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Abstract.   Drought, being a yield-limiting factor, has become a major threat to international food security. It is a complex process, and drought tolerance response is carried out by various genes, transcription factors, microRNAs, hormones, proteins, co-factors, ions and metabolites. This complexity has limited the development of crop cultivars for drought tolerance. Breeding for drought tolerance is further complicated because several types of abiotic stress, such as high temperatures, high irradiance, and nutrient toxicities or deficiencies, can challenge crop plants simultaneously. Although marker-assisted selection is now widely deployed in wheat, it has not contributed significantly to cultivar improvement for adaptation to low-yielding environments, and breeding has relied largely on direct phenotypic selection for improved performance in these difficult environments. Advances in plant breeding to produce improved and higher performing wheat cultivars are key to making dryland food-production systems more efficient and more resistant to pressure from drought, extremes of cold and heat, unpredictable rainfall, and new pests and diseases. For optimal performance, wheat cultivars can be targeted to specific farming systems, depending on local conditions and stresses. Genetic gain in wheat yield potential during the last century has been achieved by plant breeding and is well documented. It has been studied by comparing, in the same field trial, the yield of cultivars characterised by different years of release. Genomic selection (GS) and high-throughput phenotyping (HTP) have attracted the interest of plant breeders, and both approaches promise to revolutionise the prediction of complex traits, including growth, yield and adaptation to stress. This review describes the impact of drought on yield, trends in yield for boosting crop yields to meet the projected demands of rising global population by 2050, and genetic gain achieved by plant breeding in the last decades; and gathers known functional information on the genes, metabolites and traits and their direct involvement in conferring drought tolerance in wheat. In addition, it discusses recently developed techniques (i.e. GS and HTP) integrated with approaches such as breeding, genetics, genomics, and agronomic strategies for improving drought in wheat.

Additional keywords: agro-physiological traits, climate change, genetic enhancement, *Triticum aestivum*.

Introduction

Agriculture in the 21st Century is facing a daunting challenge of attaining nearly a 70% increase in crop productivity by 2050 (Friedrich 2015; Joshi *et al*. 2016; Wang *et al*. 2016). Among the various abiotic factors challenging crop production globally, drought stress is increasingly playing a crucial role. Drought is a major cause of yield and quality loss in cereal crops throughout many of the world's cereal-growing areas (Passioura 2007). Almost half (47%) of Earth's land surface, equal to 6.45×10^9 ha, comprises drylands and they are distributed worldwide. Drought continues to be an important challenge to agricultural researchers and plant breeders. However, increased demand for water from municipal and industrial users, together with water needed to maintain environmental quality, will further reduce the amount available for irrigated crops. Although changes in tillage and irrigation practices can improve production by conserving water, enhancement of the genetic tolerance of crops to drought stress is considered an essential strategy for addressing moisture deficits. FAO's latest forecast for 2016 world cereal production stands at 2571 Mt, up marginally from October's forecast and 1.5% (39 Mt) above the 2015 output. Global wheat production in 2016 is now expected to rise to 746.7 Mt, up 1.7% year- on -year and about 1.0% (4.3 Mt) more than forecast in October, reflecting increases in the Russian Federation's output now anticipated at a new record- and in Kazakhstan, where favourable weather boosted yield prospects.

Drought frequently constrains the growth and productivity of major crop species such as wheat. Although genetic increases in yield potential are best expressed in optimum environments, they are also associated with enhanced yields under drought (Slafer and Araus 2007). World wheat production increased at a rate of 3.3% year^{-1} between 1949 and 1978. Increases at the start of this period were due to both an expansion of production area and increased yields. However, starting in the 1960s, yield increases came mainly from the planting of improved varieties and a greatly expanded use of irrigation, pesticides and fertilisers. The rate of increase in world wheat production slowed to 1.5% year^{-1} between 1982 and 1991, except in China, which maintained an annual rate of increase in production of 2.6% and

became the world's largest wheat producer. During the past 50 years, most of the yield progress in wheat has been due to the gradual replacement of traditional tall cultivars by dwarf and fertiliser-responsive varieties. Height reduction has increased the proportion of carbon partitioned to grain and increased the harvest index. It has also reduced the risk of yield penalties caused by lodging (Monneveux *et al.* 2012). Wheat, as the most widely grown crop globally, is presently witnessing average yield improvements of ~0.9% year^{-1}, far slower than the rates required to double production by 2050 solely from yield gains (Ray *et al.* 2013).

In this review, we discuss breeding approaches for improving yield of wheat under drought-prone environments. We also address how knowledge of the phenological, physiological and metabolic mechanisms of wheat can contribute to reaching these goals. In addition, recent developments in integrated approaches such as breeding, genetics, genomics, and agronomic strategies for improving resistance against drought in wheat are discussed.

Trends in wheat production

In general, breeding and agronomic improvements have achieved a linear increase in food production globally, at an average rate of 32 Mt year^{-1} (Fig. 1). However, to meet the recent Declaration of the World Summit on Food Security target of 70% more food by 2050, an average annual increase in production of 44 Mt is required (Fig. 1), representing a 38% increase over historical increases in production, to be sustained for 40 years. This scale of sustained increase in global food production is unprecedented and requires substantial changes in methods for crop improvement and agronomic processes. Achieving this increase in food production would be challenging in a stable environment, but it is undoubtedly much more so given the additional pressures created by global environmental changes (Tester and Langridge 2010).

Numerous studies have shown that feeding a more populated and more prosperous world will require roughly a doubling of agricultural production by 2050 (Godfray *et al.* 2010; Tilman

et al. 2011; Foley *et al.* 2011), translating to a rate of crop production growth of 2.4% year^{-1}, while the present average wheat global yield improvement is ~0.9% year^{-1}. At the present rates, global wheat production may increase by 38% by 2050. There is a 90% chance that the total global production increase from yields alone would be 4–76% for wheat by 2050. Thus, if these rates of yield change do not increase, land clearing would likely be needed (Tilman *et al.* 2011) to increase or even maintain global food security (Table 1).

Wheat yields are only increasing at the required rate of $\geq 2.4\%$ year^{-1} in some areas of the United States, mainly in eastern South Dakota, parts of Nebraska and north-eastern Kansas (Fig. 2). Wheat yields are decreasing in many parts of the United States Great Plains (Montana; western parts of North Dakota, South Dakota, Kansas and Texas; and eastern Colorado). In Mexico, areas with the required increasing rates of wheat yields occur only in the state of Zacatecas. Nationally, wheat yields in Canada, United States and Mexico are increasing at 1.3%, 0.8% and 1.1% year^{-1}, respectively.

Wheat provides 19% of global dietary energy. It comprises an even larger portion of the diet in some countries where yields are declining, particularly the Eastern European countries of Bulgaria, Hungary, Czech Republic, Moldova, Romania, Slovakia and Ukraine. In many countries such as Bolivia, Peru, Paraguay, Afghanistan and Iraq, wheat yield increases are too low to maintain their current per-capita harvests (Ray *et al.* 2013). Many studies illustrate that intensification can be unsustainable (Rockström *et al.* 2009; Heathcote *et al.* 2013); however, several notable projects in Africa (Pretty *et al.* 2011) and elsewhere (Mueller *et al.* 2012) have shown that sustainable intensification is possible and necessary to boost global crop production.

