8 Opportunities for Improving Crop Water Productivity through Genetic Enhancement of Dryland Crops

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Introduction

The importance of water as a major limiting factor in agriculture is increasing due to the unpredictable nature of rainfall and increasing demand for water from domestic and industrial users. In arid and semi-arid regions, which experience absolute or economic shortage of water, there is an urgent need to increase crop water productivity (CWP) at the farm level through genetic enhancement and natural resources management. Natural resources and agronomic management options for higher CWP are driven by several factors related to geographic location, governmental policies, crop preferences, marketing issues and involvement of external inputs, often inconvenient or not attractive to rainfed farmers. Because of scale and resource neutrality, the genetic options are amenable to quicker and wider adoption at farm level for increasing CWP.

Pearl millet (*Pennisetum glaucum*) and sorghum (*Sorghum bicolor*) (C_4 crops) and the legumes, groundnut (*Arachis hypogaea*), chickpea (*Cicer arietinum*) and pigeonpea (*Cajanus cajan*) (C_3 crops), occupy an important place in the cropping systems of seasonally dry arid and semi-arid tropics (SAT). Maize (*Zea mays*) is an important C_4 crop grown in tropical lowlands, tropical and subtropical mid-altitudes, where drought is a major limiting factor for its production and productivity. The C_4 crops have higher photosynthetic capacity and are more efficient in nitrogen and water use efficiency (WUE). The legumes fix nitrogen through symbiotic association with *Rhizobium* bacteria, and compensate to a large extent for their lesser WUE.

Rainfed Agriculture: Unlocking the Potential (eds S.P. Wani *et al.*)

Global warming due to climate change will affect grain yields, more so in tropical than temperate regions. The global average temperatures by the year 2100 could progressively rise by up to 6 °C under the business-as-usual scenario (http://www.fao.org/docrep/005/y4252e/y4252e15.htm). Reproductive traits are highly sensitive to high temperature, leading to yield reduction. For example, rice (*Oryza sativa*) grain yield declined by 10% for each 1 °C increase in minimum temperature in the dry season in the Philippines (Peng *et al.*, 2004). A projected 10% yield reduction in maize will bring losses equal to US$2 billion in Africa and Latin America (Jones and Thornton, 2003). The wheat (*Tritium aestivum*) yields in China are expected to decline by 20% in 2070 (Hui *et al.*, 2005), while in South Australia by 13.5–32% under the most likely climate change scenario (Luo *et al.*, 2005).

In this chapter, we discuss the target growing environments and crop sensitivity of pearl millet, sorghum, maize, groundnut, chickpea and pigeonpea to drought; phenotypic screens and natural genetic variations for response to drought; empirical and trait-based breeding methods to enhance drought tolerance; and deployment of emerging biotechnological tools (DNA markers and transgene) to enhance crop adaptation and productivity under drought-stress conditions.

Adaptation in Water-limited Environments

Crop productivity versus survival mechanisms

Response of most crops to soil water deficit can be described as a sequence of three successive stages of soil dehydration. 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 to keep transpiration rate similar to the uptake of soil water for maintaining the water balance of the plant. Stage III begins when the ability of stomata to adjust to the declining rate of water uptake from the soil has been exhausted, and stomatal conductance is minimal.

Virtually all major processes contributing to 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.*, 1999). At the end of Stage II, these growth-supporting processes have reached zero and no further growth occurs in the plants. The focus of Stage III is survival and water conservation, essential for the plant to endure these severe stresses. Plant survival is a critical trait in dryland ecosystems, but for most agricultural situations, Stage III has little relevance to increasing crop yield and water productivity, especially in the case of intermittent drought.

Consequently, the amount of water extracted up to the end of Stage II determines cumulative growth by plants on a particular soil water reservoir. Research on soil water use in crop growth dating >100 years has consistently shown an intimate and stable relationship between the plant growth and transpirational water use after correcting for variations in atmospheric humidity (Sinclair *et al.*, 1984). Therefore, options to enhance crop survival do not usually mean an increase in crop yield under drought conditions. Increased crop yields and water productivity require optimization of the physiological processes involved in critical stages (mainly Stage II) of plant response to dehydration.

Target environments and crop sensitivity to drought

Pearl millet

Post-flowering (also referred to as terminal) drought stress, either alone or in combination with pre-flowering drought, is common in major pearl millet-growing environments in India. Flowering and grain-filling periods are most sensitive to water stress in pearl millet (Mahalakshmi *et al.*, 1987). Yield reduction in this stage is due to decreased panicle number and grain mass. Usually, the number of grains per panicle is less affected if terminal stress occurs after flowering. The reduction in grain mass observed during terminal drought seems to be due to restriction of the assimilate supply rather than due to reduction of the grain storage capacity (Bieler *et al.*, 1993). Under very low water potentials, stomatal closure, and a consequent reduction in photosynthetic activity, has been reported in pearl millet (Henson *et al.*, 1984). However, the supply of assimilates through the mobilization of stored soluble sugars can compensate for the impaired photosynthetic activity (Fussell *et al.*, 1980). The transfer of assimilates from the leaves, with stems serving as a buffer during the grain development, appears to be the main adaptation trait during terminal drought stress in pearl millet (Winkel and Do, 1992). From a study involving normal and extended day length, Mahalakshmi and Bidinger (1985) suggested that photoperiod control of floral initiation can provide an escape mechanism to avoid the coincidence of mid-season water stress with sensitive stages of millet growth.

Sorghum

Terminal drought is the most limiting factor for sorghum production worldwide. In sub-Saharan Africa drought at both seedling establishment and grain-filling stages is very common. In India, sorghum is grown during both rainy and post-rainy seasons. The variable moisture environment during the rainy season can have a severe impact on grain and biomass yield, affecting both pre-flowering and post-flowering stages. Climatic variability and associated genotype × environment interactions do not permit clear definition of the target environments. Opportunities to make progress in breeding for drought tolerance lie both in understanding the environmental control of crop growth and in developing simplified approaches to modelling (Bidinger *et al.*, 1996).

Drought and/or heat stress at the seedling stage often results in poor emergence, plant death and reduced plant stands. Severe pre-flowering drought stress results in drastic reduction in grain yield. Post-flowering drought-stress tolerance is indicated when plants remain green and fill grain normally. The stay-green trait has been associated with post-flowering drought in sorghum. Genotypes with the stay-green trait are also reported to be resistant to lodging and charcoal rot.

Maize

Inadequate water availability at critical stages of crop growth and development is the major limiting factor for maize production and productivity in the tropics. Mean rainfall during the crop season appears to be adequate for maize production, but its distribution during the crop cycle has a high coefficient of variability. Normal interseasonal fluctuations in rainfall have been found to be associated closely with variations in average national maize yields across quite large production regions in the tropics (Edmeades *et al.*, 1995), suggesting that water stress is the pervasive cause of yield instability in maize-based cropping systems in the tropics.

Maize is particularly sensitive to water stress in the period 1 week before to 2 weeks after flowering. Stage-sensitivity in maize to drought stress has been studied extensively. Probability of drought in maize-growing environments in the tropics is highest at the start and end of the rainy season, and therefore the crop is prone to facing water deficit at establishment and flowering/grain-filling stages (Banziger *et al.*, 2000a). Monthly rainfall totals in the tropics have a high coefficient of variability, even though mean rainfall appears adequate for maize production. Although the probability of drought stress is lower at silking, its consequences on yield can be highly severe, since the crop is highly susceptible to drought at this stage (Shaw, 1976). Stress from mid- to late grain-filling also reduces grain yields but relatively less in comparison to silking-stage water deficit.

Drought at flowering commonly results in barrenness in genotypes having a longer anthesis–silking interval (ASI). One of the main causes is reduction in the flux of assimilate to the developing ear below some threshold level necessary to sustain grain formation and growth (Westgate and Bassetti, 1990; Schussler and Westgate, 1995). Drought coinciding with this growth period can cause serious yield instability at the farm level. Understanding the nature of the higher grain potential and enhanced yield stability, especially in stress-prone environments, will provide opportunities to improve the selection of stress-tolerant genotypes.

