Chapter 5
Drought Tolerance

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Abstract Plant breeding has a limited success for developing new cultivars with enhanced adaptation to drought-prone environments, although it has been pursued for various decades. Water use efficiency and water productivity by crops are being sought by agricultural researchers to address water scarcity in drought-prone environments across the world. They may be improved through genetic enhancement. Research on the mechanisms underlying the efficient use of water by crops and water productivity remains essential for succeeding in this endeavor. Advances in genetics, “omics,” precise phenotyping, and physiology coupled with new developments in bioinformatics and phenomics can provide new insights on traits that enhance adaptation to water scarcity. This chapter provides an update on research advances and breeding main grain crops for drought-prone environments.

5.1 Introduction

Water scarcity is among the key factors that limit crop production because drought stress affects yields. Global models predict a further increase of drought under climate change (Gornall et al. 2010; Turral et al. 2011). Moreover, irrigation will be important to ensure sustainable intensification of agriculture. Adapting crops to water-limited environments and improving their efficiency for water use, which have been always major objectives of plant breeding, will be key elements for developing climate-resilient cultivars that are capable of producing “more food per drop” (Ortiz et al. 2007).

Crop yields under water scarcity are a function of the amount of water used by the crop, how efficiently the crop uses this water for biomass growth (i.e., water use

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efficiency or aboveground biomass/water use), and the harvest index, which is the proportion of "edible yield" to aboveground biomass (Passioura 2004). The ratio of total dry matter accumulation to evapotranspiration and other water losses (or water entering and lost from the system that is not transpired through the plant) is known as water use efficiency (WUE). An increase in transpiration efficiency or a reduction in soil evaporation will therefore increase WUE. The concept of water productivity (WP) was recently defined as the net return for water use (Molden et al. 2010), i.e., the ratio of biomass with economic value (e.g., grain yield of cereals) compared to the amount of water transpired. Both WUE and WP may be improved through plant breeding (Farooq et al. 2009), as can biomass accumulation and harvest index. Understanding the mechanisms underlying the efficient use of water by crops is essential succeeding this endeavor (Chaves and Oliveira 2004). Such knowledge will lead to identifying key genes that will be further used in developing cultivars with enhanced adaptation to drought-prone environments.

Global spatial data on crop production, climate, and poverty were used to identify high-priority geographic areas to target international plant breeding undertakings for drought-prone environments (Hyman et al. 2008). These areas include 15 major farming systems, especially in South Asia, the Sahel, and Eastern and Southern Africa, where high diversity in drought frequency characterizes the environments. Furthermore, the decrease in perennial drainage will significantly affect present surface water access across 25 % of Africa by the end of this century (de Wit and Stankiewicz 2006). About 13 crops (especially cereals, legumes, and root crops) make up the bulk of food production in these drought-prone areas of Africa and Asia.

5.2 Getting Terms Right

Although the term "drought resistance" has been used in the literature (Blum 2005), this author, as noted above, prefers to use the concepts of WUE or WP when breeding crops for adapting to drought-prone environments. As indicated by Passoura (2007), the word "drought" has many meanings in relation to crop production, but plant breeders—together with agronomists and crop physiologists—should seek minimizing evaporative losses from the soil surface by better matching cultivar development to its target environment. There are of course constitutive traits that allow a crop to maintain a high plant water status (i.e., dehydration avoidance) under stress but they also contribute to WUE and WP.

Water productivity could be also regarded, in its broadest sense, as "productive" because transpiration is the only water flow in a field actually passing through the crop. WP can be therefore improved through crop breeding by reducing nontranspirational uses of water, lowering transpiration without jeopardizing production, increasing production without elevating transpiration, and enhancing crop adaptation to drought stress (Bennet 2003).

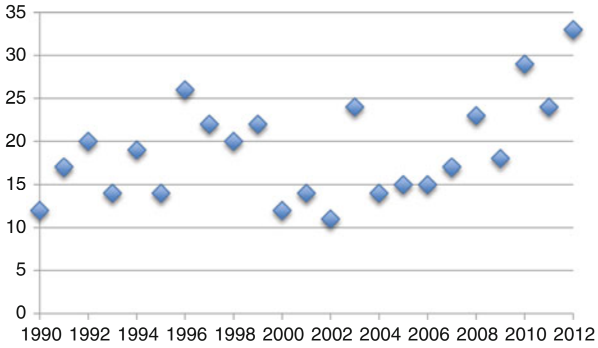

Fig. 5.1 Total number of publications per year on plant breeding for drought-prone environments or water use efficiency from leading journals: *Crop Science*, *Euphytica*, *Molecular Breeding*, *Plant Breeding*, and *Theoretical and Applied Genetics* (1990–June 2012 including online ahead of press)

