

Strategies to increase the yield and yield stability of crops under drought – are we making progress?

Neil C. Turner^{A,G}, Abraham Blum^B, Mehmet Cakir^C, Pasquale Steduto^D, Roberto Tuberosa^E and Neil Young^F

^AThe University of Western Australia Institute of Agriculture and Centre for Plant Genetics and Breeding, M080, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.

^BPlantstress.com, PO Box 16246, Tel Aviv, Israel.

^CSchool of Biological Sciences and Biotechnology, Faculty of Sustainability, Environmental and Life Sciences, Murdoch University, 90 South Street, Murdoch, WA 6150, Australia.

^DFood and Agriculture Organisation of the United Nations, Viale delle Terme di Caracalla, 00153 Rome, Italy.

^EDepartment of Agricultural Sciences, University of Bologna, Viale Fanin 44, 40127 Bologna, Italy.

^FRural Mail Box 232, Kojonup, WA 6395, Australia.

^GCorresponding author. Email: neil.turner@uwa.edu.au

Abstract. The objective of the InterDrought conferences is to be a platform for debating key issues that are relevant for increasing the yield and yield stability of crops under drought via integrated approaches. InterDrought-IV, held in Perth, Australia, in September 2013, followed previous InterDrought conferences in bringing together researchers in agronomy, soil science, modelling, physiology, biochemistry, molecular biology, genetics and plant breeding. Key themes were (i) maximising water productivity; (ii) maximising dryland crop production; (iii) adaptation to water-limited environments; (iv) plant productivity under drought through effective water capture, improved transpiration efficiency, and growth and yield; and (v) breeding for water-limited environments through variety development, and trait-based genomics-assisted and transgenic approaches. This paper highlights some key issues and presents recommendations for future action. Improved agronomic interventions were recognised as being important contributors to improved dryland crop yields in water-limited environments, and new methods for exploring root architecture and water capture were highlighted. The increase in crop yields under drought through breeding and selection, the development of high-throughput phenotyping facilities for field-grown and pot-grown plants, and advances in understanding the molecular basis of plant responses and resistance to drought stress were recognised. Managed environment phenotyping facilities, a range of field environments, modelling, and genomic molecular tools are being used to select and release drought-resistant cultivars of all major crops. Delegates discussed how individuals and small teams can contribute to progress, and concluded that interdisciplinary research, linkages to international agricultural research centres, public–private partnerships and continuation of the InterDrought conferences will be instrumental for progress.

Additional keywords: agronomy, breeding, drought resistance, genomics, InterDrought, water-limited conditions.

Received 21 February 2014, accepted 2 April 2014, published online 30 September 2014

Introduction

Food security is a major concern for all people in the world, as we are challenged by an increasing population relying on a limited area of productive land, less predictable rainfall, and less and increasingly costly water for irrigation. Adoption of more protein-rich diets, a changing climate and competing uses for the limited land and water create social and political tensions that can lead to unrest. The predicted increases in temperature and decreases in rainfall in subtropical and semiarid climates (Stocker *et al.* 2013) are predicted to decrease yields (Müller *et al.* 2009; World Bank 2010). These challenges also represent opportunities. In the face of these challenges, the Fourth InterDrought Conference (InterDrought-IV) was held in Perth,

Australia, in September 2013 to explore the most effective approaches to achieving better crop productivity under water-limited conditions and to identify the research needed to achieve greater yields and yield stability in drought-prone environments. The unique feature of previous InterDrought conferences (first held in Montpellier, France, in 1995; Rome, Italy, in 2005; Shanghai, China, in 2009) was the bringing together of scientists and students in agronomy, soil science, modelling, physiology, biochemistry, molecular biology, genetics, genomics and plant breeding in a series of plenary sessions. The 2013 conference was no different and utilised this cross-disciplinary format to present and debate the key issues and strategies that are relevant for increasing crop

productivity under drought by genetic and crop management approaches.

