



13

Drought

Salvatore Ceccarelli

Formerly International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria (now retired)

13.1 Introduction

Today, few scientists question whether climate change is occurring or not and the discussion has shifted from whether it is happening to what to do about it. Using the results from formal economic models, it has been estimated that, in the absence of effective counteraction, the overall costs and risks of climate change will be equivalent to a 5% decrease in global gross domestic product (GDP) each year (Stern, 2007). If a wider range of risks and impacts is taken into account, the estimates of damage could rise to a 20% decrease in GDP or more, with a disproportionate burden and increased risk of famine in the poorest countries (Altieri and Koohafkan, 2003).

The most likely scenarios of the future climate are the following:

- Higher temperatures, which will reduce crop productivity, are certain.
- An increase in CO₂ concentration is certain with both direct and indirect effects.
- Increasing frequency of drought is highly probable.
- Increasing in the areas affected by salinity is highly probable.
- Increasing frequency of biotic stress is also highly probable.

Among these abiotic and biotic stresses, drought is the number one limitation to crop productivity in the world. As climate changes, the incidence and duration of drought and heat stress on our major crops will increase in many regions, negatively affecting crop yields and food security (Lauer *et al.*, 2012).

Drought is the most serious constraint to agricultural production and is still one of the most difficult challenges to agricultural scientists, as shown by the devastating effects of drought on the maize and soybean production in the USA in the summer of 2012 (US Drought Monitor, 2012) with, at the time of writing, 24% of the area experiencing extreme or severe drought conditions that are the worst in 65 years. It is likely that many current crop varieties will need replacement to enable them to better suit the new and changing agroenvironments (Luck *et al.*, 2011).

Drought is not easy to define because it means different things to different people in different places in different crops and therefore can be defined in several ways: for example, to a meteorologist it could mean a rare event (for example one of the 10 driest seasons per century); to an agronomist it means yield strongly limited by water; to a plant physiologist drought means plots not watered; and eventually to a biochemist/molecular biologist drought means plants or leaves left to dry on a lab bench (Passioura, 2006). The definition that I will use is the following: drought is that level of water availability below that needed for the crop to express its potential in terms of growth and production. Defined in this way it becomes clearer that drought can occur at different times of crop development, with a different intensities, depending on the amount of water available to the crop, over different lengths of time, and can occur one or more times during the life cycle of a plant. Farmers have to cope with all these different types of drought, which are largely unpredictable in the field. In a plastic house or in a growth

chamber, where farmers usually do not plant their crops, drought is imposed artificially and hence is highly predictable. This is usually the type of drought scientists prefer to study. Whether the conclusions of these studies apply to the field drought remains to be demonstrated.

Scientists are also using, often almost as synonyms, drought tolerance and drought resistance when describing the responses of crops to limited water availability. Passioura (2006) suggested replacing these qualitative terms with water productivity, which can be quantified and expressed as units of amount of crop yield per volume of water supplied or used. The literature on drought indicates that this suggestion has not been generally followed.

Historically, drought has been the main factor limiting crop production. Water availability has been associated with the rise of several civilizations, whereas drought has caused the collapse of empires and societies, such as the Akkadian Empire (Mesopotamia, ~4200 calendar year BP), the Classic Maya (Yucatan Peninsula, ~1200 calendar year BP), the Moche IV–V Transformation (coastal Peru, ~1500 calendar year BP) (deMenocal, 2001) and the early bronze society in the southern part of the Fertile Crescent (Rosen, 1990).

Although in the past drought reached the front pages of the media only when it caused famine and death, in the past few years drought warnings have become more and more frequent. More people are now aware that drought is a permanent constraint to agricultural production in many developing countries and is increasingly causing crop losses in developed countries. The development of drought-resistant cultivars would be a major breakthrough (Ceccarelli *et al.*, 2004). From a genetic point of view, however, drought resistance is a very elusive trait because its occurrence, severity, timing and duration vary from location to location and in the same location from year to year. Cultivars successful in 1 dry year may fail in another, or cultivars resistant to late drought may not be resistant to intermittent drought or to drought occurring early in the season (Passioura, 2006). To make matters

worse, drought seldom occurs in isolation; it often interacts with other abiotic (particularly temperature extremes) and biotic stresses (for example root diseases and nematodes) (Fresco and Baudoin, 2002). Moreover, areas with high risk of drought generally have low-input agriculture (Ceccarelli *et al.*, 1991) because the risk of crop failure or low yields is so high that farmers tend to limit investments to the bare minimum, i.e. seed and tillage. Thus, breeding for drought resistance is made more difficult by its interactions with other stresses. Eventually, and in relation to the complex syndrome of climate change, drought appears as a moving target because it is expected to gradually increase with time, and to be different from place to place, with consequences on breeding strategies including the choice of germplasm that we will discuss in the later sections of the chapter.

13.2 The Genetics of Drought Resistance

Drought resistance is commonly considered an extremely complex multigenic trait controlled by several genes with small effect (Parry *et al.*, 2005; Fleury *et al.*, 2010) and this complexity of drought resistance emerges from both phenotypic and genotypic studies.

Phenotypic studies have considered several traits as possible candidates to be indicators of drought resistance (leaf water retention of excised leaves, stomatal conductance, proline content, osmotic adjustment, reduced xylem vessel size in seminal roots, abscisic acid accumulation, leaf turgor, leaf waxiness, leaf area index, stomatal density, transpiration efficiency, early growth vigour, growth habit, accumulation and remobilization of stem reserves, $\Delta^{13}\text{C}$ discrimination, canopy temperature, relative water content, water use efficiency, flowering time, cell membrane stability, cell wall rheology, root characteristics and others). When we studied the association between a number of morphological traits and grain yield under stress over a number of years in barley (Ceccarelli *et al.*, 1991), we found,

however, that individual traits play a different role in different years under different combinations of climatic stresses (Table 13.1).

In spite of large differences between the four cropping seasons (from near crop failure in 1986/87 to nearly 3 t ha⁻¹ in 1987/88), high grain yield under drought was associated with earliness, large kernels and, mainly in six-row genotypes, with plant height under drought. In 1986/87, however, when a long period of low winter temperatures prevented the crop from growing during the rainy period, the correlation between grain yield and cold tolerance in two-row genotypes was almost as strong as with days to heading. In six-row genotypes, only the correlation coefficients with cold tolerance and growth vigour were significant. In that season, only the earliest of the cold tolerant two-row barleys and the most vigorous and cold tolerant six-row barleys produced harvestable yield. A similar pattern emerged in the six-row genotypes in 1988/89 cropping season also characterized by a long period of low winter temperatures coincidental with a long winter dry spell. In the two-row genotypes, the correlation between yield and cold tolerance was again as strong as with days to heading. In the environment used in this study (dryland

Mediterranean with hot and dry summers and cold winters), earliness alone, despite its efficiency as an escape mechanism, is necessary but not sufficient to achieve maximum yield stability. The correlation coefficients between yield potential and yield in drought conditions were non-significant in five cases, negative in one case (two-row in 1988/89) and positive in two cases (two-row in 1985/86 and six-row in 1988/89). In these two cases, the variation of yield potential explained only 3% and 10%, respectively, of the sum of squares of yield in drought conditions. The multiple correlation coefficients (R) are not comparable across seasons (with the exception of 1985/86 and 1987/88) because some of the traits were not measured or scored each season. The comparison between two-row and six-row genotypes shows, however, that a given group of traits can have similar multiple correlation coefficients with yield in drought conditions in the same environment even though considerable differences exist between the correlation coefficients with individual traits.