5.3 Crop Breeding for Drought-Prone Environments: Last Two Decades

Although, as acknowledged elsewhere (Tester and Bacic 2005), there has been a limited success in breeding new cultivars with enhanced adaptation to drought-prone environments, research on the subject has been in the agenda of plant breeding, crop physiology, and more recently molecular biology. The number of articles on this subject published since the 1990s (i.e., around the time that first-generation DNA markers began its use) in the five most cited international plant breeding journals (namely, *Crop Science*, *Euphytica*, *Molecular Breeding*, *Plant Breeding*, and *Theoretical and Applied Genetics*) illustrates these research investments (Fig. 5.1).

After lowering the number of journal articles towards the beginning of the last decade, the volume of publications on crop breeding for drought-prone environment, and to a lesser extent on the application of DNA markers for assisting in this endeavor, increased and reached its peak in mid-2012. This finding may be associated to the launching in 2003 of the Generation Challenge Program (GCP) by the Consultative Group on International Agricultural Research (CGIAR). The GCP network (involving 200 partners worldwide) uses the rich pool of crop genetic diversity and advanced plant science (including genomic tools) to improve populations and cultivars for drought-prone environment. GCP facilitated plant breeding and research on 18 crops in its first phase I (2004–2008), while in its second phase (2009–2013), GCP selected 12 key crops (mainly cereals, legumes, and roots crops) for further enhancing their performance under drought stress.

Most of the 435 articles in the most cited plant breeding journals are in cereals (55.5 %) and legumes (19.4 %). Maize, rice, and wheat dominate the literature among cereals, while soybean and beans are the predominant for legumes. Such result was not surprising because it reflects the relative importance of each crop and the associated research investments. Several articles, especially in *Crop Science*, are related to cotton, forage species, sunflower, and turfgrass. Likewise, due to the scope of this journal, some articles are not solely on plant breeding but on related

Fig. 5.2 Percentage of publications according to crop groups per year on plant breeding for drought-prone environments or water use efficiency from leading journals: *Crop Science*, *Euphytica*, *Molecular Breeding*, *Plant Breeding*, and *Theoretical and Applied Genetics* (1990–June 2012 including online ahead of press). Cereals include barley, maize, pearl millet, rice, sorghum, and wheat, whereas bean, chickpea, cowpea, faba bean, groundnut (or peanut), lentil, pigeon pea, and soybean are among legumes. Other crops are cassava, canola (or oil seed rape), coconut, cotton, forages, Indian mustard, *Musa*, potato, *Salix*, sugar beet, sunflower, strawberry, and tomato. Review articles relevant to the subject (including screening methods or modeling) are also in this group

crop physiology research—especially for identifying traits or screening protocols (Fig. 5.2).

5.4 Advances in Plant Breeding Under Water Stress

Advances in genetics, “omics,” precise phenotyping, and physiology coupled with new developments in bioinformatics and phenomics are or will be providing means for dissecting integrative traits that affect adaptation to stressful environments. In this regard, Tardieu and Tuberosa (2010) indicate that analyzing the effect of traits on crop yield with the aid of modeling and confirming through field experiment (and sound biometrics) will lead to identifying alleles with favorable alleles for enhancing adaptation to a stress-prone environment.

Some traits used as proxy for selecting germplasm with enhanced adaptation to drought-prone environments (especially among grain crops) are anthesis–silk interval, early flowering (that could provide partial relief to water shortage during grain filling), floral fertility (by minimizing severe water deficit-induced damage at flowering), early vigorous growth (which improves crop establishment and reduces soil evaporation), root architecture and size (for optimizing water and nutrient harvest), and tiller inhibition (that increases tiller survival rates and carbohydrate storage in stems for ensuring further grain filling), among others (Tuberosa et al.

2007a). Likewise, indirect selection has been used for improving WUE, e.g., through canopy temperature depression, carbon isotope discrimination ($\boldsymbol{\Delta}^{13}$C) for C_3 crops (although both may differ across locations), and ear photosynthesis (Araus et al. 2007; Tambussi et al. 2007). Highlights of research advances in plant breeding for drought-prone environments are given below. They are drawn from the most important grain crops that feed the world: namely, maize, rice, wheat, and leading grain legumes.