Great advances have been made in recent years in understanding the molecular basis of plant responses and plant resistance to drought stress. Many thousands of drought-responsive genes have been identified and the function of some of these has been resolved at the cellular level. However, there is still a huge gap between the molecular-level science, and the translation and application of this knowledge at the whole-plant or crop level in the field, particularly under drought conditions (Passioura 2007; Reynolds and Tuberosa 2008; Xu and Crouch 2008). From the first conference in Montpellier, the series of InterDrought Conferences has been instrumental in continuing to address this gap through crosstalk among molecular biologists, physiologists, geneticists, breeders, crop modellers, soil scientists and agronomists.

Role of agronomy and modelling in crop performance in drought-prone environments

Analyses of crop improvement in the 1980s and 1990s in Australia concluded that changes in agronomic management, such as no-till seeding, the use of herbicides, control of root diseases, improved nitrogen management, crop rotations, yield monitoring and the use of variable seed and fertiliser rates depending on previous yield history, contributed at least three-quarters of the doubling of dryland wheat (*Triticum aestivum* L.) yields over the two decades, whereas breeding resulted in one-quarter of the increase (Anderson *et al.* 2005; Turner and Asseng 2005; Richards *et al.* 2014). Identification of the factors that restrict crops from achieving their water-limited yield potential has assisted farmers in Mediterranean climatic regions of Australia to lift yields to this potential (French and Schultz 1984a, 1984b; Richards *et al.* 2014). Nevertheless, there is still considerable scope to lift yields in many water-limited environments by the use of agronomic (Richards *et al.* 2014) and genetic (Fleury *et al.* 2010) interventions. The use of agronomic approaches was recommended particularly to delegates from countries that have access to good agronomic facilities and practices, but which lack access to the latest genetic and genomic facilities.

The importance of roots for water and nutrient capture has been rediscovered and re-emphasised in recent years. Although studying roots *per se* has been questioned (Zaman-Allah *et al.* 2011; Vadez *et al.* 2013), genetic variation for root traits and their impact on yield has been demonstrated in many studies (e.g. Kashiwagi *et al.* 2006; Gaur *et al.* 2008; Palta and Watt 2009; Landi *et al.* 2010; Uga *et al.* 2013). However, the methodologies for studying roots are highly labour-intensive and time-consuming, and cases were highlighted in which increasing root growth and depth did not benefit yield if root penetration is restricted by the depth of wetting, or chemical or physical barriers. Lynch *et al.* (2014) highlighted new technologies that can quickly identify the architectural and anatomical variations in roots that are important in water and nutrient capture. Field-based high-throughput phenotyping facilities have recently been developed and deployed in dryland regions for a range of root characteristics, but their widespread adoption in breeding programs still requires a

better understanding of the genotype \times soil environment interactions and tradeoffs that may occur. The recent development of well tested models of the interactions between roots and soils (e.g. Dunbabin *et al.* 2013) enables the value of the various root traits to be evaluated without extensive experimentation. Although models are approximations of the real world and their limitations need to be recognised, they are extremely useful in anticipating genotype \times environment \times management interactions so that the expected outcomes of a particular genotype can be evaluated without having to evaluate the genotypes at an impossibly high number of sites, seasons and agronomic inputs (Hammer *et al.* 2014). Further, as the environmental, physiological and biochemical responses of genes can now be modelled with increasing accuracy, the role of specific genes or quantitative trait loci (QTLs) in the adaptation to a particular environment or future environment can now be predicted more precisely (Hammer and Jordan 2007; Messina *et al.* 2009; Tardieu and Tuberosa 2010; Kholová *et al.* 2014). Thus crop models are part of the toolbox available to crop breeders and agronomists for improving yields in drought-prone environments, but it is extremely important that they be validated against field results.