There is an increase in the ASI and a concomitant increase in the number of barren plants in maize under drought (Zaidi *et al.*, 2003a). A short ASI is considered an indication of the diversion of an increased fraction of the plant's current photosynthesis to the ear, since it is associated with rapid ear growth (Zaidi *et al.*, 2003b). Drought at flowering also affects carbohydrate metabolism of the developing ovule, further reducing sucrose flux to the newly formed seed (Schussler and Westgate, 1995).

Groundnut

The effect of drought on groundnut is manifested in several ways, affecting both quantity and quality of the crops (Nigam *et al.*, 2002). The three patterns of drought observed in groundnut are early-season, mid-season, and end-of-season drought. A 20- to 25-day moisture stress early in the season (once the crop is established) and its subsequent release by irrigation (or rainfall) has been found to induce heavy and uniform flowering, leading to increased productivity. Groundnut shows increased sensitivity to mid-season stress compared with early- and late-season stresses (Pallas *et al.*, 1979) (Fig. 8.1). Yield progressively decreases as duration of the drought increases and as the mid-season approaches. Water deficit during the late flowering and pod-forming periods is detrimental to groundnut yield (Stansell and Pallas, 1985). End-of-season drought affects seed development and its quality (Reddy *et al.*, 1994).

Moisture-stress timing and severity during flowering decreases the number of flowers and delays the time to flower. However, since only 15–20% of flowers form pods, reduction in flowering due to moisture stress does not directly influence pod yield (Nageswara Rao *et al.*, 1988). Also, groundnut can compensate for reduced flower numbers arising from water deficits by producing a flush of flowers once the stress is relieved (Pallas *et al.*, 1979; Nageswara Rao *et al.*, 1988). Soil water deficits during pegging and pod set decrease yield primarily by reducing pod number rather than seed mass per pod (Boote *et al.*, 1976), which is true only if there is sufficient water available for the production of assimilates at the later stage (Harris *et al.*, 1988). Owing to the subterranean fruiting habit of groundnut, a reduction in soil water content can have a dual effect on peg and pod development. While the root-zone water content can directly affect plant water status and photosynthesis (and hence assimilate supply to developing pegs and pods), the water content in the pegging and podding zones can affect reproductive growth independent of the root-zone moisture content. The pod-zone water content influences peg pene-

Fig. 8.1. Contrast among groundnut genotypes for early water use and wilting.

tration and conversion into pods, and calcium and water uptake by pods (Boote *et al.*, 1982).

Variability for maturity duration in groundnut germplasm offers the possibility of selecting genotypes with desired phenology to match the environment. In the regions where the growing season is longer, cultivars belonging to the Virginia type are generally cultivated; in areas where the season is shorter, Spanish and Valencia types are cultivated. With the perceivable changes in global temperature and rainfall patterns, it may become necessary to match genotypes more carefully to the length of growing season. For example, groundnut production in Nigeria has reduced drastically over the past few years because of severe droughts. The isohyets movement towards the south has resulted in the shortening of the period of useful rains in northern Nigeria. This has necessitated the shift from growing long-duration genotypes to short-duration genotypes (Gibbons, 1978). Agroclimatological analysis of major rainfed (75–90 days) groundnut environments in the SAT indicates that growing areas in the SAT are characterized by short growing seasons, i.e. 75–110 days (Virmani and Singh, 1986). This explains the better performance of short-duration genotypes in West African regions.

Chickpea

Characterizing drought in post-rainy season crops such as chickpea is relatively simple, compared with the intermittent drought experienced by the rainy-season crops. As the crop is grown almost entirely on stored soil moisture, it is exposed mostly to progressively increasing (terminal) water deficit. 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. Hence simulation modelling of both crop growth and the effects of various crop traits is eminently feasible.

Pigeonpea

Throughout the SAT regions of South Asia and Africa, where much of the pigeonpea is grown, rainfall is erratic in its amount and distribution. However, based on the long-term rainfall pattern, it is possible to broadly characterize patterns of drought in a given environment by calculating probabilities of dry periods followed by wet periods or vice versa (Virmani *et al.*, 1982). This assessment is helpful in developing genotypes for target environments or in identifying environments with similar drought patterns. 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. Since the late 1980s, short-duration genotypes have been developed, with extra-short-duration genotypes able to reach maturity within 90 days (Nam *et al.*, 1993). However, the short-duration genotypes are usually sensitive to intermittent drought. A pigeonpea simulation model (Robertson *et al.*, 2001) could also facilitate characterization of drought patterns for environments where long-term weather data is available.

Phenotypic Screens and Natural Genetic Variations for Drought Tolerance

Pearl millet

The line-source sprinkler irrigation method, earlier developed by Hanks *et al.* (1976), is used to screen pearl millet for drought tolerance. It provides gradients of drought stress, which allows the evaluation of large numbers of genotypes at varying intensity of drought in a given environment. 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 yield performance under stress is not related to time to 50% flowering, the drought susceptibility index (DSI) is calculated based on yield under rainfed conditions and potential yield under irrigated conditions (Fisher and Maurer, 1978). The lower the DSI, the greater is the drought tolerance. Bidinger *et al.* (1987a,b) modified the DSI method 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.

Grain yield in pearl millet 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 drought-tolerant lines in pearl millet include 863B, ICMP 83720, ICMV 94472 and PTRLT 2/89–33.

Sorghum

At the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India, sorghum is evaluated for post-flowering drought tolerance during the post-rainy season. The drought is imposed at flowering/grain development stage by withholding water and lines scored for stay-green trait using curve-fitting of green leaf area retention and/or leaf chlorophyll content (using Minolta Chlorophyll Meter SPAD 502) at regular time intervals. Promising accessions from the field evaluations are further tested for drought response and root traits using a lysimetric system where plants are grown in large and long PVC cylinders, mimicking roughly the soil volume that sorghum plants would have at the usual field planting densities. The plants are grown under well-watered conditions until booting, after which a water-stress treatment is imposed.

Drought-tolerant sources in sorghum include Ajabsido, B35, BTx623, BTx642, BTx3197, El Mota, E36Xr16 8/1, Gadambalia, IS12568, IS22380, IS12543C, IS2403C, IS3462C, CSM-63, IS11549C, IS12553C, IS12555C, IS12558C, IS17459C, IS3071C, IS6705C, IS8263C, ICSV 272, Koro Kollo, KS19, P898012, P954035, QL10, QL27, QL36, QL41, SC414–12E, Segaolane, TAM422, Tx430, Tx432, Tx2536, Tx2737, Tx2908, Tx7000 and Tx7078 (www.icrisat.org). Drought tolerance of M 35–1, a highly popular post-rainy-season-adapted landrace in India, has been demonstrated (Seetharama *et al.*, 1982).

Maize

Various options have been used for screening the germplasm for identification of relative tolerance to water-limited conditions (Bruce *et al.*, 2002). Growth chamber or greenhouse screening may provide highly precise management of intensity, uniformity and timing of stress treatment. However, the findings may have least repeatability in target population environments, which closely represent farmers' fields. These evaluations generally require multiple seasons and a large number of sample environments for judicious judgement on the performance of a cultivar in target environment. Statistical procedures such as genetic correlation among environments, genotype × environment interaction and stability analysis can help improve the process of establishing the reliability of prediction on the performance of genotypes in target population environments (Cooper and DeLacy, 1994).

Managed-stress environments under rain-free season may play an essential role in assuring reproducible stress conditions targeted at specific growth stages. At CIMMYT (International Maize and Wheat Improvement Center), genotypes are screened under three moisture regimes: (i) well watered, where moisture is maintained in the plots as per normal recommendation; (ii) intermediate water stress, where plants are exposed to drought stress during late flowering and throughout grain filling by withdrawing irrigation 1 week before flowering until maturity; and (iii) severe stress, where plants are exposed to drought stress during flowering and the early grain-filling stage by withdrawing irrigation 3 weeks before flowering. Each of the managed moisture conditions is able to expose genetic variation for specific traits. The well-watered condition allows expression of yield potential; the intermediate water-stress regime exposes genetic variation for lower leaf senescence and grain yield; and the severe stress regime exposes the variability for ASI and ears per plant. Selection for drought tolerance is based on grain yield, ASI, ears per plant, stay-green and tassel size, which have shown tremendous gains across the moisture regimes (Edmeades *et al.*, 2000).