Although the situation illustrated in Table 13.1 is certainly an oversimplification, it indicates that high grain yields in drought-stressed environments can be associated with different combinations of traits rather

Table 13.1. Simple and multiple correlation coefficients (R) between grain yield in stress conditions (YD in kg ha⁻¹) and days to heading (DH), plant height in drought conditions (PHD), growth vigour (GV), growth habit (GH), cold tolerance (CT), 1000 kernel weight (KW) and yield potential (YP) in two-row and six-row barley genotypes^a in four cropping seasons (modified from Ceccarelli *et al.*, 1991).

| YD versus | Two-row | | | | Six-row | | | |
|--------------|---------|-------------------|---------|---------|---------|--------|---------|---------|
| | 85/86 | 86/87 | 87/88 | 88/89 | 85/86 | 86/87 | 87/88 | 88/89 |
| DH | -0.24** | -0.17** | -0.35** | -0.63** | -0.45** | -0.07 | -0.35** | -0.76** |
| PHD | 0.45** | n.a. ^b | 0.02 | 0.02 | 0.42** | n.a. | 0.38** | 0.55** |
| GV | -0.12 | -0.06 | -0.03 | -0.08 | -0.19 | -0.21* | -0.16 | -0.29** |
| GH | -0.09 | -0.01 | -0.08 | 0.43** | -0.20* | -0.05 | -0.20* | 0.12 |
| CT | n.a. | -0.16* | n.a. | -0.62** | n.a. | -0.21* | n.a. | -0.28** |
| KW | 0.16* | 0.21** | 0.37** | 0.31** | 0.04 | 0.03 | 0.44** | 0.61** |
| YP | 0.17** | 0.03 | -0.04 | -0.34** | -0.04 | -0.03 | -0.18 | 31** |
| R | 0.56** | 0.29** | 0.49** | 0.84** | 0.55** | 0.26* | 0.60** | 0.81** |
| YD | 1602 | 74 | 2931 | 744 | 1514 | 45 | 2869 | 567 |

^a236 two-row and 96 six-row in 85/86, 86/87 and 87/88; 203 two-row and 97 six-row in 88/89; ^bnot available; *P<0.05; **P<0.01.

than to the same specific trait, and that within these combinations the role of individual traits changes with the type, the intensity and the timing of the drought stress, which vary from year to year. It is therefore possible for each of the traits considered in Table 13.1 to find genotypes with the same value of the trait, although widely different for grain yield in drought conditions. This indicates that within a given range of values for each trait, the final performance (grain yield in drought conditions), depends on the expression of other traits. Similar results were obtained by Condon *et al.* (2002) and by Reynolds *et al.* (2007) using a general model for drought adaptation in wheat.

Phenotyping for drought resistance has recently been made more precise by the use of techniques such as nuclear magnetic resonance, canopy spectral reflectance and infrared thermography, near-infrared spectroscopy, magnetic resonance imaging and positron emission tomography (Mir *et al.*, 2012).

Most of the evidence for the genetic complexity of drought resistance comes from the molecular dissection of drought tolerance using traditional quantitative trait loci (QTL) mapping and more recently with linkage disequilibrium (LD) based association mapping. These studies have identified QTLs for drought resistance/tolerance defined as grain yield under stress and/or for characters associated with drought resistance in a number of crops; in the majority of these studies these QTLs are located on many chromosomal regions (see Table 1 in Mir *et al.*, 2012), each explaining only a small portion of the total phenotypic variance.

In gene expression studies it is not uncommon for hundreds if not thousands of genes to be found being up- or down-regulated under dehydration stress in the laboratory (Blum, 2011). A typical example of this complexity has been revealed by the analysis of the genes that are up-regulated or down-regulated by cold, drought and salinity stress in *Arabidopsis thaliana* (L.) Heynh (Seki *et al.*, 2002).

In this study, several genes were affected by drought and salinity (119 up-regulated and 31 down-regulated), and a smaller number by drought and cold and by cold and salinity. A relatively large number of genes (22 up-regulated and 17 down-regulated) were affected by all the three abiotic stresses (Seki *et al.*, 2002). As many as 128 and 26 genes were up- and down-regulated, respectively, only by drought. If these results can be extrapolated to agricultural crops and if we consider that drought and cold can occur at different developmental stages of the crop, for a variable length of time and with a variable intensity, the level of complexity of the molecular responses is likely to be higher than that shown in Fig. 13.1. In fact, data on barley show that the genes up-regulated and down-regulated at the given stress treatment are different from those up-regulated and down-regulated at a different stress treatment (Öztürk *et al.*, 2002).

A more recent example of the genetic complexity of drought resistance is the dissection of gene expression under drought stress in rice (*Oryza sativa* L. ssp. *indica*) in which the number of genes that were up-regulated in the shoot, flag leaf and panicle was 1020, 301 and 448, respectively. Further, 547, 614 and 1145 genes were down-regulated in the shoot, flag leaf and panicle, respectively (Zhou *et al.*, 2007).