Increasing need for plant breeders

As the world population continues to increase and incomes rise, the demand for agricultural products will increase by at least 50% by 2050. Although plant breeding will be a key part of meeting
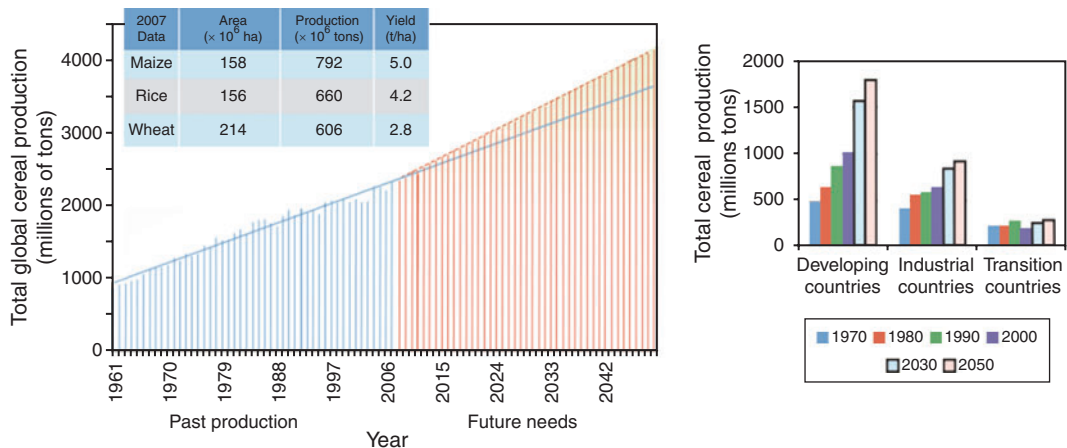
Fig. 1. Cereal production targets. Left panel: Global cereal production has risen from 877 Mt in 1961 to 2351 Mt in 2007 (blue). To meet predicted demands, production will need to rise to >4000 Mt by 2050 (red). The rate of yield increase must move from the blue trend line (32 Mt year^{-1}) to the red dotted line (44 Mt year^{-1}) to meet this demand, an increase of 37%. The inset table shows 2007 data for the three major cereals. Data from: http://faostat.fao.org/. Right panel: The greatest demand for yield increases will be from countries in the developing world (FAO 2006).

Table 1. Global summary for yield trends in wheat by 2050 (data from Ray *et al.* 2013)

Trends in yield	Values
Mean yield change per year (% year^{-1})	0.9
Mean rate of yield change per year (kg ha^{-1} year^{-1} year^{-1})	27
Projected average yield in 2025 (t ha^{-1} year^{-1})	3.4
Projected average yield in 2050 (t ha^{-1} year^{-1})	4.1
Projected production in 2025 (Mt year^{-1}) at fixed crop harvested areas of 2008	741
Projected production in 2050 (Mt year^{-1}) at fixed crop harvested areas of 2008	891
Projected production shortfall in 2025 compared with the rate that doubles production by 2050 (Mt year^{-1})	157
Projected production shortfall in 2050 compared with the rate that doubles production by 2050 (Mt year^{-1})	388
Required extra land (Mha) to the shortfall at 2025 projected yields	46
Required extra land (Mha) to the shortfall at 2050 projected yields	95
Yield in the year 2008 (t ha^{-1} year^{-1})	3.1
90% confidence limit in yield change (% year^{-1})	0.1–1.8
90% confidence limit in rate of yield change (kg ha^{-1} year^{-1} year^{-1})	4–52
90% confidence limit in production in 2025 (Mt year^{-1}) at fixed crop harvested areas of 2008	599–898
90% confidence limit in production in 2050 (Mt year^{-1}) at fixed crop harvested areas of 2008	618–1182

Rate of yield change (percent year^{-1})
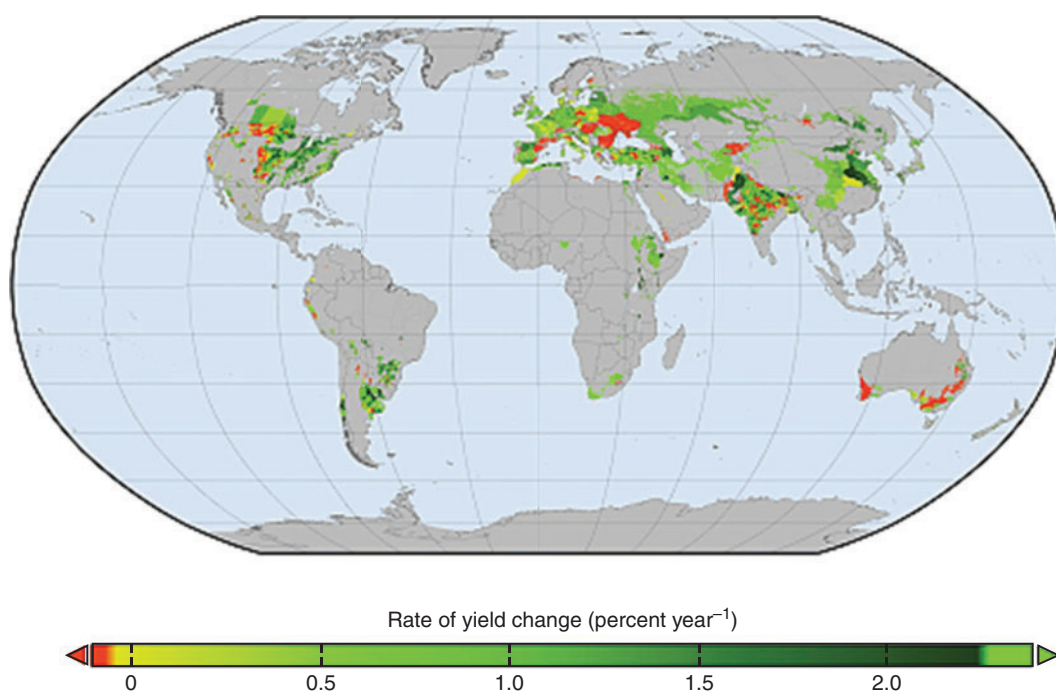
Fig. 2. Global map of current percentage rates of change in wheat yields per year. Red areas are where yields are declining; fluorescent green areas are where rates of yield increase, if sustained, would double production by 2050. Figure adapted from Ray *et al.* (2013).

that demand, recent reports in the United States and elsewhere have pointed out that too few plant breeders are being educated to fill the available positions. To be effective, plant breeders of the future will need a combination of knowledge, skills and experience in plant breeding, genetics, genomics, statistics, experimental design, genetic diversity and germplasm management (Repinski *et al.* 2011). They must be skilful communicators and have the ability to work well in interdisciplinary teams. Given rapid changes in crop science and genetic technology, breeders must continually upgrade their knowledge and skills.

Achieving genetic increases in yields under drought conditions has always been a difficult challenge for plant breeders. This is evident from the smaller genetic gains in dry regions compared with favourable environments or where irrigation is available. However, rainfed environments are characterised by unpredictable and highly variable seasonal rainfall and, hence, highly variable yields. This results in slow genetic advance in breeding programs because genetic variation in yield is masked by large genotype × environment (GE) interactions. A major challenge for breeders in dryland environments is to devise the most effective strategy for

maximising genetic gain. Substantial efforts are needed to identify representative sets of environments to evaluate the yield of breeding lines, and to devise efficient experimental designs to maximise genetic variation (Mohammadi and Amri 2013).

Breeders' efforts are focused on minimising the gap between yield potential and yield under stress conditions. Quantitative trait loci (QTLs) or underlying genes conferring a yield benefit under drought conditions need first to be identified in phenotypic screens and then incorporated into elite germplasm by using modern breeding technologies such as marker-assisted selection (MAS) (Tester and Langridge 2010). Despite some successes (Kumar *et al.* 2008; Mohammadi *et al.* 2014*a*), direct selection for yield in drought-prone environments has generally proven difficult. However, improvement in crop productivity in drought-prone environments will require genotypes with greater stress tolerance and yield stability.