Transpiration efficiency and water use

Water is a limited resource and is likely to become even more limited with climate change. As a burgeoning population and industrialisation both compete with agriculture for water, an improvement in the efficiency of water use or water productivity is demanded by both irrigated and rainfed farming systems. Genetic variation in transpiration efficiency (TE) has been a subject of considerable research for the past three decades, but there are only a few examples of crops bred for improved TE (Condon *et al.* 2004). There is also a controversy in the literature as to whether it is beneficial to breed for improved TE in water-limited environments (Blum 2009; Sinclair 2012). Bramley *et al.* (2013) pointed out that many hydraulic and biochemical processes are involved in controlling water flow through the plant and in controlling photosynthesis, and hence in controlling TE. Consequently, many genes, aquaporins and transcription factors (summarised by Bramley *et al.* (2013)) have been implicated in determining the TE of a plant during development and under water-limited conditions. Nevertheless, TE is predominantly driven by hydraulic properties, such as stomatal conductance and the anatomy of the water transport pathway, so that TE improvement in Mediterranean environments is regulated mainly by a reduction in water use rather than by an increase in assimilation (Vadez *et al.* 2014). Vadez *et al.* (2014) pointed out that water use and TE were independent variables, that improved TE was associated with increased yield in a range of crop species and that breeding for improved TE could be beneficial. However, Sinclair (2012) pointed out that TE is difficult to breed for, as it is influenced by a range of environmental factors (Feres *et al.* 2014). Ecologists have long identified isohydric (stomata close rapidly; transpiration and high leaf water status are maintained with soil drying) and anisohydric (stomata maintained open; high transpiration is maintained but leaf water status decreases rapidly with soil

drying) differences among species (Kumagai and Porporato 2012). Similarly, accessions of peanut (*Arachis hypogaea* L.), chickpea (*Cicer arietinum* L.) and pearl millet (*Pennisetum glaucum* (L.) R.Br.) have recently been shown to respond to increasing vapour pressure deficit by either closing stomata (isohydric) or by maintaining transpiration (anisohydric) (Vadez *et al.* 2013). Vadez *et al.* (2014) described a weighing lysimeter facility that enables water use and TE to be measured in a large number of genotypes in the open throughout the growing season. They concluded that genotypes with high TE and low water loss during vegetative growth, which both assist in maintaining leaf area and in making more water available for use by the crop in the reproductive stage, increase yield in late-season water-limited environments. Thus for crops grown on stored soil moisture, selection for high TE in the vegetative phase will result in increased yield (Vadez *et al.* 2014).

Another mechanism that restricts water use in the vegetative phase and increases water use in the reproductive phase is the stay-green trait (Borrell *et al.* 2014; Kholová *et al.* 2014). Plants with the stay-green phenotype use several avenues to achieve water conservation in the vegetative phase. A QTL has been shown to modify transpirational leaf area by reducing leaf size, stomatal frequency, transpiration per leaf area and possibly transpiration sensitivity to vapour pressure deficit (Borrell *et al.* 2014).

Phenotyping for drought resistance

Previous InterDrought conferences called for better means of phenotyping for drought resistance. Three major improvements in drought phenotyping have evolved between InterDrought-II and InterDrought-IV: (i) wider recognition and adoption of managed field-stress environments, (ii) development and adoption of fast and reliable field remote sensing methods of plant water status, and (iii) the development of in-house facilities using automated high-throughput phenotyping for potted plants. At InterDrought-III, Berger *et al.* (2010) described a high-throughput facility for screening for drought responses in potted plants based around infrared thermal imaging and red-green-blue digital imaging (Costa *et al.* 2013), whereas Munns *et al.* (2010) suggested that this methodology may be applicable in the field. High-throughput in-house public or commercial phenotyping facilities are now available on several continents and may provide phenotypic data derived from potted plants. Such data can be useful but should be carefully considered when applied in a specific breeding program towards a defined stress environment (Tuberosa 2012). The recent establishment of managed environment facilities (Masuka *et al.* 2012; Rebetzke *et al.* 2013; Vadez *et al.* 2014) in dryland fields, with rainout shelters, lysimeters and irrigation has enabled the phenotyping of large numbers of breeding lines for drought resistance under field conditions in the normal growing season, thereby avoiding some of the problems associated with the use of pots with limited soil volumes, and avoiding selection with day lengths or vapour pressure deficits that differ from those in the usual growing season.