The sources of drought tolerance in maize include 95TZEE-W, 95TZEE-Y, Ac7643, Ac7643S_5, Chang 3, CML 269/CML343, CML 449/CML 343, D 978, Danhuang 02, HI 209, HI 295, HI 536, HI1040, K 10, K 22, TSC 8, TZE-COMP 3 DT, X178, Xi 502, Ye 8001, Yedan-13 and Zheng 22 (www.cimmyt.org) (Fig. 8.2).

Fig. 8.2. Available genotypic variability for flowering-stage drought stress in tropical maize.

Groundnut

ICRISAT adopted a holistic approach in screening and selecting groundnut genotypes with superior performance under mid-season and end-of-season drought conditions (Nageswara Rao and Nigam, 2003). An empirical approach was first followed for selection among segregating populations and 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 is required for the selection of traits associated with drought tolerance. There has been significant improvement in physiological understanding of the genotypic response to drought 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 the total amount of water transpired (T) and transpiration efficiency (TE) has been shown (Wright *et al.*, 1994). Further studies have confirmed large cultivar differences in TE in groundnuts (Hubick *et al.*, 1988; Wright *et al.*, 1994). These studies enabled analysis of the yield variation under drought conditions using a physiological framework proposed by Passioura (1977), where HI = Harvest Index:

$$\text{Pod yield} = T \times TE \times HI$$

Research has also shown that TE and carbon isotope discrimination in leaf (CIDL) are well correlated (Wright *et al.*, 1988), suggesting the possibility of using CIDL as a rapid, non-destructive tool for selection of TE in groundnut. However, further research has shown that specific leaf area (SLA), expressed in cm^2/g, is well correlated with CIDL and TE (Wright *et al.*, 1994).

Several sources of tolerance to mid-season and/or end-of-season drought have been reported in groundnut that showed variation for physiological traits such as SLA, WUE, T, TE, and HI under drought-stress conditions (Dwivedi *et al.*, 2007a). Rucker *et al.* (1995) identified a drought-tolerant, high-yielding line, PI 315628, from pot/field experiments, with the largest root system and low in-canopy temperature.

Chickpea

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 method (Johansen *et al.*, 1994). The drought-tolerant chickpea accessions include Annigeri (high yield and short duration), ICC 4958 (large root, large seed, rapid partitioning), ICC 10448 (high yield, smaller pinnule, large sink), ICC 5680 (small leaf, fewer pinnules) and JG 62 (twin-podded, rapid partitioning) (Saxena *et al.*, 1993; Saxena, 2003). Kashiwagi *et al.* (2006) perfected a PVC-cylinder-based technique for screening chickpea root traits associated with drought tolerance. Root length density (RLD) at 35 days after sowing showed significant positive correlation with seed yield. Similarly, RLD at different soil depth (15–30 or 30–60 cm) had positive effects on seed yield, more pronounced under severe drought. RLD of plants grown in cylinders with 70% field capacity correlates well with RLD in the field trials. Using this technique, Kashiwagi *et al.* (2005) detected substantial variation in root-length density (RLD) in chickpea landraces collected from the Mediterranean and West Asian regions that showed better drought tolerance than of the known drought-tolerant genotype, ICC 4958. Promising drought-tolerant breeding lines/cultivars include ICCVs 94916–4, 94916–8, 94920–3, 94924–2, 94924–3, and 98901 to 98907, with yields similar to the high-yielding parent (Saxena, 2003).

Pigeonpea

The rainout shelter facility at ICRISAT has significantly improved the precision of drought screening. Chauhan *et al.* (1998) detected substantial genetic differences when they screened 32 pigeonpea lines for drought tolerance at flowering using DSI. ICPL 88039 showed greater drought tolerance than other genotypes. Pigeonpea hybrids ICPH 8 and ICPH 9 were the most drought tolerant and their reaction was further confirmed in multi-location trials.

The drought screening under the rainout shelter, though reliable, has limitations of space and that pigeonpea cannot be grown year after year at the same place. To overcome the latter problem, rainout shelters that can be moved to different places have been designed (Chauhan *et al.*, 1997).

Breeding programmes on pigeonpea in recent years have focused on developing genotypes of 90–150 days 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 considerable yield gap, which is largely due to the adverse effect of intermittent droughts in different environments (Nam *et al.*, 1993). The short-duration pigeonpea and extra-short-duration pigeonpea cultivars are generally shallow rooted (Chauhan *et al.*, 1993), and what they gain by being able to escape terminal drought stress is lost 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 an unstressed control (Nam *et al.*, 2001). In addition, large gaps within the rainy-season rainfall are not unusual in the semi-arid regions, when extra-short-duration and short-duration cultivars may be forced to grow with limited ability to extract water due to their shallow root system. Therefore, more work is needed for screening and selecting pigeonpea cultivars for intermittent drought tolerance.

Genetic Enhancement for Improved Water Productivity

Drought escape

Pearl millet

Drought escape is a major mechanism in pearl millet, determining relative cultivar performance in individual stress environments (Bidinger *et al.*, 1987a), often a major cause of genotype × environment interaction in multi-environment trials (van Oosterom *et al.*, 1996). For example, if rains end early, a 1-week difference in time to flowering between two cultivars is equivalent to about 30% of the grain-filling period, which enables an early flowering cultivar to escape stress (Mahalakshmi *et al.*, 1988).

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

Sorghum

Breeding for earliness has been successful for increasing the yield of rainy-season sorghums in India (Seetharama *et al.*, 1982). Earliness is more advantageous during the post-rainy season, although 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 an important adaptive trait, useful for matching the crop growth and development with the water-availability period.

Groundnut

In most of the groundnut-growing regions in the SAT, the rainfall distribution is erratic and the season length is less than 100 days (Virmani and Singh, 1986). Considerable progress has been made at ICRISAT in shortening the crop duration of groundnut without decreasing the realized yield substantially (Vasudeva Rao *et al.*, 1992). The short-duration varieties developed at ICRISAT have shown superior pod yield over local control varieties in several countries. The early-maturing genotypes usually have shallow root systems, which could make them more susceptible to intermittent drought and also result in 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 the scope for combining early maturity with efficient root system.

Chickpea

Short-duration varieties that mature before the onset of 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, reduction of crop duration below the optimum would have a yield penalty (Saxena, 1987). Depending upon the water availability, optimum crop duration for maximum yield would vary. Hence, varieties need to be matched with the length of growing period (Fig. 8.3). Significant progress has been made in developing improved short-duration chickpea varieties that mature in 80–90 days (Kumar *et al.*, 1996) and extra-short-duration varieties (<80 days), which provide options to grow chickpea in many prevailing systems and evolving new production systems, such as rice fallows (Kumar and van Rheenen, 2000).

Pigeonpea

Studies indicate that terminal drought usually reduces the 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 period of soil moisture availability. However, there is a large spectrum

Fig. 8.3. An extra-short-duration chickpea variety that escapes terminal drought.

of genotype duration available (Gupta *et al.*, 1989), and matching genotype duration with likely period of soil water availability ensures against terminal drought stress. Further, opting for a shorter-duration cultivar in a region does not necessarily mean a sacrifice in yield potential, as even extra-short-duration pigeonpea varieties can produce yields above 2.5 t/ha (Nam *et al.*, 1993).

Candidate traits for drought tolerance

Pearl millet

The panicle HI, i.e. the ratio of grain to total panicle weight, has been evaluated as a selection criterion for terminal stress tolerance in pearl millet breeding (Bidinger *et al.*, 2000). It is also currently used as one of the traits for which quantitative trait loci (QTLs) are being identified, from a mapping population made from parents that differ in the ability to maintain panicle HI under stress. Panicle HI, however, is readily and inexpensively measured in field experiments and can be used as a direct selection criterion. The main potential benefit to identifying QTLs for panicle HI 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 (Fig. 8.4).

