype, ICPL 151, which correlates with the greater leaf-area retention in ICPL 87 under drought than in ICPL 151.

QTL and marker-assisted selection (MAS) strategies

Most of the physiological traits associated with drought resistance are quantitative in nature. Using molecular markers, QTL can therefore be detected in an appropriate population of plants. A locus for any quantitative trait can be mapped as long as polymorphism is observed in the segregating populations under analysis and phenotypic information is available for the lines in the population. However, for traits as complex as drought tolerance, the success of the QTL approach is conditioned by the effectiveness of the phenotyping procedure in detecting among recombinant lines repeatable, highly heritable differences that permit the identifi-
cation of robust QTL. Therefore, a special effort is needed for the conceptualization, design and management of phenotyping programmes for drought tolerance and to maximize the chances of identifying QTL that will be useful in the future improvement of tolerance in the target crop and in the target environment.

A QTL-mapping approach is currently used at ICRISAT to dissect the genetic and physiological basis and apply marker-assisted breeding strategies for several traits linked to drought tolerance, including the PNHI and yield components of pearl millet under terminal drought, root drought-avoidance traits in chickpea and stay-green in sorghum.

For terminal drought in pearl millet, several mapping populations have been developed using restriction-fragment length polymorphism (RFLP) skeleton mapping, trait phenotyping (Hash and Witcombe, 1994) and QTL mapping (Yadav et al., 2002). Test crosses of mapping-population progenies, derived from inbred pollinators and from seed parents differing in their response to drought, were evaluated in a range of managed terminal-drought-stress environments to identify individual QTL associated with drought tolerance. A number of QTL associated with drought tolerance of grain yield and its agronomic and physiological components were identified (Yadav et al., 2002). Some of the identified QTL were common across water-stress environments and genetic backgrounds of the two mapping populations, while others were specific to a particular water-stress environment or genetic background. Interestingly, all the identified QTL contributed to increased drought tolerance through their effect on either increased maintenance of growth or harvest index or both in terminal-drought-stress environments. Programmes for marker-assisted backcross transfer of the identified QTL into the elite parent of these mapping populations have been initiated for the improvement of pearl-millet productivity in water-limited environments (Yadav et al., 2002). The development of near-isogenic lines will also provide an ideal opportunity to further test the effect of the identified QTL and to dissect the associated physiological mechanisms involved in terminal drought.

Phenotyping for chickpea root traits involved in drought avoidance has been carried out in recombinant inbred lines (RILs) of a cross (ICC 4958 × Annigeri) and a wide cross (ICC 4958 × Cicer reticulatum) (Saxena and Kumar, 2000). Currently, identification of QTL for the large root system of ICC 4958 for developing the MAS technique is in progress.

Compared with other crops, cultivated groundnut with currently available DNA markers shows limited polymorphic variation, which has made it difficult to construct a genetic map for cultivated groundnut. However, polymorphic variation in DNA has recently been detected in selected germplasm of cultivated groundnut, using molecular markers (He and Prakash, 1997; Subramanian et al., 2000). On the other hand, there is still limited information on the biochemical and molecular basis for variation among genotypes for drought resistance (Nageswara Rao and Nigam, 2003). Further research is necessary to develop linkages between the drought-resistance traits and the molecular markers so that MAS tools can be applied in drought-resistance breeding.

Material dissemination and impact

Most of ICRISAT’s genetic-enhancement programmes for the past three decades have focused on increased crop productivity and adaptation in the target semi-arid environments. The overall crop-improvement strategies pursued have, therefore, directly and indirectly contributed to increasing the selection pressure for better adaptation to water-limited conditions. With more than 400 varieties released in 170 countries, ICRISAT’s research has contributed significantly to increasing crop productivity and food security in smallholder farming across the SAT. Early-maturing varieties have generally resulted in a reduced risk of crop failure, linked to plants’ escape from end-of-season drought.

Improvements in pearl-millet and sorghum productivity under water-limited
conditions are critical for both national and household food securities in the SAT, especially in sub-Saharan Africa. Two successful examples of the impact of genetic enhancement of crop yield under rain-fed conditions are the releases of pearl-millet variety Okashana 1 in Namibia and the sorghum variety S 35 in Chad and Cameroon.

The pearl-millet variety Okashana 1, developed by ICRISAT and identified for use by the Namibian national programme, is grown on almost 50% of the national pearl-millet area, where the main limitations to crop yield are low rainfall, frequent drought and poor crop management (Rohrbach et al., 1999). Okashana 1 is early maturing, has good terminal-drought tolerance and is generally adapted to marginal environments. The development and dissemination of this variety resulted in a high value of internal rate of return in Namibia.