However, although biotechnology has revolutionized the development of new varieties with genes being identified for engineering or marker-assisted selection (MAS) for a range of 'simple' traits, and despite a substantial investment in the study of more complex traits, there are not yet success stories based on the identification of specific genes and their utilization for drought resistance (Chapman, 2008). The only markers for traits associated with drought resistance that have found their way into practical plant breeding programmes are those for boron and aluminium tolerance (Gupta *et al.*, 2010). In general, MAS has contributed very little to the release of improved cultivars with greater tolerance to abiotic stresses, and this is perhaps partly

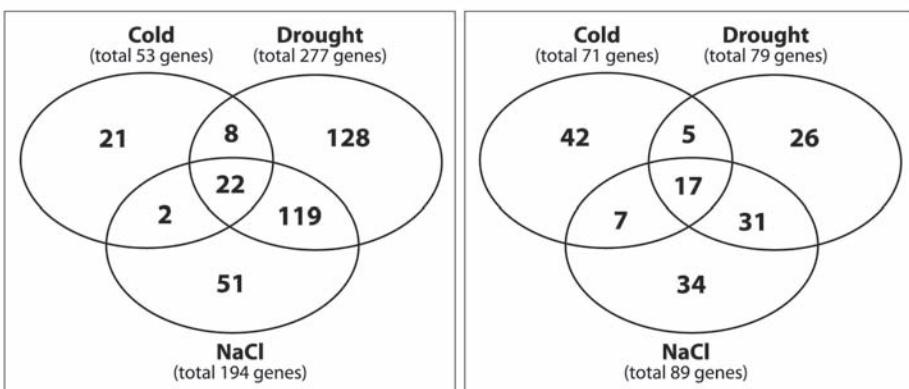


Fig.13.1. Up-regulated (left) and down-regulated (right) genes by cold, drought and salinity stress in *Arabidopsis thaliana* (from Ceccarelli *et al.*, 2004, based on Seki *et al.*, 2002).

because interactions between multiple stresses are seldom considered (Collins *et al.*, 2008).

Although QTL analysis and gene cloning have been used to investigate the same stress responses, the relationship between QTLs and stress-related sequences is still far from understood and will remain a challenge for the near future (Fleury *et al.*, 2010). This conclusion, which leaves the solutions to the near future, is common to most molecular studies.

13.3 Breeding for Drought Resistance

Two contrasting philosophies have been used to breed drought-resistant varieties. In the first, selection is done under optimum growing conditions assuming that an increased yield potential will have a carry-over effect in less favourable conditions. In the second, selection is done in the presence of drought, and can take two forms: (i) indirect selection for physiological or developmental traits (analytical breeding); and (ii) direct selection for grain yield (empirical or pragmatic breeding).

The first philosophy has been one of the main concepts upon which the 'Green

Revolution' was based (Hazell, 2003), which in high-input environments achieved large production increases but also decreased agricultural biodiversity and increased environmental degradation because the varieties it produced were able to express their superiority only if supplied with chemical inputs (fertilizers, pesticides and herbicides) (Kenení *et al.*, 2012). On the other hand, in the regions where farmers were too poor to afford chemical inputs and in those chronically affected by drought it failed to improve drought resistance.

Nearly one billion people in the world were still undernourished by 2010 (FAO, 2012) and drought continues to affect agricultural production severely, even in developed countries as mentioned earlier in the case of the USA in 2012 (US Drought Monitor, 2012). One corollary of this philosophy is that, because favourable environments tend to be similar in time and space, one or few varieties *widely adapted* can perform well in all of them, hence the reduction in agricultural biodiversity.

The second philosophy recognizes the complexity of drought and is based on breeding for *specific adaptation*. In the analytical approach, physiologists classify mechanisms for drought resistance into drought escape, drought avoidance and

drought tolerance. As discussed earlier, several traits have been associated with those mechanisms.

The analytical approach has been very successful in understanding which traits are associated with drought resistance but much less successful in developing new cultivars with improved drought resistance under field conditions where drought varies in occurrence, severity, timing and duration. Therefore, it is the interaction among traits that determines the overall crop response to drought, rather than the expression of any specific trait (Ceccarelli *et al.*, 1991). One exception could be osmotic adjustment, which is effective in a specific drought environment (Munns and Richards, 2007).

Although breeding for drought resistance on the basis of direct selection for grain yield in the target environment (empirical or pragmatic breeding) appears intuitively as the most obvious solution, it has faced criticism because the chances of progress seem low and remote. Two issues with selection in stress environments are the precision of selection and the existence of several target environments.

On the first issue, a literature review (Ceccarelli, 1996a) has shown the absence of a consistent relationship between grain yield and the magnitude of heritability and the possibility of combining precision and relevance by conducting trials in the target environment even when it is a stress environment. The second issue, how to deal with the multitude of target environments, is intimately associated with broad and specific adaptation, two concepts that have been debated in plant breeding since the early 1920s and are still highly controversial (Ceccarelli and Grando, 2002). Because of the heterogeneity of the environments affected by drought, breeding for specific adaptation is essential to increase the yield of crops grown in these environments. Breeding for specific adaptation to drought conditions is often considered an undesirable breeding strategy, because it is usually associated with lower yields under favourable conditions and produces too many varieties for the seed companies to handle. Breeding

for wide adaptation has been considered recently to be more cost-effective than selecting specifically adapted genotypes (Windhausen *et al.*, 2012). This is not necessarily true when a plant-breeding programme is organized in a participatory way (Mustafa *et al.*, 2006).

The issue of the heterogeneity and the multitude of the environments affected by drought has been addressed by developing an innovative type of breeding programme for drought prone areas based on the collaboration between farmers and scientists known as participatory plant breeding (PPB) (Ceccarelli *et al.*, 2007, 2009). PPB is based on breeding for specific adaptation to both the climatic and social environment and for wide adaptation over time (also called stability or dependability) and is conducted independently in areas that are consistently different. PPB has been shown to be able to reconcile yield increases with increased biodiversity in space and time, adaptation to climate changes and enhanced rate of adoption of new varieties (Ceccarelli *et al.*, 2009).

Genomic selection, a form of MAS that simultaneously estimates all locus, haplotype or marker effects across the entire genome to calculate genomic estimated breeding values (Heffner *et al.*, 2009), is expected to revolutionize breeding in the next decade. For the time being, however, genomic selection falls short of the expectations because its accuracy is limited by inefficiencies in the prediction of phenotype from genotype (Morrell *et al.*, 2012).

A fundamental component of a breeding strategy is the choice of the right type of germplasm and the next sections will illustrate examples of the importance of landraces and wild relatives in breeding for drought resistance.

13.4 The Value of Genetic Resources under Drought

Today there is a contradiction between the importance of biodiversity and the dangers associated with its decline, which is

recurrently emphasized by the major scientific journals (e.g. see Cardinale *et al.*, 2012; Hooper *et al.*, 2012), and the vulnerability of our crops associated with the continuous decline of agrobiodiversity (Esquinas-Alcázar, 2005; Keneni *et al.*, 2012). Modern agriculture has required the development of uniform varieties, which has been met by both public and private plant breeders with a limited number of standard, high-yielding varieties: this has characterized the Green Revolution, which has made it possible to boost food production at the price of the loss of innumerable heterogeneous traditional farmers' varieties (Esquinas-Alcázar, 2005).