Fig. 8.4. Good seed set in the long-panicle pearl millet varieties adds to drought tolerance.

Sorghum

Delayed senescence or stay-green is considered as a useful trait for plant adaptation to post-flowering drought stress, particularly in environments in which the crop depends largely on stored soil moisture for grain-filling (Fig. 8.5). Morphological traits associated with drought endurance and escape in sorghum include good seedling emergence and vigour, earliness, stay-green, tillering, pollination gap, better seed set and grain-filling, good panicle exsertion and reduced stalk lodging. Glossy trait in sorghum, characterized by light yellow-green leaves with a shiny surface, has been reported to confer a broad-spectrum tolerance to both biotic and abiotic stresses, including drought, high temperature, salinity, diseases and insects (Maiti, 1996). The glossy leaf surface is believed to be due to epicuticular wax. The majority of the 495 accessions with glossy trait identified at ICRISAT are from the Indian peninsula and belong to the taxonomic race *durra*. Many of the genotypes tolerant to drought at the seedling stage are glossy and recover faster once the stress is relieved (Maiti *et al.*, 1984).

Maize

Grain yield is commonly used as a selection criterion in crop improvement. However, inheritance of yield is complex and its heritability often declines under stress conditions (Bolaños and Edmeades, 1996). Selection on the basis of grain yield per se for improved performance under abiotic stresses has often been misleading and inefficient. Therefore, stress breeding programmes commonly use secondary traits, where heritability of some of these traits, such as ASI and ears per plant, remains relatively high, while the genetic and phenotypic correlations between grain yield and those traits increase sharply under drought and low nitrogen stresses (Bolaños and

Fig. 8.5. The stay-green trait provides enhanced drought tolerance in sorghum.

Edmeades, 1996; Banziger *et al.*, 1997). Edmeades *et al.* (1998) suggested that an ideal secondary trait should be: genetically associated with grain yield, highly heritable, genetically variable, cheap and fast to measure, stable within the measurement period, not associated with a yield penalty under unstressed conditions, easily observed at or before flowering in order to eliminate undesirable parents from being used in crossing, and a reliable estimator of yield potential before final harvest.

Key secondary traits for selecting drought tolerance include reduced barrenness on ears, ASI, stay-green, and to a lesser extent, leaf rolling (Banziger *et al.*, 2000c). Other traits such as root growth are only useful when they have been field-tested and have met the criteria prescribed for an ideal secondary trait. Roots have a very important role in water acquisition and a significant component of tolerance to water-deficit stress (McCully, 1999). When studying the relationship between early root development and grain yield under drought using recombinant inbred lines (RILs) differing in seedling root traits, the RILs with poorer early root development yielded better than those with more vigorous early root development (Bruce *et al.*, 2002). Using stress-adaptive secondary traits along with grain yield in maize has improved the selection gain in yield under low nitrogen stress by 20% in comparison to selection for yield per se (Banziger *et al.*, 1997).

Groundnut

Good scope exists for genetic improvement of the efficiency of crop water use in groundnut (Wright and Nageswara Rao, 1994). Significant genotypic variations in T and TE have been reported in groundnut (Wright *et al.*, 1988) (Fig. 8.6). Groundnut lines ICGS 76, ICGS 44, Tifton 8 and Kadiri 3 were identified with high TE values (Wright *et al.*, 1994). The extent of the root depth and RLD becomes important for soil water extraction during prolonged water deficit. Deep rooting and faster extraction may be very appropriate in tropical environments, where groundnut is grown solely on stored moisture in the dry season on high water-holding capacity soils (Prabowo *et al.*, 1990). Genotypic variability for root characteristics (root volume, root dry weight, root length and number) has been reported in groundnut (Ketring, 1984). However, only minor differences in water extraction patterns and total water use were observed among cultivars (Wright and Nageswara Rao, 1994).

Fig. 8.6. Characterization of the variation in transpiration across growing time of the reference collection of groundnut germplasm using a mini-lysimetric system.

Chickpea

Two important drought-avoidance traits have been characterized and widely used for the genetic enhancement of chickpea at ICRISAT: the large root system (which appears to be useful in greater extraction of available soil moisture) and smaller leaf area (which has been shown to reduce the transpirational water loss) (Fig. 8.7). 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 smaller leaf area, owing to either narrow pinnules (ICC 10480) or fewer pinnules (ICC 5680). Recombinants with traits of ICC 4958 and ICC 5680 showed higher midday leaf relative water content compared with the parents in field trials conducted at ICRISAT (Saxena, 2003).

End-of-season drought is often associated with increasing temperature (Calcagno and Gallo, 1993). Early pod set is considered a prime strategy for avoiding drought stress in environments prone to end-of-season moisture stress (Sedgley *et al.*, 1990). The development of early-maturing varieties may help drought escape and result in stabilizing productivity and assist in extending the chickpea crop to more drought-prone areas.

Pigeonpea

Several mechanisms seem to contribute to adaptation of pigeonpea to drought, which in some cases ensure only its survival but in other cases also have an effect on grain yield. These have been categorized under three strategies: (i) drought escape (e.g. phenological adjustment); (ii) drought avoidance (e.g. deep root systems, stomatal closure, leaf shedding and rolling, paraheliotropic movement, low epidermal conductance); and (iii) drought tolerance (osmotic adjustment, radiation use efficiency, photosynthesis, partitioning of assimilates). Important putative drought-tolerance traits for pigeonpea include early vigour, leaf area maintenance, high root and shoot growth rate, and development plasticity (Johansen, 2003). Early growth vigour is an important factor in drought

Fig. 8.7. Evaluation of chickpea germplasm for transpiration variability by use of a mini-lysimetric system.

resistance as it permits establishment of an effective root system that can extract water during later drought periods. 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 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 and leaf movements. Leaf area maintenance can be used as morphological marker in a breeding programme. Pigeonpea shows large genotypic differences for this trait (Lopez *et al.*, 1997). The short-duration genotype ICPL 87 performs better than its sister genotype, ICPL 151, which correlates with the greater leaf area retention of ICPL 87 under drought than ICPL 151.

Empirical and Trait-based Approaches to Enhance Drought Tolerance

Plant breeding provides a means of closing the gap between actual and potential yield in stressed environments (marginal and dry areas) through genetic manipulations (Acevedo and Ferreres, 1993). Crops, or cultivars within each crop, are replaced with others having a higher fitness in an environment gradient arising from uncontrolled physical limiting factors. Hence, farmers and breeders attempt to identify crop tolerance in these gradients arising from the specific abiotic stresses. However, the choice of the crop or cultivars within a crop in terms of ‘economic phenotype performance’ are driven by several intricate factors such as genotype, environment, crop management, policies (affecting both people and market), institutional arrangements and social demographics, which make the plant breeders’ job much more complicated (Ortiz *et al.*, 2002).

Pearl millet

Grain yield potential has been considered as a significant factor in determining the yield under moisture stress conditions as well (Bidinger *et al.*, 1982; Fussell *et al.*, 1991). Improvement in yield potential is expected to result in some improvement under moisture stress, especially under terminal stress and less severe stress conditions. However, this could not be validated under natural drought conditions during the main rainy season (Yadav and Weltzien, 1999). Breeding for wide adaptation has also resulted in selecting genotypes with drought tolerance, such as ICTP 8203 (in India), IKMP 3 and IKMP 5 (in Burkina Faso).

Considerable research has been conducted on the traits themselves, but there are few cases where an individual trait or mechanism has been shown to be sufficiently associated with yield to recommend it as a selection criterion (Mahalakshmi *et al.*, 1997). In pearl millet, ability to set and fill grains was found to be related to drought tolerance (Bidinger *et al.*, 1987a). Of all the responses related to drought tolerance in pearl millet, panicle HI (ratio of grain mass to the total panicle mass), which integrates both setting and filling of grains, was the best predictor. Therefore, panicle HI can be used as an inexpensive selection criterion in breeding for drought conditions in pearl millet. Panicle HI is a particularly effective variable for post-flowering stress, because the mass of the structural parts of the panicle (which complete their growth prior to flowering) is largely unaffected by stress, whereas the grain mass is significantly affected by both floret abortion and reduced grain-filling (Bidinger and Mukuru, 1995). However, the analysis of predicted response to selection for panicle HI did not indicate that panicle HI would be an effective indirect selection criterion for improved yield under stress in the test-crossed mapping population lines. This is in contrast to the results achieved in the actual selection experiments. This suggests that the requisite (genetic) preconditions for panicle HI to be an effective indirect selection criterion for improved terminal stress tolerance need to be clearly defined.