5.4.1 Maize

Drought causes 17 % of annual average losses in maize (Edmeades et al. 1989), but it can be up to 60 % in Southern Africa (Rosen and Scott 1992). Drought at 1 or 2 weeks before anthesis is a particularly sensitive period to water stress for maize (Grant et al. 1989) due to an increased anthesis–silking interval (ASI) (Edmeades et al. 1989), delayed silk emergence, and rising grain abortion, which occurs 2–3 weeks after silking (Boyle et al. 1991). Drought-induced changes in ASI are related to silk expansion, while delayed silk emergence results from reduced tissue expansion and cell division rates under water deficit (Fuad-Hassan et al. 2008). Drought stress between tassel emergence and early grain filling affects significantly grain yield due to a reduction in kernel size (Bolaños and Edmeades 1993a, b).

Hund et al. (2008) found that high WUE and sufficient water acquisition by a deep root system can increase adaptation of tropical maize lines to drought-prone environments. Although maize inbred lines with adaptation to drought-prone environments showed significantly higher Δ than susceptible ones at flowering, Monneveux et al. (2008b) indicated that carbon isotope discrimination will be only accurate for initial screening of lines or hybrids but not advanced selection among hybrids.

Significant grain yield gains have been noted under drought in maize breeding due to a significant increase in numbers of ears per plant and grains per ear and significant reductions in ASI, ovule number, and abortion rate during grain filling (Monneveux et al. 2006). Recurrent selection under drought improved tropical maize source populations for performance under water deficits (Bolaños et al. 1993). Monneveux et al. (2006) indicated that this result could ensue from enhanced partitioning of assimilates to the ear at flowering, at the expense of tassel and stem growth, whereas Zaidi et al. (2008) found that reduced 5-day ASI, barrenness, delayed senescence, and minimum loss of leaf chlorophyll can account for improved performance of maize breeding lines in Asian drought-prone environments. For further gains, maize should show more ears, larger grains, and smaller tassels (Monneveux et al. 2008a).

Bänziger et al. (2004) highlight the importance of choosing the right selection environments for breeding maize when targeting the highly variable drought stressful environments, e.g., in Southern Africa. Farmers should be further involved in selecting maize bred germplasm to ensure their suitability for such risk-prone locations (Foti et al. 2008). Due to this innovative client-oriented breeding approach, which started in the late 1990s, more than 50 new maize cultivars were released and are now grown in several million ha in sub-Saharan Africa (Bänziger et al. 2006; Tollefson 2011). Farmers and researchers managed jointly "mother–baby" trials for evaluating breeding materials in drought-prone environments. The "mother" trial involved up to 12 breeding materials sown under varied researcher-designed treatments, was close to the community, and was managed by schools, colleges, or extension agencies. The "babies" were satellite subsets of the "mother" trial, comprising approximately 4–6 cultivars in the fields of participating farmers using their own inputs and equipment. In this system public researchers and private sector partners created a network of regional "stress breeding" sites that, for the first time, provide objective information on how maize cultivars perform under drought-prone infertile soils thereby meeting the needs of poor farmers who had not previously benefited from maize breeding programs. At the beginning of 2011, the US private seed sector announced the release of new maize hybrids—bred by crossbreeding—with a yield increase of 5–15 % in water-scarce environments (Tollefson 2011). They are also developing transgenic maize cultivars aiming to tap a US$ multibillion seed market (Gilbert 2010). These genetically enhanced maize seed-embedded technologies targeting drought-prone environments may reach farmers soon.

Molecular markers have been used for mapping traits affecting maize performance under drought stress and may provide tools for continuing breeding genotypes with stable grain yields in stressful environments (Bruce et al. 2002; Ribaut and Ragot 2007). DNA-aided analysis has also provided means for the genetic dissection of maize performance under drought (Ribaut et al. 1996, 1997; Quarrie et al. 1999; Tuberosa et al. 2002; Ribaut and Ragot 2007). Table 5.1 lists some of these recent research advances. Backcrossing has been used for introgressing a few quantitative trait loci (QTLs) into elite maize lines. This breeding method does not, however, appear to be very effective when many QTLs of small effect are involved. Furthermore, QTLs are often germplasm specific and the costs for marker-aided selection (MAS) for many QTLs of small effect may be higher than those from conventional crossbreeding of maize. Likewise, many putative QTLs could be likely of limited use in applied breeding because they depend on genetic background or to their sensitivity to the environment (Campos et al. 2004). Hence, as indicated by Ortiz et al. (2007), the challenge is to identify QTLs of major effect that are independent of genetic background, not affected by the genotype-by-environment interaction, and to devise more effective breeding approaches for the application of the resultant markers. In this regard, multitrait multi-environment (MTME) QTL models can help to identify genome regions responsible for genetic correlations (useful for indirect selection through trait components) and how genetic correlations depend on the environmental conditions (Malosetti et al. 2007a). For example, Malosetti et al. (2007b) detected 36 QTLs affecting maize yield, anthesis–silking interval, male flowering, ear number, and plant height in drought and nitrogen stress. Likewise, single nucleotide polymorphisms (SNP) can be used in routine large-scale genomics-assisted marker