Impact of drought on wheat growth, development and yield

Drought is a major production constraint of agriculture worldwide. It is estimated that cultivation on Earth is possible on only 16% of the potentially arable area owing to limited availability of water (Alexandratos and Bruinsma 2012). Drought occurs on all continents with varying intensity and frequency. Wheat production was significantly affected in Australia in 2006 when drought reduced yield by 46% (van Dijk *et al.* 2013). Iran is prone to severe drought every 5–7 years. Supplemental irrigation could help to prevent crop failure during droughts and improve yields in cropping seasons with average precipitation (Mohammadi *et al.* 2011*a*). Around 17% of the global cultivated area was affected by drought during 1980–2006 (Dai 2013). Drought principally affects crops cultivated under rainfed conditions, which represent 80% of the total cultivated area worldwide. In Pakistan, ~33% of wheat, 27% of maize, 56% of sorghum and millet, and 52% of barley crops are cultivated under rainfed conditions and are consequently drastically affected by drought (GOP 2014). The proportion of the global cultivated area permanently affected by drought is estimated to be ~20% for wheat, 28% for sorghum,

19% for barley and 19% for maize (Li *et al.* 2009). Pandey *et al.* (2007) estimated that 36% of total crop production is lost through drought in eastern India. The impact of drought stress on total yield varies with the region, crop and cultivar, and the occurrence of other stresses such as high temperatures. Some examples of the impact of drought stress on yield reduction in wheat are presented in Table 2.

Drought-induced yield reduction has been reported in wheat, and it depends on the severity and duration of the stress period. The effects of drought range from morphological to molecular and are evident at all phenological stages of plant growth at whatever stage the water deficit takes place. The first and foremost effect of drought is impaired germination and poor stand establishment (Harris *et al.* 2002). Drought stress has been reported to reduce germination and seedling stand severely (Kaya *et al.* 2006). Growth is accomplished through cell division, cell enlargement and differentiation, and it involves genetic, physiological, ecological and morphological events and their complex interactions. Many yield-determining physiological processes in plants respond to water stress, and yield integrates many of these physiological processes in a complex way. For water stress, the severity, duration and timing of stress, as well as responses of plants after stress removal and interaction between stress and other factors, are extremely important (Plaut 2003). For instance, in triticale genotypes, water stress applied at pre-anthesis reduced time to anthesis, whereas at post-anthesis it shortened the grain-filling period (Estrada-Campuzano *et al.* 2008).

Mechanisms of photosynthesis under drought stress

Photosynthesis is a key physiological process affected by drought stress in plants. Drought stress produces changes in photosynthetic pigments and components (Anjum *et al.* 2003); it also damages photosynthetic apparatus and diminishes activities of Calvin cycle enzymes, causing reduced crop yield (Monakhova and Chernyadèv 2002). Another important effect of drought stress that inhibits the growth and photosynthetic abilities of plants is the loss of balance between the production of reactive oxygen species (ROS) and the antioxidant defence

Table 2.   Impact of drought stress on yield loss in wheat at various growth stages

Growth stage	Species	Yield loss	Geographic location	Reference
Reproductive phase	Bread wheat (*Triticum aestivum* L.)	20.6%	Over the world	Daryanto *et al.* 2016
Tillering to maturity	Bread wheat	22–58%	Serbia	Dodig *et al.* 2012
Late tillering to grain-filling	Durum wheat (*Triticum durum* Desf.)	61%	Turkey	Kiliç and Yağbasanlar 2010
Flowering to maturity	Durum wheat	12–59% (mild stress)	Iran	Mohammadi 2016
Post-flowering	Durum wheat	12–52% (moderate stress)	Iran	Mohammadi *et al.* 2010
Booting to maturity	Bread wheat	37% (severe stress)	Iran	Shamsi *et al.* 2010
Booting to maturity	Bread wheat	27%	Iran	Shamsi and Kobraee 2011
Heading	Bread wheat	57%	Hungary	Balla *et al.* 2011
Heading to maturity	Bread wheat	44%	USA	Prasad *et al.* 2011
Anthesis and maturity	Bread wheat	58–92% (prolonged mild stress)	India	Dhanda and Sethi 2002
Pre-anthesis	Bread wheat	18–53% (prolonged mild stress)	Pakistan	Majid *et al.* 2007
Flowering	Bread wheat	19% (mild stress)	Iran	Sangtarash 2010
Anthesis	Bread wheat	11–39%	Pakistan	Jatoi *et al.* 2011
Post-anthesis	Bread wheat	13–38%	Pakistan	Majid *et al.* 2007
Grain-filling	Bread wheat	9–78%	Hungary	Guóth *et al.* 2009
Grain-filling to maturity	Bread wheat	35%	Iran	Shamsi and Kobraee 2011
Anthesis to maturity	Bread wheat	39%	Iran	Dorostkar *et al.* 2015

(Reddy *et al.* 2004); this causes accumulation of ROS, which induces oxidative stress in proteins, membrane lipids and other cellular components. Some important components of photosynthesis affected by drought are shown in Fig. 3. Drought stress disturbs the balance between the production of ROS and the antioxidant defence, causing accumulation of ROS, and this induces oxidative stress. Upon reduction in available water, plants close their stomata (plausibly via ABA signalling), which decreases the CO_2 influx. A reduction in CO_2 not only reduces carboxylation directly but also directs more electrons to form ROS. Severe drought conditions limit photosynthesis through a decrease in the activities of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), phosphoenolpyruvate carboxylase (PEPCase), NADP-malic enzyme (NADP-ME), fructose-1,6-bisphosphatase (FBPase) and pyruvate orthophosphate dikinase (PPDK). Reduced contents of tissue water also increase the activity of Rubisco-binding inhibitors. Moreover, non-cyclic electron transport is downregulated to match the reduced requirements of NADPH production, and thus reduces ATP synthesis (Farooq *et al.* 2009).

Breeding strategies

Breeding for drought tolerance is further complicated because several types of abiotic stress can challenge crop plants simultaneously. High temperatures, high irradiance, scarcity of water and nutrient deficiencies are commonly encountered under normal growing conditions but may not be amenable to management through traditional farm practices. Certain soil

properties such as composition and structure can also affect the balance of these different stresses (Whitmore and Whalley 2009). Higher plants have evolved multiple, interconnected strategies that enable them to survive unpredictable environmental fluctuations. However, these strategies are not always well developed in wheat cultivars grown by farmers.

Genetic manipulation for increased drought tolerance

Conventional breeding approaches have demonstrated that traits conferring stress tolerance are controlled by a great variety of genes acting additively and synergistically (Yang *et al.* 2010), which makes genetic manipulation of plants for increased drought tolerance a difficult task. Drought reduces the crop yield by up to 50%, which is a great economic loss for the farming community (Akpınar *et al.* 2013). Consequently, development of drought-tolerant wheat cultivars has become a serious challenge for the plant breeders to ensure the food security of human populations (Budak *et al.* 2013). Although it may be possible to improve abiotic stress tolerance by using whole-plant phenotypic or physiological strategies and pyramiding breeding schemes, such approaches, even those based on MAS, are costly and slow, and require massive screening labour to identify specific quantitative traits; in addition, linkage of agronomically important QTLs to undesirable traits can sometimes occur. For example, selection for glycine betaine content could result in increased incidence of some insect pests (i.e. aphids) and microbial diseases (i.e. *Fusarium*). It is expected that selection supported by genetic molecular markers may help to resolve some
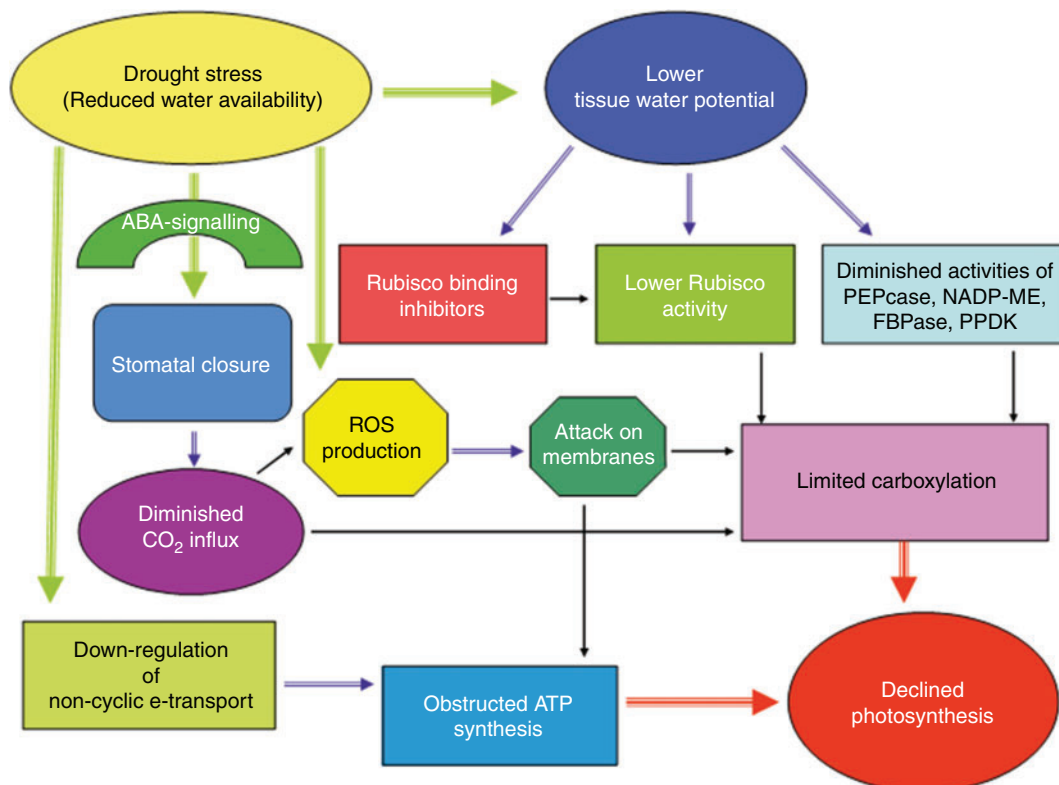
Fig. 3. Photosynthesis under drought stress. Possible mechanisms by which photosynthesis is reduced under stress. Figure adapted from Farooq *et al.* (2009).