Sorghum

Breeding for drought tolerance could be linked either to drought-resistance mechanisms and/or to yield. At ICRISAT, a combination of these two approaches with pedigree selection is followed. The drought-tolerant lines selected under mild stress showed high yield potential in stress-free environments; thus it is possible to select for drought tolerance without a concomitant yield decrease in non-stress environment (Rosielle and Hamblin, 1981).

Selections for yield and wide adaptation, determined on the basis of multi-location testing, may or may not be useful in selecting for drought tolerance as the nature, severity and duration of drought stress vary with soil type and weather variables. There is, therefore, a need for a wide range of cultivars and fine-tuning at local levels. Higher green leaf area, delayed onset of leaf senescence, and reduced rate of leaf senescence have been suggested to improve yield under terminal drought situations (Hammer and Muchow, 1994). An approach to breeding for drought tolerance and yield potential at ICRISAT includes: (i) selecting breeding materials for specific traits such as emergence under soil crust; (ii) seedling drought recovery, and grain yield under drought-prone and high-potential areas for early-stage drought; (iii) drought recovery for grain yield under drought-prone and high-potential areas alternatively for mid-season drought; and (iv) stay-green, non-lodging and grain yield under drought-prone and high-potential areas alternatively for terminal drought (Reddy, 1986).

Sorghum hybrids are known to have reduced growth duration, due to higher growth rates, and increased HI (Blum *et al.*, 1977), and early-maturing genotypes have shown relative yield advantage under late-season moisture stress (Saeed and Francis, 1983; Saeed *et al.*, 1984). Selection for improved productivity under water-stress conditions resulted in a genetic shift towards early flowering but with some yield penalty. Nevertheless, the increased yield potential coupled with greater vigour and earliness of hybrids has been very well exploited to breed for drought tolerance through escape mechanism. The rainy-season hybrids rapidly became the primary components of various production systems in India because of their higher productivity, wider adaptability, short duration and stature (Rana *et al.*, 1997). Under terminal water stress during the post-rainy season, early-maturing sorghum genotypes produce equal grain but less dry matter than late-maturing cultivars. Some popular sorghum hybrids with higher water productivity include CSH 8, CSH 18, CSH 16 and JKSH 22. The superior performance of sorghum hybrids over varieties in semi-arid dry areas has been demonstrated in several countries (Kebede and Menkir, 1987; House *et al.*, 1997). Hybrids perform better than varieties under moisture conditions, and also recover faster when moisture stress is released (Osmanzai, 1994).

The stay-green trait expresses best in environments in which the crop is dependent on stored soil moisture but where this is sufficient to meet only a part of the transpiration demand. Sufficient expression of the trait for selection is thus dependent upon the occurrence of a prolonged period of drought stress of sufficient severity during the grain-filling period to accelerate normal leaf senescence but not of sufficient magnitude to cause premature death of the plants (Mahalakshmi and Bidinger, 2002). The stay-green trait from IS 12555 (SC 35) has been successfully used in Australia to develop post-flowering drought tolerance and lodging resistance in parental lines and commercial hybrids (Henzell *et al.*, 1992). Conventional breeding for stay-green has been primarily based on B 35 and KS 19 (Mahalakshmi and Bidinger, 2002). The partially converted (B 35) and fully converted (SC 35C-14E) versions of IS 12555 (Rosenow *et al.*, 1983) have provided the best sources of the trait used in the Australian programme (Henzell *et al.*, 1997). Sorghum hybrids containing the stay-green trait yield significantly more under water-limited conditions compared with hybrids not possessing this trait (Rosenow *et al.*, 1983; Borrell and Douglas, 1996). This advantage is reported to be due to maintenance of photosynthetic capacity and reduced mobilization of stem reserves to grain during the late grain-filling period, combined with lodging resistance (Borrell and Douglas, 1996). In this study, stay-green was not associated with lower HI, as was reported in an earlier study (Rosenow *et al.*, 1983).

Maize

Plant breeders traditionally evaluate their advanced materials in a range of environments. The approach relies on multiple tests of progenies in the environments representing a random selection of the variation in drought stress in the target environment and selection largely on the basis of grain yield (Rosielle and Hamblin, 1981). More recently, Zaidi *et al.* (2004) have demonstrated that with conventional selection under optimal conditions it is likely that some of the best materials with tolerance to drought and/or low-nitrogen stress might have been rejected, while other less desirable materials for marginal and less favourable environments are selected on the basis of their superior performance under optimal input and favourable environments. Plant response to limited water conditions in terms of drought-adaptive traits is only expressed when they are exposed to such conditions, and genetic variability can be identified. Castleberry *et al.* (1984) examined Corn Belt hybrids developed under optimal input conditions from a period of more than 50 years and found very low selection gains under low soil fertility. Similarly, Martinez-Barajas *et al.* (1992) reported that progress from selection for high yield under well-watered conditions was greatly reduced under water-deficit conditions. These results suggest that positive spillover effects from selection under optimal conditions to stress conditions may be limited. Duvick (1995) proposed that the major goal of the tropical maize improvement programme should be to improve and stabilize yield, and broaden adaptation through increased tolerance to various abiotic stresses. For areas where the average maize yield is less than 2.0–2.5 t/ha, selecting genotypes for high yield in these target environments is preferred (Fig. 8.8).

While comparing the suitability of managed-stress versus multi-location testing for improving drought tolerance in maize, Byrne *et al.* (1995) concluded that evaluating the genotypes under managed drought stress, rather than that which occurs randomly during multi-location testing, is relatively more effective and efficient in selecting maize germplasm for water-deficit tolerance. Elapsed time per selection cycle is often less when testing under a few managed environments than under multi-location testing at several sites. Use of modern experimental designs, such as alpha lattices or row and column designs, can further increase selection efficiency (Yau, 1997). Relating the environmental classification, crop modelling and the identification of the target population environments the crop encounters over time suggests

Fig. 8.8. A high-yielding CIMMYT maize hybrid at ICRISAT campus.

that considerable gains can be expected in this area (Chapman *et al.*, 2000).

Recurrent selection for drought tolerance

CIMMYT has made a concerted attempt to select and improve mid-season drought tolerance in tropical maize and identified 50–80 best-performing families that produced high grain yield across the water-stress regimes, small ASI and delayed foliar senescence under severe and intermediate stresses, and adequate yield and small tassels under well-watered conditions (Byrne *et al.*, 1995).

Edmeades *et al.* (1994) demonstrated that gain in yield across two populations (La Posta Sequia and Pool 26 Sequia) averaged 259 kg/ha (12.4% per cycle) under drought, and 115 kg/ha (1.5% per cycle) under well-watered conditions. Yield improvements under drought were paralleled by increases in ears per plant (0.075 per cycle) and in HI, while ASI declined (1.3 days per cycle). Principal component analysis of yields in the ten different environments showed that well-watered and drought environments were generally orthogonal, which indicates that selection only in well-watered environments is unlikely to give improvements in yield under drought. They concluded that selection for drought tolerance has improved broad adaptation, as well as specific adaptation to dry environments. Further studies under two water regimes (well watered and severe drought stress) revealed that yield gains in La Posta Sequia and DTP (drought-tolerant population) averaged 218 and 239 kg/ha/cycle under drought and 55 and 41 kg/ha/cycle under well-watered conditions, respectively. Yield improvements under drought were paralleled by increases in ears per plant and HI, while ASI declined (Srinivasan *et al.*, 2003). Bruce *et al.* (2002) also reported average improvement in grain yield of 126 kg/ha/cycle, following recurrent selection under drought conditions.