Table 5.1 Some recent research advances in mapping quantitative trait loci (QTLs) affecting maize performance under drought

Trait and major finding(s)	Reference
Maximum leaf elongation rate per unit thermal time accounted for by five QTL, among which three co-localized with QTL for anthesis–silk interval (ASI) of well-watered plants. Alleles conferring high leaf elongation rate conferred a high silk elongation rate (i.e., low ASI)	Welcker et al. (2007)
81, 57, 51, and 34 QTLs were noted for target traits (male flowering, anthesis-to-silking interval, grain yield, kernel number, 100-kernel fresh weight, and plant height) in water stress and well-watered trials in Mexico and Zimbabwe, respectively. About 80, 60, and 6 % of the QTLs did not show significant QTL-by-environment interactions (QTL × E) in the joint analyses per environment, per water regime, and across all experiments. QTL clusters for different traits were identified in chromosomes 1, 3, and 5 in water stress trials	Messmer et al. (2009)
Specific seedling QTLs water stress: root dry weight, shoot dry weight, and leaf area-to-root length ratio. Ear number QTLs collocated with QTLs for shoot-to-root dry weight and leaf area-to-root length ratios. ASI QTLs collocated with QTLs for the numbers of crown roots and seminal roots irrespective of water supply	Ruta et al. (2010)

development and gene discovery. Very recently, Lu et al. (2010) used 2,052 SNPs (including 659 from drought-response candidate genes) in joint linkage–linkage disequilibrium mapping to detect QTLs underlying maize adaptation to drought-prone environments.

5.4.2 Rice

Rice production systems are very vulnerable to drought stress, which affects 10 million ha of upland rice and over 13 million ha of rainfed lowland rice in Asia alone (Wassmann et al. 2009 and references therein). Rainfall distribution seems to be more important than total seasonal rainfall. A short dry spell at flowering leads to a significant decrease of grain yield and harvest index (Serraj et al. 2008), because water stress at this stage reduces grain formation more significantly than at other reproductive stages (Boonjung and Fukai 1996). A reduction on spikelet fertility and panicle exertion due to drought affects significantly grain yield. Drought can also inhibit the development of reproductive organs (egg and pollen) and processes (anther dehiscence, pollen shedding and germination, and fertilization).

Although the physiological basis of genetic variation in drought response remains unclear (Laffite et al. 2004), research advances in physiology, molecular biology, and genetics have contributed tremendously to the understanding of rice performance under drought (Table 5.2). A deep root system seems to be the most important target trait for improving rice grain yield in drought-prone environments (Gowda et al. 2011; Kato et al. 2011). Near-isogenic lines (NILs) have been very important tools for dissecting traits accounting for adaptation to drought stress in rice.

Table 5.2 A sample of progress of rice physiology, molecular biology, and genetic research under drought stress

Ensuing knowledge	Reference
Grain percentage (spikelet fertility) is the most sensitive yield component. Spikelet fertility in the top four rachis branches was reduced due to decreasing anther dehiscence and lowering stigma pollen density	Liu et al. (2006)
There was a significant variation on water use efficiency among the five upland and three lowland cultivars used. Cultivars showing high photosynthesis and conductance were more productive across a soil moisture gradient	Centritto et al. (2009)
Near-isogenic lines (NILs) with broad leaves had higher biomass (and its individual components), less stomatal conductance, and higher transpiration efficiency under drought than NILs with narrow and short leaves, which explain their improved performance	Farooq et al. (2010)
Dehydration avoidance (characterized by significantly higher growth rate and biomass, efficient partitioning (measured by improved harvest index)) and drought escape by accelerated heading under water scarcity are the main mechanisms for adapting to drought-prone environments	Guan et al. (2010)
Leaf water status and leaf elongation are not particularly sensitive to water deficit but poor root system may account for drought sensitivity	Parent et al. (2010)
Adaptation to drought related to deep root growth and water uptake ability	Gowda et al. (2011)
Enhanced rooting depth enhances dehydration avoidance and rice adaptation to drought stress, but there are other mechanisms contributing to significant yield increase in lowland drought-prone environments	Venuprasad et al. (2011)
Cytokinin-mediated source–sink modifications delay stress-induced senescence under drought	Peleg et al. (2011)
High-yielding lines had maximum root length and root volume compared, thereby indicating positive influence of drought avoidance root traits contributing to adaptation to this stress	Gouda et al. (2012)