13.4.1 Landraces

In many developing countries, and for crops grown in low input conditions and in stress environments, landraces are still the backbone of agricultural production (Ceccarelli, 1984; Flower, 1996; Kelley *et al.*, 1996; Sthapit *et al.*, 1996; Grando *et al.*, 2001). The reasons why farmers prefer to grow only landraces or continue to grow landraces even after partial adoption of modern cultivars are many, often including quality attributes such as food and feed quality (Kelley *et al.*, 1996), and seed storability (Ceccarelli and Grando, 1999). Landraces are often able to produce some yield even in difficult conditions where modern varieties are less reliable. For example, where farmers have adopted modern cultivars they have kept the landraces in the most unfavourable areas of the farm (Cleveland *et al.*, 2000). The value of landraces as sources of drought tolerance has been well documented in the case of barley in Syria (Ceccarelli *et al.*, 1995; Grando *et al.*, 2001) and in several other crops elsewhere (Brush, 1999). The comparison between barley landraces and modern cultivars under a range of conditions from severe stress (low input and low rainfall) to moderately favourable conditions (high inputs and high rainfall) has consistently indicated that:

- 1.** On average, landraces yield more than modern cultivars under low-input and stress conditions (see Table 13.2).
- 2.** Within landraces, there is considerable variation for grain yield under low input and drought stress conditions, but all the landrace-derived lines yield something, whereas some modern cultivars fail (see Table 13.3).
- 3.** Landraces are responsive to both inputs and rainfall and the yield potential of some lines is high, though not as high as modern cultivars (see Table 13.3).
- 4.** The superiority of landraces is not associated with mechanisms of escape to drought stress, as shown by their heading date (see Table 13.4).
- 5.** It is possible to find modern cultivars which under low-input and stress conditions yield almost as well as landraces, but their frequency is very low.

The data in Table 13.2 suggest that selection conducted only in high-input conditions or in intermediate conditions is likely to miss most of the lines that would have performed well under low input conditions. The assumption of most breeding programmes that landraces are genetically inferior is based on work conducted in research stations. Even those breeding programmes addressing target environments that have a low yield potential because of the combination of biotic and abiotic stresses have rarely challenged this assumption.

An example of the potential value of landraces in marginal environments is given in Table 13.3 where barley breeding lines, unrelated to local barley landraces, were compared with 77 pure lines extracted from Syrian landraces in two contrasting environments, one affected by drought stress represented by two locations with 186 mm and 185 mm rainfall, respectively (YS), and the second not affected by drought and represented by three locations with 504 mm, 234 mm and 317 mm, respectively.

The landraces have an average yield advantage of 60% under stress, whereas the modern cultivars have an average yield advantage of 14% in the absence of stress. In

Table 13.2. Grain yield (kg ha^{-1}) of pure lines derived from Syrian landraces and modern cultivars at three levels of stress^a in northern Syria (from Ceccarelli, 1996b).

| Environment | Landraces (n = 44) | Modern (n = 206) | Difference | P ^b |
|--------------|-----------------------|---------------------|------------|----------------|
| Stress | 1038 | 591 | 447 | <0.01 |
| Intermediate | 3105 | 3291 | 186 | NS |
| Non-stressed | 4506 | 6153 | 1647 | <0.01 |

^a as defined by average precipitation and soil fertility (Ceccarelli, 1996b); ^b based on *t*-tests for groups of unequal size; NS, not significant.

Table 13.3. Grain yield (kg ha^{-1}) under stress (YS) and grain yield under non-stress (YNS) of barley breeding lines classified according to the germplasm type (from Ceccarelli, 1994).

| Type of germplasm | YS ^b | | | YNS ^c | |
|------------------------|-----------------|-------|----------|------------------|-----------|
| | N ^a | Yield | Range | Yield | Range |
| Non-landraces | 155 | 488 | 0–893 | 3901 | 2310–4981 |
| Landraces ^d | 77 | 788 | 486–1076 | 3413 | 2398–4610 |
| Best check | | | | 4147 | |

^aNumber of entries; ^baverage of two stress sites; ^caverage of three non-stress sites; ^dpure lines obtained by pure line selection within landraces.

Table 13.4. Means of morphological, developmental and agronomic traits in 1041 modern (unrelated to Syrian landraces) barley genotypes compared with 322 pure lines extracted from Syrian landraces^a (from Ceccarelli, 1994).

| Traits | Non-landraces (n = 1041) | Landraces (n = 322) |
|--|-----------------------------|------------------------|
| Early growth vigour (1 = good; 5 = poor) | 2.5 b | 3.2 a |
| Growth habit (1 = erect; 5 = prostrate) | 2.8 b | 4.0 a |
| Cold tolerance (1 = tolerant; 5 = susceptible) | 3.0 a | 1.3 b |
| Days to heading (from emergence) | 117.9 b | 121.2 a |
| Grain filling duration (days) | 39.3 a | 35.5 b |
| Yield potential (kg ha^{-1}) | 4398.0 a | 3293.0 b |
| Yield under stress (kg ha^{-1}) | 483.1 b | 984.0 a |

^aMeans followed by the same letter are not significantly ($P < 0.05$) different based on *t*-test for samples of unequal size.

addition to the mean performance of the two types of germplasm, the interval of variation is very informative. All 77 lines from landraces yielded something under stress, whereas some of the modern cultivars failed; the best modern cultivars yielded almost as much as the best landraces. Under non-stress conditions, it was interesting to find that the yield of some landraces was not significantly inferior to that of the best modern cultivars.

In the attempt to understand the basis of the adaptation of landraces to drought

stress conditions, we evaluated a number of morphological and developmental traits in landrace and non-landrace material hoping to find a relatively simple explanation to the superiority of the landraces under drought stress. The choice of the traits was limited to those that are easy, cheap and quick to measure because these are essential requisites for use in a breeding programme. The results were discouraging (Table 13.4). Landraces differ from non-landraces in a number of traits that together appear to form an adaptive complex.

If the genetic structure of landraces is considered as an evolutionary approach to survival and performance under arid and semi-arid conditions (Schulze, 1988), then it appears that during millennia of cultivation under adverse conditions, natural and artificial selection have not been able to identify either an individual genotype possessing 'a trait' associated with its superior performance or an individual genotype with a specific architecture of different traits. On the contrary, the combined effects of natural and artificial selection have led to an architecture of genotypes representing different combinations of traits each able to respond to different types of drought and different combinations of various abiotic and biotic stresses.

The value of landraces and their contribution to plant breeding has been recently summarized in the case of cereals by Newton *et al.* (2010). In the case of legumes, there is also quite a considerable body of evidence suggesting the presence of useful genes both in landraces and wild relatives (Teshome *et al.*, 2010). In these reviews, examples of the contribution of landraces to plant breeding include contributing useful genes both for resistance to abiotic stresses, particularly to drought and high temperatures, and for resistance or tolerance to biotic stresses. The latter has probably been the most common and widespread contribution of landraces that in several crops have been used as donors of resistance genes to virtually all the most important diseases. This is also highly relevant in the case of climate change because one of the expected side effects is an increase in the frequency of both pest and disease epidemics.