drawbacks of conventional breeding methods. Meanwhile, efforts to engineer improved tolerance by using transfer of genes (single- or multigene) via genetic transformation offer far more rapid and promising improvements in stress tolerance (Cushman 2001).

Genetic engineering of plants has opened the possibility of manipulating the plant genome towards more specific and ambitious objectives, studying gene structure and function as well as determining the relation of gene expression to causal factors. Plant response to drought stress has been analysed at the ecological, cellular, physiological and molecular levels. The knowledge gained by studies in these research areas has settled the technological basis now utilised for increasing the drought tolerance of plants by genetic manipulation. In recent years, genomics knowledge based on next-generation sequencing, gene-editing systems (Shan *et al.* 2013), gene silencing (Yin *et al.* 2014), and overexpression methods (Saad *et al.* 2013) have increased our understanding about drought-signalling pathways. At the transcriptome level, RNA deep sequencing (Akpınar *et al.* 2015) and microarray analyses (Ergen *et al.* 2009) are employed to elucidate the differential expression of RNA transcripts involved in drought response. Moreover, microRNAs (miRNAs; Budak and Akpinar 2015), hormones (Reddy *et al.* 2014), QTLs (Barakat *et al.* 2015), metabolites (Xiao *et al.* 2012), and transcription factors and drought-related proteins (Alvarez *et al.* 2014) are key players in drought signalling.

Molecular markers can be used to explore germplasm through segregation and association mapping to identify useful alleles in both crop cultivars and wild relatives. Drought tolerance is a typical quantitative trait; however, single genes, such as those controlling flowering time, plant height, spike type and osmotic adjustment, may have important roles in adaptation to drought-prone environments (Forster *et al.* 2004). During the last 10 years, the application of QTL analysis has provided unprecedented opportunities to identify chromosome regions controlling variations in almost all of the physiological, morphological and developmental changes observed during plant growth in water-limiting conditions. Most QTLs for drought tolerance in wheat and its close relatives have been identified through yield and yield-component measurements under water-limited conditions (Quarrie *et al.* 2006; Mathews *et al.* 2008). Although yield is the most relevant trait to breeders, it is very difficult to describe accurately with respect to water use and to identify candidate regions for positional cloning. Few studies have identified QTLs associated with specific components of drought response. Although the development of gene-based molecular markers and genome sequencing should accelerate positional cloning (Collins *et al.* 2008), the genomic regions associated with individual QTLs are still very large and are usually unsuitable for screening in a breeding program.

High water-use efficiency (WUE) is an important breeding target for major crops. Direct measurement of WUE relies on leaf gas-exchange data and long-term measurement of plant water consumption and biomass production, and it is logistically difficult in large-scale plant screening. Differences in carbon isotope discrimination ($\Delta^{13}C$) have been used as an indirect indicator of WUE. Ishimaru *et al.* (2001) found six QTLs for $\Delta^{13}C$ that explained 0.628 (r) of the total phenotypic variation. Xu

et al. (2009) identified seven QTLs for $\Delta^{13}C$, and the contributions of these QTLs to the total phenotypic variation ranged from 7.6% to 22.2%. However, there were no common QTLs reproduced in these two studies.

Canopy temperature has also been commonly used in evaluating drought avoidance. In a wheat doubled-haploid population (RAC875/Kukri), two QTLs located on chromosome 3B had a considerable effect on canopy temperature and accounted for up to 22% of the variation (Bennett *et al.* 2012).

Plant roots play a vital role in plant growth, development and fitness and are responsible for water and nutrient uptake. Root development is directly affected by environmental factors, and possession of a deep and thick root system that allows access to water deep in the soil has been considered important for drought resistance in crops. Among the numerous QTLs for different root traits, a significant proportion is located in the same chromosome regions or in close proximity, and such colocalised QTLs were detected even in different populations. A QTL for root volume identified by Yue *et al.* (2006) was found to overlap with the QTL for root thickness and root weight detected by Zheng *et al.* (2003). Yue *et al.* (2006) detected QTLs affecting different traits, including deep-root rate, maximum root length and root volume under drought stress, that overlapped with the QTLs for root thickness, root penetration and penetrated root dry weight in a different population.

Crop improved varieties

Crop programs that aim to release commercial varieties typically grow many thousands of genotypes in target areas in order to undertake phenotypic selection for grain yield and other key traits. An increase in yield is a function of selection intensity, the extent of phenotypic variability for yield and its heritability. Heritability is reduced if GE interactions are significant, as they usually are in variable rainfed environments. Crop management is equally important as breeding to improve yields (Passioura and Angus 2010). Optimising time of sowing and timing and amount of nitrogen application in relation to rainfall, rotation sequence, tillage, sowing rate and row spacing all are important to maximise grain yield in dry environments. Beneficial interactions between variety and management provide an additional avenue to achieve further yield gains (Fischer 2009).

Traits associated with drought tolerance

Knowledge of traits associated with drought tolerance would be useful for developing breeding materials for target environments. Efforts have been made to enhance the efficiency of selection for drought-tolerant genotypes based on yield and specific physiological traits (Monneveux *et al.* 2012). The disadvantage of this approach is that GE interaction for yield is always large and there is a lack of precise screening techniques not influenced by environmental conditions during measurement for trait selection. Selecting a physiological trait for screening drought tolerance requires comprehensive understanding of the trait, its contribution to yield and its responsiveness to the environment (Mutava *et al.* 2011). Genetic gains in grain yield improvement will increase if more traits conferring better agronomic and physiological performance and disease resistance are brought together in the same variety in a breeding program. Several

main traits show correlations with yield (Olivares-Villegas *et al.* 2007). Measuring these traits in a large set of germplasm is not an easy task, because major traits (such as plant height and days to heading or to maturity) can interact with the trait of interest, such as canopy temperature or early groundcover. It is advisable to measure all of these traits, including plant height and phenology, in order to ensure that the traits of interest are not confounded by either phenology or plant height (Lopes *et al.* 2012). Selection efficiency can be greatly improved with the identification of biochemical markers. Lopez *et al.* (2003), working on dehydrins (a class of proteins expressed in plants exposed to dehydration stress), observed a positive association of dehydrin expression with drought tolerance. Several researchers have made similar findings. Cseuz *et al.* (2002) used different selection methods such as water-retention ability, chemical desiccation and carbohydrate accumulation to screen different drought-tolerant wheat genotypes.