Appropriate choice of parents, selection criteria, and robustness of the managed screening protocols will contribute to the success of breeding rice germplasm for drought-prone environments (Wassmann et al. 2009). Intermittent stress, which is imposed by withholding irrigation during the period bracketing the entire flowering and grain-filling stages, seems to be a reliable screening for ranking cultivars' performance under drought (Laffite and Courtois 2002). Significant progress has been achieved in breeding upland and aerobic cultivars for water-scarce environments (Bernier et al. 2008). The breeding gains on rainfed lowland germplasm have been however relatively slow until recently, when several lines were released in India and the Philippines (Verulkar et al. 2010). The use of drought-selected introgression lines for rainfed or water-scarce rice-growing regions (Laffite et al. 2006) contributed to this achievement.

Serraj et al. (2009) provide a recent overview on rice breeding for drought-prone environment. They found that increased crop yield and water productivity need optimizing physiological processes at the initial critical stages of plant response to soil drying, water use efficiency, and dehydration-avoidance mechanisms. They advocate a holistic interdisciplinary approach that integrates plant breeding with physiological dissection of resistance traits and molecular genetic tools together with agronomical practices. Such an approach, according to these authors, should lead to a better conservation and use of soil moisture and matching rice cultivars with the environment.

QTL analysis of rice traits in drought-prone environments has been widely used (Laffite et al. 2004). QTLs were noted for some secondary traits associated with drought response, e.g., rooting depth, membrane stability, and osmotic adjustment. Most QTL research has been useful for identifying promising genome regions for potential use in rice breeding for drought-prone environments. For example, seven QTLs for carbon isotope discrimination were mapped in five chromosomal regions through composite interval analysis (Xu et al. 2009). Likewise, Bernier et al. (2009) found one QTL improving grain yield under severe drought stress (*qtl12.1*) mainly through a slight improvement (7 %) in plant water uptake under water scarcity. Very recently, 23 QTLs linked to plant phenology and production traits under stress were identified with the aid of a meta-analysis (Sellamuthu et al. 2011). Chromosomes 1 and 9 seem to bear QTLs for reproductive-growth traits and grain yield under drought stress. Serraj et al. (2011) indicated further that high-throughput, high-precision phenotyping systems will allow to map genes for yield components under stress and to assess their effects on drought-related traits. Such undertaking will assist to simultaneously incorporate the most promising genes into widely grown rice cultivars and enhance gene detection and delivery for use in marker-aided breeding.

African rice (*Oryza glaberrima*) shows adaptation to harsh growing environments and has been used for breeding a new rice for Africa (Jones et al. 1997). Bimpong et al. (2011a) found that the fraction of transpirable soil water was higher in some African rice accessions than in Asian rice lines. Such finding shows the ability of these African rice accessions to close their stomata early in response to drought stress to keep transpiration rate similar to the rate of uptake of soil water, thereby resulting in maintenance of the water balance of the plant. Further research by Bimpong et al. (2011b) using BC_2F_3 offspring deriving from IR64 and African rice found one QTL on chromosome 2, which accounts for 22 % of the genetic variation, affecting positively grain yield under stress.

5.4.3 Wheat

Water scarcity could be the most important abiotic stress affecting grain yield and quality of wheat. Climate change may exacerbate this stress due to more random weather events or by extending drought, especially in rainfed environments. Early drought in the growing season affects seed germination and crop establishment in wheat. Leaf expansion and tillering are also very sensitive to water stress in the vegetative stage. Water deficit before flower initiation can decrease the number of spikelet primordia and grain number during the spike growth period. Moreover, water stress 10 days before spike emergence decreases spikelets per spike of fertile tillers (thereby maximizing grain yield loss), while water deficit prior to anthesis accelerates plant development. Furthermore, water stress during grain reduces grain weight because of the shortening of the grain-filling period due to accelerated plant senescence.

There are various traits that could improve wheat yield in dry environments. They may enhance plant establishment, early canopy development, root growth and depth, or soil water use (Richards et al. 2001). WUE can be improved in wheat by traits such as deep roots, plant phenology, seedling vigor, tiller inhibition, high transpiration efficiency, or osmotic adjustment. Furthermore, canopy temperature, stomatal conductance, stay-green intermediate, or leaf rolling may indicate deep roots in the crop. These drought-adaptive traits can be associated to distinct genes controlling early (pre-anthesis) growth, access to water, WUE, and photoprotection (Reynolds et al. 2005).