The S 35 sorghum variety has been described as a non-photoperiod-sensitive, high-yielding, early-maturing and drought-tolerant pure line; it originated from ICRISAT's breeding programme in India and was later advanced and promoted in Cameroon and Chad (Yapi et al., 1999). Its introduction into drought-prone areas of Chad has been very successful, resulting in an estimated yield advantage of about 51% over farmers’ local varieties and consequently in a very high internal rate of return (Yapi et al., 1999).

For chickpea, extra-early kabuli genotypes were developed at ICRISAT through the introgression of desi-kabuli, which matured in less than 3 months. Among these lines, the variety ICCV 2 was released in India as ‘Swetha’ and in Sudan as ‘Wad Hamid’ (http://grep.icrisat.org/archives/kabuli.htm). This variety has performed well in Egypt, Tanzania and Ethiopia. ICCV 2 is currently the world’s shortest-duration kabuli chickpea, able to grow fast on the conserved receding soil moisture and to mature before the moisture is depleted from the deeper soil layers. However, being an extra-short-duration variety, ICCV 2 has a limited yield potential, lower than the traditional desi types (Kumar and van Rheenen, 2000).

The chickpea line ICC 4958 was confirmed as a drought-tolerant source in many field trials, both at ICRISAT and by the Indian national agricultural research system (NARS) partners (Saxena, 2003). It also proved to be the most drought-tolerant in spring-planted chickpea in Mediterranean types of climate. Seven other varieties (ICCV 98901 to ICCV 98907) were developed in order to incorporate drought-tolerant traits in agronomically superior cultivars. Additional promising drought-tolerant, Fusarium-wilt-resistant lines developed with high yield are ICCVs 94916–4, 94916–8, 94920–3, 94924–2 and 94924–3 (Saxena, 2003).

Groundnut research on drought in ICRISAT has been mainly targeted on south Asia and West Africa. As the growing season is becoming short, particularly in West Africa, drought-escape and early-maturing genotypes have significantly contributed to maintaining crop productivity under terminal drought. Examples of groundnut varieties released in India are ICGS 11 and ICGS 37, which are tolerant to end-of-season drought. Other cultivars released with tolerance to mid-season drought in India include ICGS 44, ICGS 76 and ICG(FDRS) 10.

In pigeonpea, the adoption of the SDP cultivar ICPL 87 in southern India led to 93% yield gains, in addition to improved soil fertility and reduced production costs (Bantilan and Parthasarathy, 1999). Line UPAS 120, another SDP cultivar, released in northern India, has also shown great drought-tolerant levels (Chauhan et al., 1998). In addition to the short-term economic impact of its cultivation as a second crop in the post-rainy season, the widespread adoption of SDP improves long-term yield stability and system sustainability through the improvement of soil fertility.

**Future Thrust**

Integrated strategies for crop genetic improvement in drought-prone environments have recently been reviewed (CIMMYT, 2000). A
A framework for their specific application to ICRISAT mandate crops is outlined in Fig. 8.3. A systematic characterization of the SAT drought environments where the mandate crops are grown is still to be done, in order to enable adequate targeting of drought-resistant traits, using historical climatic series, GIS tools, water balance and crop-simulation models.

With improved knowledge of probable soil-moisture availability over time, it becomes easier to further exploit the drought-escape option, considering the spectrum of crop durations and germplasm available for all mandate crops.

The ideotype approach for incorporating the relevant drought-resistance traits requires a better knowledge of the physiological mechanisms involved in drought resistance and their genetic control. Simple mechanistic models that can reliably simulate crop growth and yield in different environments can also be used for the assessment of the putative drought-tolerant traits in a wide range of target environments.

Despite the methodological difficulties, genetic enhancement of root systems for more effective water extraction would seem a high-priority effort for rain-fed chickpea and ESDP. Dissection of root traits and development of a screening system relevant to field conditions are therefore needed, in parallel with extensive genotyping and the search for molecular markers. Other promising integrated traits for improving drought resistance and crop water productivity include the PNHI in pearl millet, stay-green in sorghum and transpiration-use efficiency in groundnut. There seems to be much scope for improving such characters, using QTL and molecular breeding techniques, aided by physiological characterization and conventional breeding, in order to significantly improve the ability of the mandate crops to withstand drought stress in defined target environments.

![Fig. 8.3. Framework of an integrated strategy for genetic enhancement of crop grain yield (GY) and its components under water-limited conditions at ICRISAT. TR, total plant water transpired; TE, transpiration efficiency; HI, harvest index.](image-url)
References