Genes conferring drought tolerance

During the last decade, several important and major genes and QTLs for drought-mediated grain yield and its components have become available in wheat (Table 3). Drought is a complex trait and drought-tolerance response is carried out by various genes, transcription factors, miRNAs, hormones, proteins, co-factors, ions and metabolites (Budak *et al.* 2015). This complexity has limited the development of crop cultivars for drought tolerance by classical breeding. Adaptation of plants to drought and to the consequent cellular dehydration induces an active plant molecular response. Many stress-related genes have been isolated and characterised in the last two decades in a variety of crop species; however, the complexity of the entire molecular response to drought in crop plants has only recently been revealed by large transcriptome analyses (Hazen *et al.* 2005). Transgenic plants have been developed to upregulate the general stress response or to reproduce specific metabolic or physiological processes previously shown to be related to drought tolerance by classical physiological studies. Transcription factors as well as

components of the signal transduction pathways that coordinate expression of downstream regulons are thought to be optimal targets for engineering of complex traits such as drought tolerance. Successful examples are transgenic crops engineered with genes encoding the dehydration-responsive element-binding (DREB)/C-repeat binding factor (CBF) transcription factors in wheat (Pellegrineschi *et al.* 2004). The transgenic plants showed increased stress tolerance as well as the over-induction of downstream stress-related genes and/or higher levels of soluble sugars and proline. Metabolic engineering for increasing osmolyte contents was successful in several plants subjected to stress, although real advantages of such a strategy are always a subject of debate (Serraj and Sinclair 2002). An improvement of drought tolerance in wheat was reported by Abebe *et al.* (2003) through the ectopic expression of the mannitol-1-phosphate dehydrogenase (*mtlD*) gene, which caused a small increase in the level of mannitol.

Equations for assessing the drought tolerance

Drought is an important limiting factor for crop production in most areas of the world, influencing yield, quality and plant architecture. With climate change, water deficits will increase as a major challenge for sustainable crop production (Wassmann *et al.* 2009). The intensity and frequency of droughts are expected to increase, resulting in decreased food production and food security, and increased vulnerability of the crop to drought (Bates *et al.* 2008). Several regression techniques of yield against environmental indices as independent variables were developed to evaluate genotype adaptability. Several indices were proposed to describe yield performance of a given genotype under stress and non-stress conditions or compared with the average yield or the yield of a superior genotype (Mohammadi 2016). On order to estimate the water stress experienced by crop plants, Idso *et al.* (1981) suggested a crop water-stress index derived from the increase in average canopy temperature in relation to that of a well-watered reference plot and evaluated by infrared thermometry. In a study on wheat,

Table 3. Genes conferring drought tolerance in wheat

Gene(s)	Function	Reference
DREB1A	Stress-induced transcription factors	Pellegrineschi *et al.* 2004
*DREB*s	Stress-induced transcription factors	Lucas *et al.* 2011
Argonaute	Signal transduction, stress response	Gupta *et al.* 2014
CCAAT-box TF	ABA-responsive transcription, drought tolerance	Ma *et al.* 2015
HVA1, OsLEA3	Stress induced LEA proteins	Bahieldin *et al.* 2005
TaDREB2/TaDREB3	Improving survival under severe drought conditions	Morran *et al.* 2011
TaNAC69	Enhancing transcript levels of stress-upregulated genes and dehydration tolerance	Xue *et al.* 2011
TaMYB33	Enhancing salt and drought tolerance	Qin *et al.* 2012
TaPIMP1	Overexpressing of wheat *MYB* gene	Liu *et al.* 2011
QHd.idw-2A.2	Early flowering	Maccaferri *et al.* 2008
QDm-7D.b	Early maturity	Lopes *et al.* 2013
qGYWD.3B.2	Improve grain yield	Shukla *et al.* 2015
QTgw-7D-b	Enhancing 100-grain weight	Lopes *et al.* 2013
Qchl.ksu-3B	SPAD/chlorophyll content	Kumar *et al.* 2012
QSrm.ipk-2D	Stem reserve mobilisation	Salem *et al.* 2007
QWsc-c.aww-3A	Water-soluble carbohydrate	Bennett *et al.* 2012
Rht-B1b/Rht-D1b	Coleoptile length	Rebetzke *et al.* 2007

a water-potential index was suggested by Karamanos and Papatheohari (1999) as a measure of the total water stress experienced by a crop in a given environment for a specific time interval. Other approaches aim to quantify the degree of drought based on specific environmental factors (weather, soil water availability, etc.) in order to provide a measure that is independent of the GE interaction. Araus *et al.* (2003) found that yield was well correlated with water input under different water-stress conditions. Motzo *et al.* (2001) proposed a seasonal water-stress index based on soil–plant–atmosphere interaction, where stress was quantified as: 1 – (fraction of transpirable soil water). Rizza *et al.* (2004) proposed an integrated water stress index (WSI), based on a simple soil-water balance and the integrated reduction of plant transpiration relative to potential transpiration. They proposed that yield potential and adaptability of cultivars could be related to water stress by means of the intercept, *a*, and slope of a linear regression, *b*, of yield vs WSI.

Relative yield performance of genotypes in drought-stressed and non-stressed environments can be used as an indicator of drought tolerance in breeding for drought-prone environments. Based on their comparative yield performance in stress and non-stress environments, genotypes were categorised into four groups by Fernandez (1992). These groups were genotypes with high performance under both stress and non-stress conditions (group A), genotypes with high yield in non-stress conditions (group B), genotypes with high yield in stress conditions (group C), and genotypes with low yield in both stress and non-stress conditions (group D). Several yield-based drought-tolerance indices based on mathematical relationships between yield under irrigated and drought conditions have been proposed to characterise the behaviour of genotypes in stress and non-stress environments, and to screen for drought-tolerant genotypes. Fischer and Maurer (1978) suggested a stress-susceptibility index (SSI) for measurement of yield stability that considered the changes in both potential and actual yields in variable environments. Mohammadi (2016) used SSI to evaluate drought tolerance of durum wheat genotypes and found year-to-year variation in SSI for genotypes; this enabled ranking of their patterns of response. Guttieri *et al.* (2001) assessed SSI in spring wheat cultivars and suggested that an SSI >1 indicated above-average susceptibility to drought stress. Rosielle and Hamblin (1981) defined stress tolerance (TOL) as the difference in yield between stress and irrigated environments and mean productivity (MP) as the average yield of genotypes under stress and non-stress conditions. Fernandez (1992) proposed the stress-tolerance index (STI) as a useful tool for predicting high yield and stress-tolerance potential of genotypes. The geometric mean productivity (GMP) is often used by breeders interested in relative performance because drought stress varies in severity in field environments over years. Yield index (YI) (Gavuzzi *et al.* 1997) and yield-stability index (YSI) (Bouslama and Schapaugh 1984) were proposed in order to evaluate genotypic stability in the both stress and non-stress conditions. These indices are based on either drought tolerance or drought susceptibility of genotypes and have been used in many crops, including bread wheat (Sio-Se Mardeh *et al.* 2006), barley (Shakhatreh *et al.* 2001; Rizza *et al.* 2004; Benmahammed *et al.* 2010) and durum wheat (Mohammadi *et al.* 2011*a*). However, multi-environment selection, covering a wide range of climatic variability, seemed more suitable to

identify stress-tolerant and high-performing genotypes (Kirigwi *et al.* 2004).

However, the different indices have different levels of precision, making comparisons between genotypes difficult. On the other hand, each index has to be interpreted according to its physiological meaning and optimal value. For example, good performance under both drought and irrigated conditions leads to high values of STI, MP, GMP, YSI and YI, and to generally low values of TOL and SSI (Mohammadi 2016).