13.4.2 Crop wild relatives

Crop wild relatives have particular value because of their potential to contribute beneficial traits to crops, such as biotic and abiotic resistance, leading to improved yield and stability (Maxted *et al.*, 2006). Crop wild relative species tend to contain greater genetic variation than crops because they have not passed through the genetic bottleneck

of domestication that has reduced the diversity available to breeders, and so they are expected to present a reservoir of useful variation for crop improvement (Vollbrecht and Sigmon, 2005).

Crop wild relatives have contributed significantly to improving food production and have been used particularly in barley (Lakew *et al.*, 2011, 2012, 2013), cassava (Nassar, 2003), potato (Bradshaw *et al.*, 2006), rice (Brar, 2005), tomato (Rick and Chetelat, 1995), lentil (Erskine *et al.*, 1994), chickpea (Singh and Ocampo, 1997) and wheat (Valkoun, 2001; Zaharieva *et al.*, 2001). Wild relatives have been mostly used as sources of pest and disease resistance genes (80% of the traits according to Hajjar and Hodgkin, 2007, 56% of the papers according to Maxted *et al.*, 2012), much less as sources of genes for drought tolerance (17% of the references cited abiotic stress as an objective in Maxted *et al.*, 2012) although several studies in a number of crops have identified useful genes for drought resistance in the corresponding wild relatives.

Barley breeders have long recognized the inherent value of wild species for the improvement of important agronomic, disease and quality traits. For example, the introgression of germplasm from wild barley, *Hordeum vulgare spp. spontaneum* (hereafter *H. spontaneum*), has been considered useful to increase the genetic variation for characters that contribute to drought tolerance in barley (Nevo, 1992; Forster *et al.*, 1997; Ivandic *et al.*, 2000; Grando *et al.*, 2001; Baum *et al.*, 2003; Ceccarelli *et al.*, 2004). One example of using wild relatives in a breeding programme was ICARDA's barley breeding programme that routinely used *H. spontaneum* for drought stressed environments. One of the reasons for choosing *H. spontaneum* was its ability to maintain a long stem even under severe drought. Plant height in very dry years is very important to farmers for two reasons: firstly, it allows mechanical harvesting, which is much cheaper than hand harvesting, and second it is associated with higher straw yield and the price of straw in dry years can nearly match the price of grain. Lodging susceptibility associated with tall plants is

seldom a problem because of the prevailing low input and dry conditions.

The decisive year for including *H. spontaneum* in ICARDA's breeding programme for stress environments was 1987 when a *H. spontaneum* collection was evaluated at a very dry site in Syria. That year rainfall was only 176.2 mm and there was a crop failure (Ceccarelli, 1994) with virtually no breeding lines in the entire programme able to produce grain. The only lines able to head and to produce some grains were two accessions of *H. spontaneum*. In these, some photosynthetic activity was found between 0700 and 0800 hours, the average net photosynthesis was $2.7 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and stomatal conductance was $0.060 \pm 0.003 \text{ mol m}^{-2} \text{ s}^{-1}$. At the same time, the stomata of the locally adapted landrace, Arabi Aswad, considered to be drought resistant, were closed. By midday, the stomatal conductance of the *H. spontaneum* accessions decreased to $0.025 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at a leaf water potential of -4.6 Mpa while the leaf water potential of Arabi Aswad was -3.5 Mpa and the stomatal conductance was zero. These lines combined earliness with an acceptable level of cold resistance, they were able to maintain good plant height under drought conditions and, despite the very dry conditions, they were also able to extrude part of the last internode outside the flag leaf (Grando *et al.*, 2001). The two *H. spontaneum* accessions have been used routinely in the crossing programme ever since.

Recently Lakew *et al.* (2011, 2012, 2013) used barley lines with various levels of introgression of the same two *H. spontaneum* accessions described above with the objective of identifying chromosomal regions in the two wild barleys responsible for increasing barley yields in marginal environments characterized by severe moisture stress. The lines were tested in a range of locations/years from highly drought stressed (about 0.7 t ha^{-1}) to favourable conditions (4.5 t ha^{-1}) (Fig. 13.2). The top yielding lines in the two driest environments (BR04 and KH05) were derived mostly from crosses with one of the two *H. spontaneum* accessions, whereas most of the improved varieties

(group 8 with no *H. spontaneum* introgression) showed a positive genotype by environment (GE) interaction with the highest yielding environments (TH04, TH05 and TH06). The results of the field experiments indicated that there was variation for grain yield under drought stress among barley genotypes, and that some of the lines derived from *H. spontaneum* had consistently superior specific adaptation to the range of severe stress conditions used in this study even if the study was unable to associate this superiority with specific chromosomal regions. The usefulness of *H. spontaneum* in breeding programmes for stress conditions is likely to increase in view of the predicted increase in the occurrence of high temperatures and droughts.

13.5 A Dynamic Response to Climate Change

As landraces and wild relatives are likely to become important sources of useful genetic variation when trying to cope with increased levels of drought resistance in the varieties needed to cope with climate change, the emphasis will be on where to access this type of germplasm.

The two most obvious sources of novel genetic variation are the gene banks and/or the farmers' fields. The major difference between the two sources of genetic variation is that the first is static, in the sense that it represents the genetic variation available in the collection sites at the time the collection was made, whereas the second is dynamic because landraces and wild relatives are heterogeneous populations and, as such, they evolve and can generate continuously novel genetic variation. The difference can be relevant as shown recently by Nevo *et al.*, (2012) who found that accessions of wild wheat and barley relatives collected in Israel in 2008 were significantly earlier than the accessions collected in the same locations 28 years earlier and kept in a gene bank. The finding is important because it confirms that even populations of predominantly self-pollinated plants can evolve, as also shown by Morran *et al.* (2009).

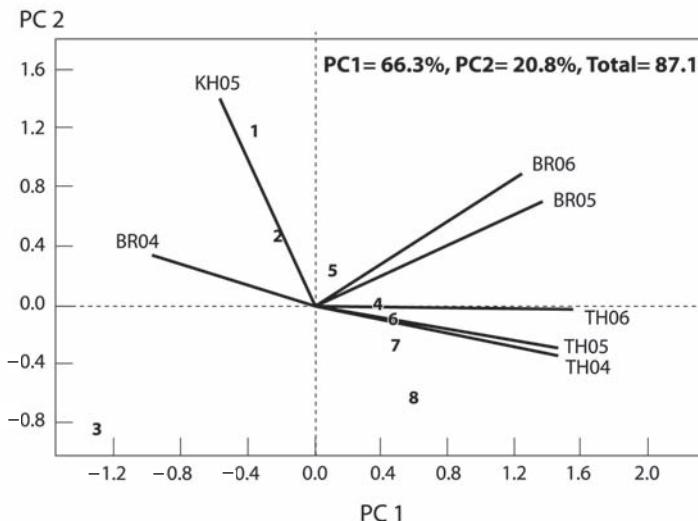


Fig. 13.2. GGE biplot for grain yield data in seven year \times location combinations of eight groups of barley genotypes differing for the percentage of observed introgression with *H. spontaneum* (group 1 = 44.5%, group 2 = 24.2%, group 3 = 22.6%, group 4 = 45.4%, group 5 = 19.0%, group 6 = 15.5%, group 7 = 11.4%, group 8 = 0%). Groups 1, 2, 3 and 6 are introgressed with one accession of *H. spontaneum*, and groups 4, 5 and 7 with a different accession (from Lakew *et al.*, 2011).