Gains from multi-environments evaluation

Zaidi *et al.* (2004) examined the performance of hybrids of DTP across stress (drought and low nitrogen) and unstressed environments. The normal single cross (NSC) hybrids were slightly better than DTP topcrosses under unstressed conditions. However, under stressed conditions NSC hybrids performed very poorly. The NSC hybrids yielded only 3.3–4.8% under drought and 34.8–36.2% under low nitrogen, while DTP hybrids yielded up to 31.8–42.4% under drought and 48.9–63.6% under low nitrogen. Improved performance of DTP hybrids across the environments was related to improvements in secondary traits under stress conditions: reduced ASI, increased ears per plant, delayed senescence and relatively high leaf chlorophyll. Correlation and regression analysis showed a strong relationship between grain yield under drought and low-nitrogen stress in the germplasm improved for mid-season drought tolerance. However, the relationship was not significant with germplasm improved for yield per se under optimal conditions.

The improved sources from CIMMYT exhibited an equally good level of drought tolerance in Southern Africa, and when introgressed in local germplasm, the newly developed hybrids have shown superior and stable performance across the wide range of growing conditions in Southern and eastern Africa. The open-pollinated varieties developed using these source germplasms showed 35% superiority over commercial hybrids under moderate to severe levels of water stress (Banziger *et al.*, 2000b).

Improved drought tolerance using stress-adaptive traits

Several traits for drought and low-nitrogen tolerance in maize were evaluated and their value as a secondary trait assessed (Bolaños and Edmeades, 1996; Banziger *et al.*, 1997), and a few traits with proven value in selection for drought tolerance were used extensively for improving maize productivity under limited moisture conditions.

EARS PER PLANT Drought at flowering causes severe barrenness and destabilizes the grain yield. Ability of a genotype to produce an ear under such adverse conditions is certainly an important characteristic of drought tolerance in maize. More than 75% of the yield variation under drought was accounted for by variation in the number of ears and kernels per plant (Bolaños and Edmeades, 1996; Edmeades *et al.*, 2000). Grain yield under drought stress showed a strong relationship with ears per plant (r = 0.90 ± 0.14) and, across the trials, a strong curvilinear relationship with ears per plant ($r^2 = 0.94^{**}$). Being highly heritable (Bolaños and Edmeades, 1996; Edmeades *et al.*, 2000) and having a stronger relationship with grain yield, ears per plant has been used as a trait in the selection for water-limited environments and is important in the selection index for drought tolerance (Banziger *et al.*, 2000a).

ANTHESIS–SILKING INTERVAL The ASI is a symptom of ear growth rate, and the difference in ASI among genotypes growing in the same environment reflects differences in partitioning efficiency to the ear. The genetic correlation between grain yield and ASI in a diverse array of genotypes grown under drought at flowering is about −0.6 (Bolaños and Edmeades, 1996; Edmeades *et al.*, 2000), and the strong curvilinear relationships observed with yield under severe drought stress suggest that ASI is a visual indicator of underlying processes affecting reproductive success. Recurrent selection for mid-season drought tolerance in several diverse tropical maize populations at CIMMYT over two to ten cycles has increased grain yield under stress by about 100 kg/ha/year and reduced ASI by 0.6 days/year. Reduction in ASI was associated with decline in spikelets per ear, increase in rate of ear growth, spikelets and silk growth, and increase in HI (Edmeades *et al.*, 2000).

LEAF SENESCENCE Studies at CIMMYT revealed little adaptive value of this trait because of lack of association between green leaf area longevity and grain yield and the apparent lack of progress in selecting for delayed senescence (Bolaños *et al.*, 1993). Nevertheless, delayed senescence and stay-green is an important trait under drought stress, indicative of plant water status, and is useful for selection of maize genotypes under drought stress, although relatively less weight is given in the selection index (Banziger *et al.*, 2000a). The stay-green characteristic of maize facilitates a long grain-filling period and a long duration of harvesting in silage varieties (Choi *et al.*, 1995). Bekavac *et al.* (1998) detected highly significant genetic and phenotypic correlations between stay-green, stalk water content, leaf water content, vegetative period and grain moisture in two synthetic maize populations (Syn103NS and Syn140NS), with most consistent genetic correlations established between stay-green and leaf water content (r = 0.85–0.90).

TASSEL SIZE The maize plant is a prolific pollen shedder, and a vigorous maize plant can produce

25 million pollen grains, which is much more than required for pollinating the 500–1000 ovules present in a female flower (cob). The tassel has no role to play after completion of pollination. A small-sized tassel is preferred to reduce the sink competition, particularly when there is high competition for limited assimilates under stressed condition. A negative correlation between tassel size and grain yield under drought was observed in tropical maize populations (Bolaños and Edmeades, 1996). Tassel size is a highly heritable trait and can be easily altered by selection (Fischer *et al.*, 1987). Eight cycles of recurrent selection for mid-season drought tolerance resulted in a reduction of (−0.45) primary tassel branches per plant and tassel biomass (−2.6%) per cycle, although the trait was not under direct selection (Bolaños and Edmeades, 1993). In another study, direct selection for reduced tassel branches led to a significant increase in female inflorescence biomass at 50% silking, a reduction in tassel biomass and an increase in HI (Fischer *et al.*, 1987). These findings indicate that reduced tassel size in tropical maize is directly associated with increase in ear growth at flowering and in HI.

Groundnut

The segregating populations, derived from crosses involving known drought-tolerant germplasm and widely adapted high-yielding cultivars, are generation-advanced/evaluated under rainfed conditions at ICRISAT, Patancheru, India. The advanced breeding lines are yield tested in both rainy (rainfed conditions at ICRISAT (Patancheru) and Anantapur, India) and post-rainy (simulated mid-season stress conditions at ICRISAT (Patancheru)) seasons in replicated trials. The promising drought-tolerant varieties identified on the basis of their pod and seed yield, after 3 years of evaluation, are included in the international drought trial, tested by cooperators in Asia and Africa. From such evaluation, we identified ICGVs 87354, 86187 and 86647, which consistently outyielded controls in acute drought-prone areas in India, and ICGV 86635 in Thailand and Indonesia (Reddy *et al.*, 1994). ICGV 87354 has been shown to possess higher T, TE and HI (Rachaputi and Wright, 2003), contributing to its higher performance under water-limiting conditions. Further, simultaneous evaluations for drought tolerance under imposed drought conditions at ICRISAT revealed that ICGSs 11, 37, 44 and 76, ICG (FDRS) 10 and ICGV 86021 are drought tolerant. The first four varieties were released in India, the fifth in India and Myanmar, and the sixth in Indonesia.

Short-duration, high-yielding groundnut cultivars are required for many agroecological situations in the SAT. Using predetermined cumulative thermal time as a basis to select for earliness (Vasudeva Rao *et al.*, 1992), ICRISAT developed several short-duration varieties, with potential to escape terminal drought; some of these varieties have been released for cultivation in some countries (Fig. 8.9).

New breeding approaches utilizing physiological traits have been proposed to improve the understanding and efficiency of selection of superior drought-tolerant genotypes. Variations for T, TE and HI have been reported in groundnut. More recently, it has been shown that the negative association observed between TE and HI can be broken, thus offering scope to combine TE and HI in groundnut for improved yield performance. Interestingly, genotypes involving ICGSs 44 and 76 or ICGVs 86754 and 87354 in their pedigrees, all reported to be tolerant to drought, had superior yield performance because of higher TE and HI or all the three traits, while for the other genotypes, the dominant contribution to the yield was from T and/or HI (Rachaputi and Wright, 2003). There is therefore scope for pyramiding physiological traits associated with drought tolerance into improved genetic background. Yield performance of some of these selected lines was superior even under irrigated conditions (Nigam *et al.*, 2002), indicating that the physiological traits such as TE and HI could be used as a selection criterion for high water productivity under irrigated conditions and in high rainfall areas.