Major physiological factors

The physiological basis of yield maintenance under drought conditions remains poorly understood, owing to both the numerous mechanisms that plants can use to maintain growth in conditions of low water supply and the complexity of the stress itself. Physiological traits relevant for the responses to water deficits and/or modified by water deficits span a wide range of vital processes. Consequently, it can be expected that no single response pattern is highly correlated with yield under all drought environments. The different crop developmental stages show different sensitivity to drought stress. In wheat, most of the floret primordia that reach the fertile floret stage become grains after anthesis. The number of fertile florets or grains per m^2, the most relevant component in ensuring high yield in drought conditions (Slafer and Whitechurch 2001), is determined during stem elongation, a few weeks before anthesis.

Several studies have addressed yield under drought stress as a function of single physiological traits in attempts to understand which metabolic processes and/or morpho-physiological traits are crucial in ensuring high yield performance under a wide range of environments (Lopes and Reynolds 2012; Monneveux *et al.* 2012; Rebetzke *et al.* 2016). In a study conducted with durum wheat, Mohammadi *et al.* (2014*b*) demonstrated how yielding capacity is related to an environment-related agro-physiological trait such as canopy temperature, SPAD reading, plant height, flag-leaf length and heading date, which suggests that these traits could be useful for screening durum wheat genotypes for drought tolerance.

Stay-green is an important trait in several crops (e.g. wheat, maize, rice, sorghum). Stay-green plants are characterised by a post-flowering drought-resistance phenotype that provides resistance to premature senescence, stalk rot and lodging when subjected to drought during grain-filling (Campos *et al.* 2004). Improvement in grain-filling capacity under terminal drought could also be achieved by increasing the mobilisation of vegetative reserves from stems to spikes (Monneveux *et al.* 2012).

Rebetzke *et al.* (2016) reported another example of a successful breeding program for dry environments based on a physiological trait. They used $\Delta^{13}C$ as a surrogate for WUE to select wheat lines with high WUE in drought-prone environments. During photosynthesis, plants discriminate against the heavy isotope of carbon (^{13}C), and as a result, in several C_3 species, $\Delta^{13}C$ is positively correlated with the ratio of internal leaf CO_2 concentration to ambient CO_2 concentration (Ci/Ca) and negatively associated with transpiration efficiency. Thus, a high Ci/Ca leads to a higher $\Delta^{13}C$ and a lower transpiration efficiency (Farquhar and Richards 1984). When employing divergent selection in wheat, the resulting low $\Delta^{13}C$ lines had

increased aboveground biomass and kernel weight. Yield was increased by ~2% under mild stress conditions and up to ~10% under the driest conditions (Rebetzke *et al.* 2002).

Watt *et al.* (2005) developed a wheat breeding line for aboveground vigour with a 40% faster growing root system in the unploughed soil of conservation systems compared with the conventional cultivar. Seed size has a major influence on seedling vigour (Richards and Lukacs 2002), and so for selection, seeds with about the same weight are sown. Visual selection is then made to eliminate plants with the smallest leaf width; a ruler may be required to make the final selections. Screening large numbers of genotypes in the field for deeper roots that increase water supply to the growing grains may be feasible by selecting lines for specific shoot traits after flowering. This must be done in a managed environment where there is little late-season rainfall and lines are grown with a receding soil moisture supply. Selection can be made for genotypes that maintain green leaf area and have a high stomatal conductance, low canopy temperature or high grain $\Delta^{13}C$. These traits are expected to be good indicators of which genotypes have deep roots in moist soil. Table 4 provides a description of the most important traits recommended to improve the grain yield of wheat crops where water is limited. These traits may not be universally important in rainfed environments; some may have greater impact in specific environments.

Genetic gain for drought tolerance in wheat

Increasing crop productivity

Genetic improvement of wheat performance can be achieved by introducing improved alleles at existing loci through conventional crossing, aided by marker and other technology, and by adding new loci by transformation. In general, a genetic gain of $10–50\,kg\,ha^{-1}\,year^{-1}$ has been recorded for cereals and legumes over the last century in all countries, including those characterised by vast, drought-prone regions. Information obtained on genetic gain by comparing cultivars of different release years is not absolute, owing to the influence of environment (mainly water availability) on the performance of the varieties. When grain-yield values of wheat and barley were estimated in environments with different levels of water availability, yield progress attributed to genetic improvement was, in absolute terms, higher in the environments characterised by a low level of water stress (Cattivelli *et al.* 2008). However, when yield increases were expressed as a percentage, no differences were recorded for environments with different degrees of water stress. This suggests that some of the traits selected to improve yield also led to yield increases in dry environments. In mild–moderate drought conditions characterised by a wheat or barley grain yield of $2–5.0\,t\,ha^{-1}$, selection for high yield potential has frequently led to some yield improvements (Araus *et al.* 2002). In these cases, the breeders have selected plants characterised by high yield potential and high yield stability, with the latter being attributed to a minimal GE interaction (Mohammadi and Amri 2013). This indicates that traits maximising productivity normally expressed in the non-stress conditions can still sustain a significant yield improvement under mild–moderate drought (Slafer *et al.* 2005; Tambussi *et al.* 2005). An example is the success of wheat and

rice varieties bred at the Maize and Wheat Improvement Center (CIMMYT) and the International Rice Research Institute (IRRI), where selection under well-watered environments identified genotypes with high yield in a wide range of conditions including regions with a low yield potential (Trethowan *et al.* 2002).

Molecular breeding for enhancing drought tolerance

Recent research breakthroughs in biotechnology have revived interest in targeted drought tolerance breeding and use of new genomics tools to enhance yield productivity. Marker-assisted breeding is revolutionising the improvement of temperate field crops and will have similar impacts on the breeding of tropical crops. Other molecular breeding tools include development of genetically modified crops that can tolerate plant stress. As a complement to the recent rapid progress in genomics, a better understanding of physiological mechanisms of drought response will also contribute to progress in genetic enhancement of crop drought tolerance. It is well accepted that the complexity of the drought syndrome can only be tackled with a holistic approach. This would involve integration of physiological dissection of crop drought avoidance and tolerance traits by using molecular genetic tools such as MAS, microarrays and transgenic crops with agronomic practices that lead to better conservation and utilisation of soil moisture, and better matching of crop genotypes with the environment.

Because drought brings about many changes in gene expression, identification of candidate genes being expressed in drought-stress conditions is a major strategy, and the technology of microarray has been quite helpful in achieving that objective (Umezawa *et al.* 2006). Zhang *et al.* (2005) reported a dwarf mutant of wheat named 's-dwarf', which showed a remarkably low rate of transpiration with higher WUE than the Chinese wheat cultivar Jingdong 6. Khan *et al.* (2001) described two mutant lines (DHML-50 and DHML-9) developed through haploid breeding and mutagenesis that appeared to be promising with regard to drought tolerance. Similarly, in a search for drought-resistant wheat varieties in the marginal areas of Kenya, Njau *et al.* (2006) compared introductions, mutants and doubled-haploid lines; the doubled-haploid technique proved the most efficient and effective means of breeding for drought tolerance.

Genomic-based approaches can ultimately help us to determine QTLs for drought tolerance that enable the crop to survive better in water-limited conditions. However, despite all of the technological advancements, the success of molecular-based approaches in developing drought-tolerant cultivars is marginal (Zhao *et al.* 2008).