Mexico's diverse landraces, as per DNA fingerprinting, showed superior ability for water extraction from soil depth and an increased concentration of soluble carbohydrates in the stem shortly after anthesis, whereas resynthesized wheat lines, using wild ancestors, had increased partitioning of root mass to deep soil profiles (between 60 cm and 120 cm) and increased ability to extract moisture from these depths (Reynolds et al. 2007). Izanloo et al. (2008) noted that the capacity for osmotic adjustment was the main physiological trait related for adaptation to cyclic water stress in South Australian bread wheat cultivars, thereby enabling their plants to recover from water deficit. Carbon isotope discrimination (Δ) could be another useful trait because it can indirectly measure yield potential, harvest index, and water status under irrigated and rainfed conditions, as shown by Zhu et al. (2008) when researching on wheat cultivars in northern China. Rebetzke et al. (2002) suggest that Δ could be used for indirect selection in water-limited environments because it may increase the probability of recovering high-yielding lines in a wheat breeding program. Hoffman et al. (2010) found that increasing the root/shoot ratio and decreasing the water potential and grain-filling duration enhanced adaptation to water deficiency in wheat–barley introgression lines.

Although wheat breeders may have interest in the above traits (especially those with high heritability and showing low genotype-by-environment interactions), a few of them have been used to develop cultivars because of the little capacity of breeding programs to screen for these traits, their lack of validation through relevant field experiments, and the limited knowledge regarding their economic benefit for selecting one trait against another. A reliable drought screening may need to use managed environment facilities (MEF) that control water availability and remove the impact of seasonal changes and timing of rainfall on the performance of trial crops. The accuracy of performance measurements can, therefore, increase, as well as the precision for attributing phenotypic effects to individual traits and their underlying genetics.

Progress in international wheat breeding aiming drought-affected environments was measured for a 20-year period using data from global semiarid wheat yield trials (Trethowan et al. 2002). The yearly progress was determined by measuring change in the percentage of trial mean (%TM) and change in trial mean (TM) between 1979 and 1998. The increases were 4.38 and 0.09 % per year for %TM and TM, respectively, in environments whose average grain yield was below 4 t ha^{-1}, while in those environments yielding 4 t ha^{-1} or above, these rates were 0.85 and 2.87 % per year. Further analysis for the period 1994–2010 (Manès et al. 2012) shows a rate of 1 % per year (or 31 kg ha^{-1} per year) when grain yield was expressed as a percentage of the long-term check cultivar "Dharwar Dry," being the yield increase rate twice in high-yielding environments than in low-yielding environments. "Attila" and "Pastor," which are key parents in international wheat breeding, and their derivatives were high-yielding lines in several environments. A resynthesized wheat derivative ("Vorobey"), which includes "Pastor" as parent, had outstanding yields in recent multi-environment trials. A data subset from these trials (122 locations) was also used for assessing the relationship among international drought-prone test sites and further clustering of environments (Trethowan et al. 2001). Some weak associations among locations could be attributed to their inherent variability, which is a major characteristic of most rainfed, drought-prone environments.

As noted above, several traits contribute to wheat performance under drought stress. Hence, none of them alone will be able to improve wheat yields in environments affected by water scarcity. Moreover, adaptation to drought seems to be a quantitative trait controlling a complex phenotype, which may be often confounded by plant phenology (Fleury et al. 2010). Breeding for drought-prone environments may be further confused due to interaction with other stress factors (e.g., high temperature and irradiance, nutrient toxicity, or deficiency), which explains so far the limited success using physiological and molecular breeding approaches. Nonetheless DNA markers can assist dissecting some of these traits (Table 5.3) and mapping QTLs, e.g., for plant height at distinct water regimes, flag leaf senescence, and grain yield under drought stress. An interdisciplinary approach that takes into account interactions among stress factors and plant phenology, integrates physiology and genetics of traits for enhancing adaptation to drought, and uses high-throughput MEF and genomic tools will facilitate wheat breeding under water scarcity.

5.4.4 Legumes

Adaptation of legumes to drought-prone environments remains challenging because of the complexity of the various traits involved as well as the broad variability in the environments where water scarcity occurs. This section includes research highlights for cowpea, chickpea, groundnut (or peanut), bean, and soybean.