The CIDL and SLA have been identified as surrogate traits associated with TE in groundnut. SLA is a crude but easily measurable parameter, and can be used as a rapid and inexpensive selection criterion for high TE. Further, it has been demonstrated that SPAD chlorophyll metre readings (SCMR) serve as a rapid, low-cost and non-destructive technique to screen large breeding populations for SLA

Fig. 8.9. Drought-tolerant groundnut varieties enhance adaptation to varied cropping systems.

(Nageswara Rao *et al.*, 2001) and specific leaf nitrogen (Madhava *et al.*, 2003). Screening of groundnut germplasm for SLA indicated significant variability within and between taxonomic groups of groundnut. Genotypes belonging to the variety *hypogaea* (Virginia bunch and runner types) had a lower mean SLA than those of variety *fastigiata* (Valencia and Spanish types), suggesting the likelihood of higher TE. However, the former had lower partitioning ability than the latter. Groundnut genotypes with lower SLA (high TE) have shown more stability in dry matter production under drought (Nigam *et al.*, 2002).

Chickpea

One way for the chickpea crop to escape end-of-season drought is to develop varieties with early growth vigour, early flowering and early maturity (Calcagno and Gallo, 1993). Kumar *et al.* (1985) developed an extra-early chickpea, ICCV 2, from a transgressive segregant of a cross involving five chickpea lines (Kumar and Abbo, 2001). A major recessive gene, *efl-1*, responsible for about 3 weeks difference in flowering time has been identified (Kumar and van Rheenen, 2000). A super-early chickpea segregant, ICCV 96029, which flowers about a week earlier than either of the parents, was selected from a cross involving two extra-early varieties (Kumar and Rao, 1996). These early-flowering genotypes will be useful in combining earliness with other drought-tolerance traits to develop genotypes with stable yields.

Pigeonpea

Short- and extra-short-duration pigeonpea

Pigeonpea in India is traditionally grown during the rainy season (180–270 days duration) as an intercrop. However, since the late 1970s it has been shown that genotypes of shorter duration (120–150 days), when grown during the rainy season, can give yields similar to, or even higher than, long-duration genotypes in northern India (Saxena and Yadav, 1975). In Australia, properly managed photoperiod-insensitive genotypes could produce grains up to 8.8 t/ha (Wallis *et al.*, 1983). The development and release of short-duration pigeonpea varieties that mature in about 120 days has helped the expansion of the crop to newer areas (Singh *et al.*, 1990). These varieties are relatively insensitive to photoperiod and show high per day productivity.

Pigeonpea hybrids

The world's first pigeonpea hybrid (ICPH 8), based on genetic male sterility, was released in 1991 for cultivation in India, with 20–34% yield advantage (Saxena, 2002). ICPH 8 also showed drought, disease and waterlogging tolerance (Saxena *et al.*, 1996). Further, using short-duration male sterile lines (Reddy *et al.*, 1995), the Indian programme released five short-duration hybrids (COPH 1, COPH 2, PPH, AKPH 2022 and AKPH 4104), with 11–64% yield advantage over the controls (Saxena, 2002). These hybrids have revealed a higher seedling vigour, crop growth rate and pod/seed density, and higher plasticity with no yield reduction at suboptimal population levels compared with controls (Fig. 8.10) (Saxena *et al.*, 1992).

Enhancing Drought Tolerance Using Biotechnological Tools

Introgression breeding using wild relatives

Wild relatives of groundnut, chickpea and pigeonpea are endowed with important traits necessary for the improvement of the three legumes: *Arachis glabrata*, *Arachis cardenasii* and *Arachis pintoi* in groundnut with multiple resistance to drought, diseases and insects (Fisher and Cruz, 1994); *Cicer stapfianum*, *Cicer subaphyllum* and *Cicer pungens* in chickpea with drought tolerance and deep root system (van der Maesen, the Netherlands, personal communication); and *Cajanus acutifolius* and *Cajanus confertiflorus* in pigeonpea with silvery hairs, which confer drought tolerance (van der Maesen, 1986). Some of the above wild species are cross compatible with their respective cultigens, and work is in progress at ICRISAT to introgress drought-tolerance traits into improved genetic background in these legumes. An interspecific derivative in chickpea, BG 1103 (renamed as Pusa 1103), has been released for cultivation in northern India because of its high yield and tolerance to fusarium wilt and drought (Abbo *et al.*, 2007).

Marker-aided introgression of QTL associated with drought tolerance

Pearl millet

Linkage groups (LG) 2, 4 and 6 are reported to harbour several QTLs associated with drought tolerance, flowering, stover and grain yield, panicle numbers, HI, and panicle HI, with some common QTL across stress environments and tester backgrounds (Yadav *et al.*, 2002, 2003,

Fig. 8.10. Hybrid pigeonpea cultivars have shown better drought tolerance.

2004). Bidinger *et al.* (2005) demonstrated that QTL-based hybrids outyielded under stress but with yield penalty under non-stress environments. More recently, Bidinger *et al.* (2007) identified three QTLs as primary candidates for marker-assisted selection (MAS) for improved grain yield across variable post-flowering moisture environments. The QTLs on LG2 and LG3 also co-mapped with QTLs for HI across environments for grain numbers and individual grain mass under severe terminal stress. Neither had a significant QTL × environment interaction, indicating their predictive effects should occur across a broad range of available moisture environments. ICRISAT has initiated a large-scale marker-aided breeding programme to enhance post-flowering drought tolerance in pearl millet.

Sorghum

An integrated, interactive sorghum linkage map based on all available published information, incorporating RFLP (restriction fragment length polymorphism) and SSR (simple sequence repeat) marker locus positions as well as approximate map positions of stay-green QTLs, has been developed and made available globally (www.icrisat.org). Post-flowering drought in sorghum is associated with the stay-green phenotype. Xu *et al.* (2000) reported several QTLs with large effects for stay-green and chlorophyll content under post-flowering drought-stress environments; few QTLs for stay-green coincided with the chlorophyll content QTL. Some of the sorghum stay-green QTLs also corresponded with stay-green QTLs in maize and were congruent with other drought-related traits in maize and rice (Kebede *et al.*, 2001). More recently, Harris *et al.* (2007) demonstrated that some of the sorghum stay-green QTLs individually reduced post-flowering drought-induced leaf senescence when near-isogenic lines (NIL) containing individual QTLs were evaluated under drought-stress environments. ICRISAT initiated marker-assisted backcross to transfer stay-green QTLs with major effects from stay-green donors (B35 and E 36–1) into a range of diverse genotypes from Asia, Africa and Latin America (Fig. 8.11). Thus there is now an opportunity to assess the efficacy of marker-assisted backcrossing for this trait, which can be scored phenotypically only under conditions of terminal drought stress.

Fig. 8.11. Expression of stay-green trait (in sorghum) under receding soil moisture conditions in a vertisol.

Maize

Large numbers of QTLs associated with grain yield, yield components, and for secondary traits such as ears per plant, ASI and leaf abscisic acid concentration (L-ABA) have been reported in maize under different water regimes including severe drought stress. QTLs for leaf growth co-localized with QTLs for ASI (Welcker *et al.*, 2007). QTLs for seminal root growth co-localized with QTLs for grain yield and drought tolerance index (Tuberosa *et al.*, 2002). Giuliani *et al.* (2005) field evaluated near-isogenic hybrids containing a major QTL for L-ABA for 2 years under well-watered and water-stressed conditions. They reported that the QTL allele for high L-ABA markedly reduced stomatal conductance and root lodging. Across water regimes, the QTL confirmed its effect on L-ABA and showed a concurrent effect on root angle, branching, number, diameter and dry weight. This QTL affects root lodging through a constitutive effect on root architecture. Landi *et al.*

(2005) validated a major QTL for L-ABA that affects root traits and relative water content. Tuberosa *et al.* (2003) reported several chromosome regions affecting root traits and grain yield under well-watered and/or drought-stressed conditions, with most important QTL effects on few chromosome bins. Two QTLs with major effects on yield and stay-green under post-flowering drought had pleotropic effects on yield under non-stressed conditions (Sari-Gorla *et al.*, 1999).