Recent and promising techniques in wheat breeding

Achieving adequate levels of genetic gain for yield, and all target traits, is increasingly difficult, but effective strategies for implementing the new technologies of genomic selection (GS) and high-throughput phenotyping (HTP) can help to predict and identify the best lines and parent combinations. Such strategies will initiate a GS and HTP prediction methodology, integrating remote sensing, genomic and pedigree data, which will be developed specifically for breeding candidates before yield

Table 4.   Morpho-physiological traits relevant for response to drought conditions in wheat

Trait(s)	Function or effect on yield productivity	Reference(s)
Stomatal conductance	More–less rapid water consumption	Cattivelli *et al.* 2008
Leaf temperature	Leaf temperature reflects the evaporation and hence is a function of stomatal conductance	Lawlor and Cornic 2002
Photosynthetic capacity	Modulation of concentration of Calvin cycle enzymes and elements of the light reactions	Lawlor and Cornic 2002
Phenological traits	Early–late flowering, maturity and growth duration, synchrony of anthesis, reduced grain number	Slafer *et al.* 2005
Starch availability during ovary/embryo development	A reduced starch availability leads to abortion, reduced grain number	Boyer and Westgate 2004
Partitioning and stem reserve utilisation	Lower–higher remobilisation of reserves from stems for grain-filling, affecting kernel weight	Slafer *et al.* 2005
Stay-green	Delayed senescence	Lopes and Reynolds 2012
Single plant leaf area	Plant size and related productivity	Walter and Schurr 2005
Root length	Higher–lower tapping of soil-water resources	Hoad *et al.* 2001
SPAD value	Delayed leaf senescence, better maintenance of photosynthetic rate	Lopes and Reynolds 2012
Photosynthetic pathway	$C_3/C_4/CAM$; higher WUE and greater heat tolerance of C_4 and CAM	Cushman 2001
Osmotic adjustment	Accumulation of solutes: ions, sugars, poly-sugars, amino acids, glycinebetaine	Serraj and Sinclair 2002
Membrane composition	Increased membrane stability and changes in aquaporin function	Tyerman *et al.* 2002
Anti-oxidative defence	Protection against active oxygen species	Reddy *et al.* 2004
Accumulation of stress-related proteins	Involved in the protection of cellular structure and protein activities	Ramanjulu and Bartels 2002
Large seed size	Emergence, early groundcover, initial biomass	Monneveux *et al.* 2012
Long coleoptiles	Emergence from deep sowing, desirable to avoid extremely hot soil surface temperatures and rapid soil drying	Monneveux *et al.* 2012
Early groundcover (visual)	Decrease of evaporation and increase of radiation-use efficiency (RUE)	Daryanto *et al.* 2016; Monneveux *et al.* 2012
Specific leaf dry weight	Thinner, wider leaves, early groundcover	Merah *et al.* 2001
Growth habit (visual)	Lower soil evaporation and higher RUE	Richards *et al.* 2007
Tiller survival	Survival and recovery	Monneveux *et al.* 2012
Long and thick stem internodes	Storage of carbon products	Monneveux *et al.* 2012
Vegetation indices (normalised difference vegetation index, NDVI)	Green biomass	Royo *et al.* 2003
Earliness	Drought escape	Monneveux *et al.* 2005
Number of grains per spike	Spike sterility	Hafsi *et al.* 2007
Canopy temperature depression	Stomatal conductance, extraction of water from soil	Reynolds *et al.* 2000
Carbon isotope discrimination	Stomatal conductance, extraction of water from soil	Monneveux *et al.* 2005
Ash content	Stomatal conductance, extraction of water from soil	Misra *et al.* 2006
Spike photosynthetic capacity	Contributes to remobilisation during grain filling	Monneveux *et al.* 2012
Leaf colour (visual, SPAD)	Delayed senescence, maintenance of photosynthesis	Christopher *et al.* 2016
Leaf waxiness	Lower transpiration rate and reduced photo-inhibition	Izanloo *et al.* 2008
Leaf pubescence	Lower transpiration rate and reduced photo-inhibition	Izanloo *et al.* 2008
Leaf thickness and posture	Lower transpiration rate and reduced photo-inhibition	Reynolds *et al.* 2000
Presence of awns	Contribute to photosynthesis and efficient water use	Rebetzke *et al.* 2016
Leaf rolling	Lower transpiration rate and reduced photo-inhibition	Reynolds *et al.* 2001
Glume pubescence	Lower transpiration rate and reduced photo-inhibition	Tiwari *et al.* 2014
Delayed senescence	Higher RUE	Hafsi *et al.* 2007
Fructanes in stem	Storage of carbon products	Tiwari *et al.* 2014
Solute concentration in cells	Osmotic adjustment	Tiwari *et al.* 2014
Accumulation of ABA	Reduced stomatal conductance and cell division	Blum 2010
Accumulation of proline	To diminish reactive oxygen species levels in cells, thus preventing programmed cell death	Chen and Dickman 2005
Leaf relative water content	Indicates maintenance of favourable plant water status	Wang *et al.* 2017
Relative water loss	Indicates maintenance of favourable plant water status	Jäger *et al.* 2014
Chlorophyll fluorescence (Fv/Fm)	Indicates changes in actual quantum yield of PSII	Zivcak *et al.* 2014
Cell membrane stability	Allows leaves to continue functioning at high temperature	Bita and Gerats 2013
Water-use efficiency	Indicates greater carbon gain per unit of water lost by transpiration	Condon *et al.* 2004
Fast early growth	Minimise evaporation of moisture from the soil surface and maximise soil-water available for transpiration and growth	Monneveux *et al.* 2012

testing where selection accuracies for yield are currently low because of smaller field plots and limited seed availability. Developing methodologies for HTP on small plot sizes and with no replication of breeding candidates will be critical. Methodologies developed will be validated by using replicated yield-trial data to identify a suitable HTP methodology for these early-stage breeding candidates. One of the novel proposed methodologies, the Wheat Walker, is a low-cost field-mobile robot platform. It is small, tactical, semi-autonomous and ground-based with sensors capable of mapping the physical structure of a cereal canopy *in situ* and measuring its local climatic parameters.

The GS and HTP technologies have been attracting the interest of the plant-breeding community in both the public and private sectors worldwide. Both approaches promise to revolutionise the prediction of complex traits including growth, yield and adaptation to stress. Whereas HTP may help to improve understanding of crop physiology, the most powerful applications for high-throughput field phenotyping are empirical rather than analytical and comparable to GS (Cabrera-Bosquet *et al.* 2012). We below discuss these two methodologies in wheat.

Genomic selection

Improving wheat yield and breeding efficiency is vital for feeding an expanding population. GS is a new form of MAS that offers gains in efficiency over phenotypic selection or conventional MAS. Conventional MAS focuses on a few genes with large effects, whereas GS uses markers covering the entire genome to estimate the value of an individual (Meuwissen *et al.* 2001; Ayers and Cordell 2010; Reynolds *et al.* 2011).

The prediction accuracy of GS is estimated by the correlation of the genomic estimated breeding value (GEBV) with the trait phenotype. The use of GS in plant breeding has been evaluated for several important traits. These include: grain moisture and grain yield in maize (Zhao *et al.* 2012); soybean cyst nematode resistance (Bao *et al.* 2014); amylase activity in barley (Lorenzana and Bernardo 2009); grain yield and plant height in rice (Spindel *et al.* 2015); and diameter, pulp yield, and rust resistance in eucalyptus (Grattapaglia and Resende 2011). In wheat, the use of GS has been assessed for breeding of important quantitative traits such as grain yield and quality traits including flour yield, flour protein, solvent-retention capacity for sucrose, lactic acid, water absorption, sodium carbonate and softness equivalent, as well as resistance to Fusarium head blight and stem rust (Heffner *et al.* 2011; Poland *et al.* 2012; Rutkoski *et al.* 2015). The accuracy of GS for predicting these traits differs depending on the GS models, marker imputation methods, population size and number of markers being used (Heffner *et al.* 2011; Poland *et al.* 2012).

In order to achieve genetic gains for complex traits, breeders often evaluate trait stability and GE interactions when performing phenotypic selection. Trait stability will likely become increasingly important as global climate change increases environmental variation. Many studies have proposed different concepts and statistical approaches to estimate trait stability (Rubio *et al.* 2004; Mohammadi *et al.* 2011*b*; Huang *et al.* 2016).

Huang *et al.* (2016) used GS for wheat traits and trait stability in winter wheat. They genotyped 273 lines of a soft winter wheat population by using 90 000 single-nucleotide polymorphism markers and phenotyped for four agronomic and seven quality traits. They used the additive main effect and multiplicative interaction (AMMI) model and Eberhart and Russell regression (ERR) to estimate trait stability. The accuracy of GS ranged from 0.33 to 0.67 for most traits and trait stability. Accuracy of trait stability was greater than of trait itself for yield (0.44 using AMMI vs 0.33) and heading date (0.65 using ERR vs 0.56). The magnitude of GS accuracies for all traits and most of the trait stability indices suggests the possibility of rapid selection for these trait and trait stabilities in wheat breeding.