A strategy to cope with drought resistance, defined earlier as a moving target in the case of climate change, is to use population (evolutionary) breeding which produces heterogeneous varieties better able to cope with the year-to-year variability expected to increase with climate change. Evolutionary plant breeding can also produce uniform varieties capable of responding to market demand by superimposing artificial selection within the evolving population.

Evolutionary breeding (Suneson, 1956) is based on populations with large genetic variability, such as mixtures of F_2 s, which can be handled directly by farmers in a multitude of environments while they slowly evolve and adapt. At ICARDA, evolutionary breeding was combined with the participatory programmes for barley and wheat and implemented in Syria, Jordan, Iran, Eritrea, Algeria, Ethiopia, and recently in Italy as a component of a European project on organic agriculture. The aim is to increase the probability of recombination within a population, which is constituted deliberately

to harbour a very large amount of genetic variation.

In the case of barley such a population consisted of a mixture of nearly 1600 F_2 s (Ceccarelli *et al.*, 2010), whereas, in the case of durum and bread wheat, the population consisted of a mixture of slightly more than 700 crosses and more than 2500 F_2 -derived F_3 and F_4 generations, respectively. The barley population was planted at 19 locations in five countries, whereas the durum and bread wheat populations have been planted at five locations. The three populations have been left evolving under the pressure of changing climate conditions with the expectation of an increase in the frequency of genotypes with adaptation to the conditions (climate, soil, agronomic practices, abiotic and biotic stresses) of the location where each year the population is grown. The simplest and cheapest way of implementing evolutionary breeding is for the farmers to plant and harvest in the same location. The breeder and the farmers can, however, superimpose artificial selection with criteria that may change from location

to location and with time. While the population is evolving, lines can be derived and tested as pure lines in the participatory breeding programmes, or can be used as multilines, or a sub-sample of the population can be directly used for cultivation exploiting the advantages of intra-population genetic diversity described earlier. The key aspect of the method is that, while the lines are continuously extracted, the population is left evolving for an indefinite amount of time, thus becoming a unique source of continuously better adapted genetic material directly in the hands of the farmers. This approach generates a large agrobiodiversity both in space and in time. In all the countries where the evolutionary populations are currently grown (including some developed countries), the farmers share the excess seed with others so that the populations are rapidly spreading across the farmers' communities. This guarantees that the improved material will be readily available to farmers without the bureaucratic and inefficient systems of variety release and formal seed production.

13.6 Conclusions

Drought is a complex problem that affects the livelihoods of millions of poor every year and most likely will become more frequent as the climate changes. Current knowledge on the molecular basis of drought resistance is not yet sufficient to develop more drought resistant crops or varieties. Therefore, for the time being, conventional breeding based on specific adaptation and evolutionary strategies, and with the collaboration of farmers seems to be the only realistic avenue to develop in the short-term drought-resistant varieties quickly available on the ground. As our knowledge of the genetic basis of drought resistance improves, biotechnological techniques and genomic tools might offer the possibility of introducing new traits and regulatory mechanisms that would improve the efficiency of selection. As this is now admittedly recognized as an avenue for the future, there is a need to re-address the allocation of resources, which

are currently grossly unbalanced in favour of approaches that are not likely to accelerate the production of new varieties in the timeframe of climate change.

References

- Altieri, M.A. and Koohafkan, P. (2003) *Enduring Farms: Climate Change, Smallholders and Traditional Farming Communities*. Third World Network, 131 Jalan Macalister, 10400 Penang, Malaysia, p. 72.
- Baum, M., Grando, S., Backes, G., Jahoor, A., Sabbagh, A. et al. (2003) QTLs for agronomic traits in the Mediterranean environment identified in recombinant inbred lines of the cross 'Arta'×*H. spontaneum* 41 - 1. *Theoretical Applied Genetics* 107, 1215–1225.
- Blum, A. (2011) Drought resistance – is it really a complex trait? *Functional Plant Biology* 38, 753–757.
- Bradshaw, J.E., Bryan, G.J., and Ramsay, G. (2006) Genetic resources (including wild and cultivated *Solanum* species) and progress in their utilisation in potato breeding. *Potato Research* 49, 49–65.
- Brar, D. (2005) Broadening the gene pool and exploiting heterosis in cultivated rice. In: Toriyama, K., Heong, K.L. and Hardy, B. (eds) *Rice is Life: Scientific Perspectives for the 21st Century*. Proceedings of the World Rice Research Conference, Tokyo and Tsukuba, Japan, 4–7 November 2004, pp. 157–160.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C. et al. (2012) Biodiversity loss and its impact on humanity. *Nature* 486, 59–67.
- Ceccarelli, S. (1984) Utilization of landraces and *Hordeum spontaneum* in barley breeding for dry areas. *Rachis* 3, 8–11.
- Ceccarelli, S. (1994) Specific adaptation and breeding for marginal conditions. *Euphytica* 77, 205–219.
- Ceccarelli, S. (1996a) Adaptation to low/high input cultivation. *Euphytica* 92, 203–214.
- Ceccarelli, S. (1996b) Positive interpretation of genotype by environment interactions in relation to sustainability and biodiversity. In: Cooper, M. and Hammers, G.L. (eds) *Plant Adaptation and Crop Improvement*. CAB International, Wallingford, UK, ICRISAT, Andhra Pradesh, India, and IRRI, Manila, Philippines, pp. 467–486.
- Ceccarelli, S., and Grando, S. (1999) Barley landraces from the Fertile Crescent: a lesson for plant breeders. In: Brush, S.B. (ed.) *Genes in the Field: On-Farm Conservation of Crop*