More recently, Ribaut and Ragot (2007) demonstrated that introgression of favourable alleles at five target regions, involved in the expression of yield components and flowering traits, increased grain yield and reduced the asynchrony between male and female flowering under water-limited conditions. They recovered 85% of the recurrent parent's genotype at non-target loci only in four generations of marker-assisted backcrossing (MABC) by screening large segregating populations for three of the four generations. Mean grain yield of MABC-derived hybrids was consistently higher than that of control hybrids under severe water stress. Under those conditions, the best five MABC-hybrids yielded, on average, at least 50% more than the control hybrids. However, under mild stress, defined as resulting in <50% yield reduction, no difference was observed between MABC-derived hybrids and the control hybrids, confirming that genetic regulation for drought tolerance is dependent on stress intensity.

Groundnut

Krishnamurthy *et al.* (2007) evaluated TE in a set of 318 RILs, derived from a cross between a high TE (ICGV 86031) and a low TE (TAG24) parent, using SLA, SCMR and carbon isotope discrimination (δ^{13}) as surrogate of TE under progressive soil drying in a pot culture. Large and consistent variation exists for TE in this population; however, surrogate traits turned out to relate little (r <0.13–0.15) with TE. New sources of drought tolerance have been identified, which need to be further assessed for drought-tolerance traits. A new set of SSR markers has been generated, which is currently being assessed to identify genetically diverse, drought-tolerant parents for developing new mapping populations.

Chickpea

Research efforts have been made at ICRISAT to characterize and map QTLs associated with drought-avoidance root traits. RILs involving ICC 4958 (a genotype with large roots) and Annigeri, when evaluated under terminal drought conditions, showed large variations for rooting depth and root biomass at 35 days after sowing, shoot biomass and seed yield at maturity, and partitioning. However, no direct relationship between seed yield and root depth or root biomass could be established from this study, probably owing to moderate drought intensity observed during the crop season. The root-trait benefits on the yield were clearly shown to be visible in environments with a productivity level of <1.0 t/ha (Saxena, 1987).

New sources of genetic variation, ICCs 1431, 8350, 15697, 3512 and 11498, with deep root traits and drought tolerance have been identified (Kashiwagi *et al.*, 2005). New mapping populations involving ICC 8261 and ICC 4958 (large root) with ICC 283 and ICC 1882 (small root) have been developed, and the F_1, F_2, BC_1 and BC_2 populations are being analysed for the estimation of genetic components and evaluated for root traits and field agronomic performance. A large number of SSR markers are now available to genotype these populations using ABI3700 at ICRISAT. A major QTL contributing to one-third of variation for root length and root biomass has been identified (Chandra *et al.*, 2004).

Association mapping

Conventional linkage mapping for identification of trait markers relies on the development of defined genetic populations: NILs, RILs and advanced backcross derivatives. The development of such populations takes several years and is expensive, and the resultant markers must be validated in diverse populations before application in breeding programmes. Therefore, there has been considerable interest in the development of methodologies that do not require the creation of mapping populations and generate markers that can be more immediately applied in diverse breeding programmes. Linkage disequilibrium analysis is an alternative means of identifying a close association between trait (such as drought tolerance) and marker loci. It relies on population-level associations among alleles at trait loci and those at nearby markers. Such associations typically arise when all or most of the trait alleles in a population share a common ancestral origin. This approach is based on the use of natural populations rather than genetic populations, which has the added advantage that the resultant marker tends to be both genetically and physically close to the gene of interest and, therefore, more readily applied in a diverse range of breeding programmes. Marker-trait association using this approach has been established in crop plants (Dwivedi *et al.*, 2007b). However, this approach has its own limitation with respect to population structure, which needs to be taken care of to avoid false discovery.

Transgenic

Maize

AtNF-YB1, a transcription factor from the nuclear factor Y (NF-Y) family, confers improved performance in *Arabidopsis* under drought conditions. Nelson *et al.* (2007) identified maize homologues (ZmNF-YB2) of AtNF-YB1, which they used to transform inbred elite maize. The transgenic maize plants constitutively expressing ZmNF-YB2 showed less leaf rolling, cooler leaf temperature and a higher chlorophyll index, photosynthetic rate and stomatal conductance; all these stress-adaptive traits contributed to grain yield advantage under water-limited environments. The best-performing transgenic lines produced about 50% increase in grain yield relative to the irrigated control. Qin *et al.* (2007) isolated *ZmDREB2A*, a *DREB2* homologue from maize, which is induced in response to cold, drought, salt and heat stresses in seedlings. Maize transgenic lines with *ZmDREB2A* improved drought and heat-stress tolerance, which could be due to induction of late embryogenesis abundant protein (LEA), heat shock and detoxification genes.

Glycine betaine plays an important role in confering abiotic stress tolerance in some plants including maize. Quan *et al.* (2004) transformed a maize inbred line with the beta gene from *Escherichia coli* encoding choline dehydrogenase, a key enzyme in the biosynthesis of glycine betaine from choline. The transgenic plants accumulated higher levels of glycine betaine, were more tolerant to drought, and produced significantly higher grain yield than wild-type plants after drought treatment. The enhanced glycine betaine accumulation in transgenic plants provides greater protection of the integrity of the cell membrane and greater activity of enzymes compared with wild-type plants under drought stress.

Groundnut

Water use efficiency under drought conditions is one of the promising traits to improve and stabilize crop yields under drought conditions. The recent work at ICRISAT revealed that when a popular groundnut cultivar, JL 24, was introduced with *DREB1A* from *Arabidopsis* (through *Agrobacterium tumefaciens*), driven by the stress-inducible promoter *rd29A*, the transgenic plants did not show growth retardation. When T3 progenies were exposed to progressive soil drying in a pot-culture experiment, all the transgenic plants were able to maintain a transpiration rate equivalent to the well-watered control in soil dry enough to reduce the transpiration rate in wild-type JL 24, with most of these plants achieving higher TE. One of the plants under water-limited conditions showed 40% higher TE than the wild-type JL 24 (Bhatnagar-Mathur *et al.*, 2007). Vadez *et al.* (2007) reported that *DREB1A* seems to be involved in the development of groundnut roots under drought conditions, as they noted excessive root growth in transgenic plants whereas roots remained unchanged in wild-type JL 24, which resulted in higher water uptake from the soil.

Conclusion

Globally, the five ICRISAT crops and rainfed maize play a predominant role in enhancing the rural livelihood opportunities in arid and semi-arid regions, which experience acute water shortage. A combination of approaches has been employed to enhance the adaptation of these crops under drought conditions. These include matching the genotypes to the environment, developing short-duration varieties, selecting for stable yield and wide adaptability, screening and breeding under water-limiting environments and/or imposed stress conditions, and employing cultivar options (varieties versus hybrids). However, these approaches have resulted in moderate success in breeding cultivars that have given enhanced water productivity under drought conditions.

Recently, a more focused research on drought has enabled researchers to identify simple and effective traits associated with drought tolerance. For example, panicle HI and individual grain mass in pearl millet; glossy and stay-green in sorghum; deep root in chickpea; T, TE and HI in groundnut; and ASI, ears per plant, leaf senescence and tassel size in maize. Using these approaches, several genetically enhanced products have been developed, some of which have reached the farmers' fields.

Recent advances in genome mapping have enabled researchers to apply DNA markers technology to dissect the genetic structure of the germplasm collection, identify QTLs associated with drought-tolerance traits, and apply MAS in combination with conventional breeding to enhance drought tolerance in these crops. Products of MAS in pearl millet and maize have conclusively shown superior performance under severe drought-stress conditions, but no advantage under mild drought stress or under well-watered conditions. Genetically transformed groundnut with the *DREB1A* gene driven by the stress-inducible promoter *rd29A* has shown promise in enhancing drought tolerance, with no symptoms of growth retardation. Transgenic maize containing ZmNF-YB2 or *ZmDREB2A* has contributed to enhanced drought tolerance and/or grain yield advantage under drought-stress conditions. A combination of approaches (trait-based selection, QTLs and transgene) needs to be deployed to support the empirical approach in order to enhance drought tolerance in these crops.

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