Table 5.3 QTL sample for wheat characters measured in drought-prone environments

Trait	Finding	Reference
Flag leaf senescence	Complex genetic mechanism (in chromosomes 2B and 2D) of this trait involving the remobilization of resources from the source to the sink during senescence	Verma et al. (2004)
Grain yield	A grain yield QTL on the proximal region of chromosome 4AL (contributed by cv. "Dharwar Dry") with a significant effect on performance under reduced moisture	Kirigwi et al. (2007)
Adaptive QTL	QTL located on 4A accounts for 27 % of grain yield variation under drought QTL on 3B-b explains 14 % of canopy temperature variation Common QTL for drought and heat stress traits on 1B-a, 2B-a, 3B-b, 4A-a, 4B-b, and 7A-a, thereby confirming their generic value across both stress factors	Pinto et al. (2010)
Plant height (PH)	No single QTL continually active in all periods of PH growth QTL with additive effects expressed in the period from the original point to the jointing stage formed a foundation for PH development PH development under control of a network of genes with additive and epistatic effects, but the former are more important than the latter or QTL × environment interactions	Wu et al. (2010)

Cowpea—the most important legume crop of the semiarid tropics of Africa—shows an inherent adaptation to drought but yet suffers significant damage leading to grain yield loss in the Sahel and dryland savannas, which are affected by unstable rainfall patterns and frequent droughts. Agbicodo et al. (2009) provide the most recent overview of cowpea breeding for drought-prone environments. Research on this crop under drought stress includes the analysis of the relationship between drought response and grain yield components, plus other morphological and physiological traits. The extensive research on drought screening was only successful for selecting cowpea parents showing distinct mechanisms to adapting to drought. There have been some recent advances in identifying DNA markers defining QTLs for traits related to adapting the crop to drought stress. Table 5.4 provides a summary of some research findings regarding the genetics of traits favoring adaptation of this crop to environments affected by water scarcity.

Chickpea could be the most investigated legume crop under drought stress (Dwivedi et al. 2013 and references therein). Its adaptation to drought seems to be related to drought avoidance root traits (root length density, root to total dry plant weight ratio, root depth, and root to shoot length density), transpiration efficiency (TE), carbon isotope discrimination, SPAD chlorophyll meter reading, and canopy temperature. Plant breeders have used some of these traits to enhance chickpea performance in drought-prone environments. Krishnamurthy et al. (2010) and Zaman-Allah et al. (2011) were able to identify various chickpea lines with enhanced adaptation to terminal drought.

Table 5.4 Research advances on trait analysis, physiology, and genetics for adapting cowpea to drought-prone environments

Findings	Reference
Water stress regulates the synthesis and the activity of superoxide dismutase isoforms, which contribute to protect photosynthesis against the damageable effects of superoxide radicals in cowpea	Brou et al. (2007)
Delayed leaf senescence associated with adaptation to drought	Muchero et al. (2008)
10 QTLs associated with seedling drought-induced senescence on linkage groups 1, 2, 3, 5, 6, 7, 9, 10, each contributing between 5 and 12 % to the phenotypic variance	Muchero et al. (2009)
Germplasm with enhanced adaptation to drought had more pods and seeds per plant and grain yield per plant and show high harvest index	Hegde and Mishra (2009)
Genetic variation in water-saving traits such as lower plant transpiration rate (Tr) under no stress and restricted Tr under high vapor pressure deficit (VPD)	Belko et al. (2012)

There are various *Arachis* germplasm sources for adapting groundnuts to mid- and end-of-season terminal drought (Cruickshank et al. 2003 and articles therein), e.g., subspecies *hypogaea* and *fastigiata* show variation for physiological traits such as specific leaf area (SLA), chlorophyll content, amount of water transpired (*T*), TE, WUE, and harvest index under drought stress (Dwivedi et al. 2013 and references therein). Most groundnut breeding programs follow an empirical approach (largely based on pod yield as selection criterion for adaptation to drought), which explains its slow genetic progress (Nigam et al. 2005). Recently Ravi et al. (2011) found a few major, many minor, and epistatic QTLs, thereby revealing that the groundnut adaptation to drought is a complex and multigenic trait.