- Diversity. IPGRI, IDRC and Lewis Publishers, Boca Raton, Florida, pp. 51–76.
- Ceccarelli, S. and Grando, S. (2002) Plant breeding with farmers requires testing the assumptions of conventional plant breeding: Lessons from the ICARDA barley program In: Cleveland, D.A. and Soleri, D. (eds) *Farmers, Scientists and Plant Breeding: Integrating Knowledge and Practice*. CAB International, Wallingford, UK, pp. 297–332.
- Ceccarelli, S., Acevedo, E. and Grando, S. (1991) Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. *Euphytica* 56, 169–185.
- Ceccarelli, S., Grando, S., and van Lier, J.A.G. (1995) Barley landraces of the Fertile Crescent offer new breeding options for stress environments. *Diversity* 11, 112–113.
- Ceccarelli, S., Grando, S., Baum, M. and Udupa, S.M. (2004) Breeding for drought resistance in a changing climate. In: Rao, S.C. and Ryan, J. (eds) *Challenges and Strategies for Dryland Agriculture*. CSSA Spec. Publ. 32. ASA and CSSA, Madison, Wisconsin, pp. 167–190.
- Ceccarelli, S., Grando, S. and Baum, M. (2007) Participatory plant breeding in water-limited environments. *Experimental Agriculture* 43, 411–435.
- Ceccarelli, S., Guimaraes, E.P. and Weltzien, E. (eds) (2009) *Plant Breeding and Farmer Participation*. FAO, Rome, Italy.
- Ceccarelli, S., Grando, S., Maatougui, M., Michael, M., Slash, M. et al. (2010) Plant breeding and climate changes. *Journal of Agricultural Science* 148, 627–638.
- Chapman, S.C. (2008) Use of crop models to understand genotype by environment interactions for drought in real world and simulated plant breeding trials. *Euphytica* 161, 195–208.
- Cleveland, D.A., Soleri, D. and Smith, S.E. (2000) A biological framework for understanding farmers' plant breeding. *Economic Botany* 54, 377–390.
- Collins, N.C., Tardieu, F. and Tuberrosa, R. (2008) Quantitative trait loci and crop performance under abiotic stress: where do we stand? *Plant Physiology* 147, 469–486.
- Condon, A.G., Richards, R.A., Rebetzke, G.J. and Farquhar, G. (2002) Improving intrinsic water-use efficiency and crop yield. *Crop Science* 42, 122–131.
- deMenocal, P.B. (2001) Cultural responses to climate change during the late holocene. *Science* 292, 667–673.
- Erskine, W., Tufail, M., Russell, A., Tyagi, M.C., Rahman, M.M. et al. (1994) Current and future strategies in breeding lentil for resistance to biotic and abiotic stresses. *Euphytica* 73, 127–135.
- Esquinas-Alcázar, J. (2005) Protecting crop genetic diversity for food security: political, ethical and technical challenges. *Nature Reviews Genetics* 6, 946–953.
- Food and Agriculture Organization of the United Nations (2012) Hunger. Available at: www.fao.org/hunger/en/ (accessed 21 November 2012).
- Fleury, D., Jefferies, S., Kuchel, H. and Langridge, P. (2010) Genetic and genomic tools to improve drought tolerance in wheat. *Journal of Experimental Botany* 61, 3211–3222.
- Flower, D.J. (1996) Physiological and morphological features determining the performance of the sorghum landraces of northern Nigeria. *Experimental Agriculture* 32, 129–141.
- Forster, B.P., Russell, J.R., Ellis, R.P., Handley, L.L., Robinson, D. et al. (1997) Locating genotypes and genes for abiotic stress tolerance in barley: a strategy using maps, markers and the wild species. *New Phytologist* 137, 141–147.
- Fresco, L.O. and Baudoin, W.O. (2002) Food and nutrition security towards human security. In: *ICV Souvenir Paper*, International Conference on Vegetables: World Food Summit Five Years Later. 11–13 June 2002, Rome, Italy.
- Grando, S., von Bothmer, R. and Ceccarelli, S. (2001) Genetic diversity of barley: use of locally adapted germplasm to enhance yield and yield stability of barley in dry areas. In: Cooper, H.D., Spillane, C. and Hodgkin, T. (eds) *Broadening the Genetic Base of Crop Production*. CABI, New York, FAO, Rome, and IPGRI, Rome, pp. 351–372.
- Gupta, P., Langridge, P. and Mir, R. (2010) Marker-assisted wheat breeding: present status and future possibilities. *Molecular Breeding* 26, 145–161.
- Hajjar, R. and Hodgkin, T. (2007) The use of wild relatives in crop improvement: a survey of developments over the last 20 years. *Euphytica* 156, 1–13.
- Hazell, P.B.R. (2003) The Green Revolution. In: Mokyr, J. (ed.) *Encyclopaedia of Economic History*. Oxford University Press, Oxford, UK, pp. 478–480.
- Heffner, E.L., Sorrells, M.E. and Jannink, J-L. (2009) Genomic selection for crop improvement. *Crop Science* 49, 1–12.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A. et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–108.