Genomic selection offers the potential to accelerate selection gain (Crossa *et al.* 2010; Burgueño *et al.* 2012; Poland *et al.* 2012) especially by shortening the lengths of breeding cycles (Sallam *et al.* 2015). Encouraging prediction accuracies have been reported for GS for grain yield in wheat despite the use of wheat line populations of only 200 (Poland *et al.* 2012) to 800 (Lopez-Cruz *et al.* 2015). The prediction ability of GS is influenced by the genetic composition of the training population, the relatedness between the training and the test populations, and the heritability within the training population (Isidro *et al.* 2015). Recent studies examined the potential to reduce costs by decreasing the training population size while keeping the prediction ability constant (Rincent *et al.* 2012; Akdemir *et al.* 2015). The findings suggested that using criteria such as the mean prediction error variance facilitates a resource-efficient establishment of training populations.

High-throughput phenotyping

Rates of genetic improvement are below those needed to meet projected demand for staple crops such as wheat (Ray *et al.* 2013). The grand challenge remains in connecting genetic variants to observed phenotypes, followed by predicting phenotypes in new genetic combinations. Extraordinary advances over the last 5–10 years in sequencing and genotyping technology have driven costs down and they are providing an abundance of genomic data, but this is only half of the equation to understand the function of plant genomes and predict plant phenotypes (White *et al.* 2012; Cobb *et al.* 2013). HTP platforms could provide the key to connecting the genotype to phenotype by both increasing the capacity and precision and reducing the time to evaluate huge plant populations. To reach the point of predicting the real-world performance of plants, HTP platforms must innovate and advance to the level of quantitatively assessing millions of plant phenotypes. Plant phenotyping involves a wide range of plant measurements such as growth development, canopy architecture, physiology, disease and pest response, and yield. In this context, HTP is an assessment of plant phenotypes on a scale and with a level of speed and precision not attainable with traditional methods (Dhondt *et al.* 2013), many of which include visual scoring and manual measurements. To be useful to breeding programs, HTP methods must be amenable to plot sizes, experimental designs and field conditions in these programs.

One of the emerging technologies in aerial-based platforms is unmanned aerial system (UAS), which have undergone

remarkable development in recent years and are now powerful, sensor-bearing platforms for various agricultural and environmental applications (Dunford *et al*. 2009; Chao *et al*. 2010; Baluja *et al*. 2012; Gonzalez-Dugo *et al*. 2013; Chapman *et al*. 2014). UAS can cover an entire experiment in a very short time, giving a rapid assessment of all of the plots while minimising the effect of environmental conditions that change rapidly, such as wind speed, cloud cover and solar radiation. UAS enables measuring with high spatial and temporal resolution capable of generating useful information for plant-breeding programs.

Platforms for HTP support the discovery and analysis of genome-wide genetic markers (genotypes) in populations in a routine manner (Davey *et al*. 2011; Edwards *et al*. 2013). Recently, the introduction of techniques for HTP has boosted the area of plant phenomics, where new technologies such as non-invasive imaging, spectroscopy, robotics and high-performance computing are combined to capture multiple phenotypic values at high resolution and high precision, and in high throughput. This will ultimately enable plant scientists and breeders to conduct numerous phenotypic experiments in an automated format for large plant populations under different environments to monitor non-destructively the performance of plants over time (Eberius and Lima-Guerra 2009). Various automated or semi-automated HTP platforms for plants have been developed and are applied to investigate plant performance under different environments (Arvidsson *et al*. 2011; Golzarian *et al*. 2011; Nagel *et al*. 2012).

Field-based HTP is an emerging tool with the potential to accelerate genetic discovery and to identify genetic combinations that will allow more rapid selection of high-yielding varieties (Shi *et al*. 2016; Sperry *et al*. 2016; Tattaris *et al*. 2016). These platforms have been successfully deployed in wheat and barley (Munns *et al*. 2010), cotton (Andrade-Sanchez *et al*. 2014), maize (Vergara-Díaz *et al*. 2016), rice (Tanger *et al*. 2017) and barley (Honsdorf *et al*. 2014), and the rapid nature of data collection has even enabled analyses of temporally dynamic traits.

It is concluded that new high-throughput imaging technologies in controlled environments can provide a useful way of screening large numbers of genotypes and identifying small differences in growth rate or expression of certain traits.

Berger *et al*. (2010) used high-throughput shoot imaging to study drought responses, describing some of the traits that contribute to drought tolerance in plants and the HTP techniques available to measure those traits. The authors employed non-destructive imaging techniques that allowed temporal resolution and monitoring of the same plants throughout the experiment. Information was obtained on the physiological changes in response to drought over time, which is vital for identifying and characterising different drought-tolerance mechanisms. The authors concluded that the technique provides a valuable new tool to allow the dissection of plant responses to drought into a series of component traits.

New crop varieties for drought-prone environments

Recurrent drought associated with climate change is among the principal constraints to global productivity of wheat.

Numerous efforts to mitigate drought by breeding resilient varieties are under way around the world, but progress is hampered because drought tolerance is a complex trait that is controlled by many genes and its full expression is affected by the environment (Mwadzingeni *et al*. 2016). However, significantly improved crop varieties are urgently needed to feed the rapidly growing human population under changing climates (Chen *et al*. 2014). Advances in crop science to produce improved and higher performing crops are key to making dryland food-production systems more efficient and more resistant to pressure from drought, extremes of cold and heat, unpredictable rainfall, and new pests and diseases. For optimal performance, varieties can be targeted to specific farming systems, depending on local conditions and stresses. Releases of plant genetic materials for drought-prone environments from the gene banks of the International Center for Agricultural Research in the Dry Areas (ICARDA), which hosts wild relatives of wheat, barley and legumes, have led to the development of crops with higher yields and greater resistance to a range of biotic and abiotic stresses. Some varieties also offer large improvements in bread-making quality, nutritional value, and other traits. More than 900 improved cereal and legume varieties have been released by national programs in partnership with ICARDA and adopted by farmers worldwide. These varieties generate estimated net benefits of ~US$850 million each year. Our ability to breed the improved crops of tomorrow has been advanced by a new approach to mining agricultural gene banks to speed the pace of research innovation for food security. Focused identification of germplasm strategy (FIGS) is the first scientific approach to agricultural gene bank mining and is a scientifically proven tool that helps breeding programs identify useful traits in plant genetics (Bari *et al*. 2012).

Conclusion

Several studies have shown that global crop production needs to double by 2050 to meet the projected demands of rising population. Meanwhile, drought stress is one of the major limiting factors among abiotic stresses hampering crop production. Although significant progress has been made in elucidating the genetic mechanisms underlying drought tolerance, considerable challenges remain. Worldwide, plant breeding in wheat was very successful during the second half of the 20th Century, contributing substantially to maintaining production ahead of population growth. The effect of plant breeding on wheat yield potential and its physiological determinants has been widely studied in many reports, and a positive genetic gain has been recorded. These results were achieved through an empirical selection for high yield potential and high yield stability, with the latter being attributed to a minimal GE interaction. This implies that traits maximising productivity normally expressed in the optimal conditions can still sustain a significant yield improvement under drought condition. However, most difficulties encountered in the identification of accurate drought-tolerance traits occur because wheat crops are cultivated under very different climatic conditions and face very different drought scenarios worldwide. Multidisciplinary approaches involving breeders, physiologists, gene bank managers and biotechnologists are still scarce,

holding back the exploitation of genetic diversity and the use of MAS for drought tolerance improvement. Two new techniques (i.e. GS and HTP) have recently attracted the interest of plant breeders worldwide. Both approaches promise to revolutionise the prediction of complex traits including growth, yield and adaptation to drought stress. HTP may help to improve understanding of crop physiology; the most powerful techniques for high-throughput field phenotyping are empirical rather than analytical and comparable to GS.

Conflicts of interest

None.

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