Common beans show significant plasticity at the biochemical and cellular levels under drought, especially for stomatal conductance, photosynthetic rate, abscisic acid synthesis, and resistance to photoinhibition (Lizana et al. 2006). Deep rooting system, maximization of WUE, greater photosynthate transport to seed under stress through efficient remobilization, early maturity, and recovery from drought are among the traits that confer enhanced adaptation in common bean in water-limiting stressful environments (Dwivedi et al. 2013 and references therein). Several germplasm and breeding lines showing these traits have been selected worldwide. Some recently bred lines outyielded the commercial checks by 15–25 % under favorable environments or up to 36 % under drought stress (Beebe et al. 2008). This enhanced adaptation to drought seems to be multigenic (Beebe et al. 2008), and recurrent selection could be an effective breeding method. Few QTLs that enhance adaptation to drought have been noted (Blair et al. 2012). Asfaw et al. (2012) mapped nine QTLs for ten traits enhancing adaptation of common bean to drought-prone environments on 6 of the 11 linkage groups. Six of these QTLs had a significant interaction with the environment.

There has been a tremendous progress for identifying the physiological and genetic basis of traits for water-limited environments and quantifying their impact on soybean grain yield (Sadok and Sinclair 2011 and references therein). Such advances translated in the release of the first ever N-fixing soybean cultivars for drought stressful environments and the use of "slow-wilting" germplasm in soybean breeding programs. Their success ensued from an interdisciplinary approach relying on field-based phenotyping, dissecting traits using physiological tools and genetic analysis, and crop modeling.

5.5 Outlook

Water remains as one of the most serious limiting factors for world agriculture and it may likely worsen with the anticipated global climate change. Adaptation to drought is a complex, multigenic phenotype that may be affected by both the environment and other stress factors. Mir et al. (2012) suggest that genomics and genetics coupled with precise phenotyping methods could unravel the genes and metabolic pathways that confer crop adaptation to drought. "Omics" research, which emerged mostly in the last one and a half decades, provides further insights for breeding WUE in crops, while phenomics will assist to quantify precisely the traits enhancing crop adaptation to water scarcity. Phenotyping protocols (within a plant breeding strategy for improving crop yields under drought) should screen for water use, WUE, and harvest index (Salekdeh et al. 2009). Digital imaging could be used for accurately doing high-throughput phenotyping of ground cover and early vigor traits (Mullan and Reynolds 2010). It may replace the destructive sampling methods, which are regarded as time consuming by plant breeding programs.

Modeling offers means for simulating how virtual plants—bearing a diverse combination of alleles—could respond to distinct drought scenarios (Tardieu 2003). Chapman (2008) indicated that this approach has the additional advantage of manipulating separately "biological and experimental noise." Crop simulation models are, therefore, an important tool for genomics research and breeding crop adaptation to drought.

The focus of the recent years in crop-drought research has been on dissecting traits that enhance adaptation to this stress (Collins et al. 2009). QTL mapping or gene discovery through linkage and association mapping, QTL cloning, candidate gene identification, transcriptomics, and functional genomics has been used to understand crop responses to drought. In some crops several QTLs controlling characters that enhanced adaptation to drought have been detected. Dissecting complex phenotypes into their constituting QTLs offers a more direct access to tap valuable genetic diversity regulating the adaptive response to drought (Tuberosa et al. 2007b). As suggested by Courtouis et al. (2009) for rice roots traits, compiling these data could significantly assist on identifying candidate genes through positioning consensus QTLs with more precision through meta-QTL analysis.

Gene expression microarrays are useful for gaining insights into physiological and biochemical pathways of crop adaption to drought. This technology can also lead to identifying new candidate genes that can be used for enhancing plant breeding for environments affected by water scarcity. For example, Luo et al.

(2010) examined some gene expression patterns in several maize stress response-associated pathways and found that specific genes were responsive to drought stress positively, while Kathiresan et al. (2006) noted contrasting drought responses when comparing upland- and lowland-adapted rice cultivars and between traditional and improved upland rice types.

"Omics" tools can address the multi-genecity of plant responses under stress (Bohnert et al. 2006). The analysis of genomes, transcriptomes, protein dynamics, and metabolomes will provide means for comparing adaptation to drought across species. Advances in crop genome sequencing and resequencing will further provide means for dissecting genetically the basis for adapting crops to stressful environments (Roy et al. 2010). Likewise, molecular-aided breeding, which includes marker-assisted backcrossing, marker-assisted recurrent selection, and genome-wide selection, may offer means for developing new cultivars with enhanced adaptation to drought stressful environments. The judicious use of plant genetic resources, precise phenotyping, and knowledge-intensive crop breeding led by physiology and "omics" sciences should be also able to deliver germplasm with enhanced water productivity. The success in this endeavor will contribute towards ensuring food, feed, fiber, and other feedstocks under the likely unstable and more variable climate to be brought by global warming.

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