- Ivandic, V., Hackett, C.A., Zhang, Z.J., Staub, J.E., Nevo, D. et al. (2000) Phenotypic responses of wild barley to experimentally imposed water stress. *Journal of Experimental Botany* 51, 2021–2029.
- Kelley, T.G., Parthasarathy Rao, P., Weltzien, E. and Purohit, M.L. (1996) Adoption of improved cultivars of pearl millet in an arid environment: straw yield and quality considerations in western Rajasthan. *Experimental Agriculture* 32, 161–171.
- Kenen, G., Bekele, E., Imtiaz, M. and Dagne, K. (2012) Genetic vulnerability of modern crop cultivars: causes, mechanism and remedies. *International Journal of Plant Research* 2, 69–79.
- Lakew, B., Eglinton, J., Henry, R.J., Baum, M., Grando, S. et al. (2011) The potential contribution of wild barley (*Hordeum vulgare* spp. *spontaneum*) germplasm to drought resistance of cultivated barley (*Hordeum vulgare* spp. *vulgare*). *Field Crops Research* 120, 161–168.
- Lakew, B., Henry, R.J., Eglinton, J., Baum, M., Ceccarelli, S. et al. (2012) SSR analysis of introgression of drought tolerance from the genome of *Hordeum spontaneum* into cultivated barley (*Hordeum vulgare* spp. *vulgare*). *Euphytica* DOI 10.1007/s10681-012-0795-9.
- Lakew, B., Henry, R.J., Ceccarelli, S., Grando, S., Eglinton, J. et al. (2013) Genetic analysis and phenotypic associations for drought tolerance in *Hordeum spontaneum* introgression lines using SSR and SNP markers. *Euphytica* 189, 9–29.
- Lauer, J.G., Bijl, C.G., Grusak, M.A., Baenziger, P.S., Boote, K. et al. (2012) The scientific grand challenges of the 21st century for the Crop Science Society of America. *Crop Science* 52, 1003–1010.
- Luck, J., Spackmand, M., Freedman, A., Trębicki, P., Griffiths, W. et al. (2011) Climate change and diseases of food crops. *Plant Pathology* 60, 113–121.
- Maxted, N., Ford-Lloyd, B.V., Jury, S.L., Kell, S.P. and Scholten, M.A. (2006) Towards a definition of a crop wild relative. *Biodiversity Conservation* 15, 2673–2685.
- Maxted, N., Kell, S., Ford-Lloyd, B., Dulloo, E. and Toledo, A. (2012) Toward the systematic conservation of global crop wild relative diversity. *Crop Science* 52, 774–785.
- Mir, R.R., Zaman-Allah, M., Sreenivasulu, N., Trethowan, R. and Varshney, R.K. (2012) Integrated genomics, physiology and breeding approaches for improving drought tolerance in crops. *Theoretical Applied Genetics* 125, 625–645.
- Morran, L.T., Parmenter, M.D. and Phillips, P.C. (2009) Mutation load and rapid adaptation favour outcrossing over self-fertilization. *Nature* 462, 350–352.
- Morrell, P.L., Buckler, E.S., Ross-Ibarra, J. (2012) Crop genomics: advances and applications. *Nature Reviews Genetics* 13, 85–96.
- Munns, R. and Richards, R.A. (2007) Recent advances in breeding wheat for drought and salt stresses. In: Jenks, M.A.P., Hasegawa, M. and Jain, S.M. (eds) *Advances in Molecular Breeding toward Drought and Salt Tolerant Crops*. Springer-Verlag, Dordrecht, the Netherlands, pp. 565–586.
- Mustafa, Y., Grando, S. and Ceccarelli, S. (2006) *Assessing the Benefits and Costs of Participatory and Conventional Barley Breeding Programs in Syria*. ICARDA, Aleppo, Syria.
- Nassar, N.M.A. (2003) Cassava, *Manihot esculenta* Crantz genetic resources: VI Anatomy of a diversity center. *Genetics and Molecular Research* 2, 214–222.
- Nevo, E. (1992) Origin, evolution, population genetics and resources for breeding of wild barley, *Hordeum spontaneum*, in the Fertile Crescent. In: Shewry, R.P. (ed.), *Barley: Genetics, Biochemistry, Molecular Biology and Biotechnology*. CAB International, Wallingford, UK, pp. 19–43.
- Nevo, E., Fu, Y.-B., Pavlicek, T., Khalifa, S., Tavasi, M. et al. (2012) Evolution of wild cereals during 28 years of global warming in Israel. *Proceedings of the National Academy of Sciences USA* 109, 3412–3415.
- Newton, A.C., Akar, T., Baresel, J.P., Bebeli, P.J., Bettencourt, E. et al. (2010) Cereal landraces for sustainable agriculture. A review. *Agronomy for Sustainable Development* 30, 237–269.
- Öztürk, Z.N., Talamé, V., Michalowski, C.B., Gozukirmiz, N., Tuberosa, R. et al. (2002) Monitoring large-scale changes in transcript abundance in drought- and salt-stressed barley. *Plant Molecular Biology* 48, 551–573.
- Parry, M.A.J., Flexas, J. and Medrano, H. (2005) Prospects for crop production under drought: research priorities and future directions. *Applied Biology* 147, 211–226.
- Passioura, J.B. (2006) Increasing crop productivity when water is scarce – from breeding to field management. *Agricultural Water Management* 80, 176–196.
- Reynolds, M., Dreicer, F. and Trethowan, R. (2007) Drought-adaptive traits derived from wheat wild relatives and landraces. *Journal of Experimental Botany* 58, 177–186.
- Rick, C. and Chetelat, R. (1995) Utilization of related wild species for tomato improvement. *Acta Horticulturae* 412, 21–38.
- Rosen, A.M. (1990) Environmental change at the

- end of early Bronze Age Palestine. In: De Miroshchedji, P. (ed.) *L'Urbanisation de la Palestine à l'Âge du Bronze Ancient*. BAR International, Oxford, UK, pp. 247–255.
- Schulze, E.D. (1988) Adaptation mechanisms of non cultivated arid-zone plants: useful lesson for agriculture? In: Bidinger, F.R. and Johansen, C. (eds) *Drought Research Priorities for the Dryland Tropics*. ICRISAT, Hyderabad, India, pp. 159–177.
- Seki, M., Narusaka, M., Ishida, J., Nanjo, T., Fujita, M. et al. (2002) Monitoring the expression profiles of 7000 *Arabidopsis* genes under drought, cold and high-salinity stresses using a full-length cDNA microarray. *Plant Journal* 31, 279–292.
- Singh, K.B. and Ocampo, B. (1997) Exploitation of wild *Cicer* species for yield improvement on chickpea. *Theoretical and Applied Genetics* 95, 418–423.
- Sthapit, B.R., Joshi, K.D. and Witcombe, J.R. (1996) Farmer participatory crop improvement. III. Participatory plant breeding, a case study for rice in Nepal. *Experimental Agriculture* 32, 479–496.
- Stern, N. (2007) *The Economics of Climate Change: The Stern Review*. Cambridge University Press, Cambridge. Also available at: www.hm-treasury.gov.uk/independent_review_ws/stern_review_economics_climate_change/stern_review_Report.cfm (accessed 20 November 2012).
- Suneson, C.A. (1956) An evolutionary plant breeding method. *Agronomy Journal* 48, 188–191.
- Teshome, A., Brown, A.H.D. and Hodgkin, T. (2010) Diversity in landraces of cereal and legume crops. *Plant Breeding Reviews* 21, 221–261.
- US Drought Monitor (2012) Available at: www.droughtmonitor.unl.edu/ (accessed 21 November 2012).
- Valkoun, J. (2001) Wheat pre-breeding using wild progenitors. *Euphytica* 119, 17–23.
- Vollbrecht, E. and Sigmon, B. (2005) Amazing grass: developmental genetics of maize domestication. *Biochemical Society Transactions* 33, 1502–1506.
- Windhausen, V.S., Wagener, S., Magorokosho, C., Makumbi, D., Vivek, B. et al. (2012) Strategies to subdivide a target population of environments: results from the CIMMYT-led maize hybrid testing programs in Africa. *Crop Science* 52, 2143–2152.
- Zaharieva, M., Gaulin, E., Havaux, M., Acevedo, E. and Monneveux, P. (2001) Drought and heat responses in the wild wheat relative *Aegilops geniculata* Roth: potential interest for wheat improvement. *Crop Science* 41, 1321–1329.
- Zhou, J., Wang, X., Jiao, Y., Qin, Y., Liu, X. et al. (2007) Global genome expression analysis of rice in response to drought and high-salinity stresses in shoot, flag leaf, and panicle. *Plant Molecular Biology* 63, 591–608.