Although field phenotyping for drought resistance has made great progress, phenotyping in growth chambers and greenhouses has been trying to cope with the problems of

protocols and correct measurement of drought stress since the early 1990s (Blum *et al.* 1996), and even though problems still occasionally persist (Blum 2013), there are recent examples of successful genomics projects that used correct protocols and phenotyping from their inception to the final proof of function in the field (e.g. Uga *et al.* 2013). Greater effort and attention are still needed in applying the correct protocols in order to produce results and data that are relevant for research that eventually aims to enhance crop productivity under drought conditions.

Phenotyping in laboratories and in managed environment facilities generates large volumes of data. Meta-analysis of data produced in these facilities across the world is rapidly progressing and is being utilised in international breeding programs. However, suitable correlation and consistency of protocols will be required to obtain the full value of this approach.

Selection and breeding for drought resistance

Yield under drought (the definition of drought resistance in crop plants) is polygenic and has low heritability; hence it is difficult to select. Nevertheless, breeding for drought resistance and for water-limited environments has been making steady progress over the last 80 years, particularly in the major cereal crops, rice (*Oryza sativa* L.), wheat and maize (*Zea mays* L.) (see Duvick (2005) for well documented studies in maize), but rates of genetic advance in crop productivity have slowed and even stagnated in many environments, particularly the drier areas (Graybosch and Peterson 2010; Trethowan 2014). The rate of yield increase in dryland environments has generally ranged from 0.3% to 0.7% per annum, depending on the crop studied. In the face of current and future demand, this past rate of increase is not sufficient to meet the predicted demand for food security. New field technologies and the automation applied to breeding in the field referred to in the section entitled “Role of agronomy and modelling in crop performance in drought-prone environments” are expected to enhance progress. Furthermore, genetic resources such as landraces, crop plant progenitors and wild relatives are being used successfully to enhance drought resistance (e.g. Lopes and Reynolds 2011). The integration of plant physiology into breeding programs was effective in moving forward breeding programs for drought resistance such as those for maize in Africa (Bänziger *et al.* 2006), cowpea (*Vigna unguiculata* (L.) Walp.) in Africa (Hall 2004), rice in China (Luo 2010) and wheat in Australia (Richards *et al.* 2014). International institutional involvement at the International Maize and Wheat Improvement Center, the International Rice Research Institute, the International Crops Research Institute for the Semi-arid Tropics, the International Center for Agricultural Research in the Dry Areas and the Global Challenge Program has been very effective in breeding for drought resistance, compared with the research on drought breeding in the 20th century when the concept of breeding for high potential yield was considered the best solution for stress environments. The role of crop models in integrating the disciplines of agronomy, physiology, breeding and molecular genetics has also played a role in advancing drought resistance breeding (Hammer and Jordan 2007; Hammer *et al.* 2014).

Education in breeding for drought resistance, which has long been missing from the university curricula, is now being increasingly addressed by universities, as well as in special international courses offered by institutions such as the University of California, Colorado State University and the Mediterranean Agronomic Institute of Zaragoza, Spain. Therefore, in perspective (Blum 1988; Blum 2011), there has been considerable progress, and an exponential combination of ideas, knowledge, investment and education towards breeding for higher crop production in water-limited environments.

At the same time, huge progress has been made in genomics, especially regarding gene discovery and marker-assisted selection (Fleury *et al.* 2010). The challenge now is to merge genomics with breeding in order to enhance delivery to the farmer (Xu and Crouch 2008; Varshney and Tuberosa 2013).

Molecular research for improving drought resistance

Significant effort has been devoted to transgenic research for improving drought resistance in several crops such as canola (*Brassica napus* L.), potato (*Solanum tuberosum* L.), maize and rice. Drought has a strong impact on gene expression, resulting in many genes being up- and downregulated. EST analysis has been used extensively for comparing well watered plants with stress-treated plants. Differentially expressed gene sequences allow comparisons between the existing sequence databases and gene identities (Gorantla *et al.* 2007; Talamè *et al.* 2007), enabling the discovery of candidate genes (Cal *et al.* 2013; Yu *et al.* 2013). Several genes have been tested and a summary of these genes has been provided by Deikman *et al.* (2012). Receptor-like kinases were recently identified as significant genetic elements that are able to improve drought resistance in water-limited environments. Receptor-like kinases are now considered to be key regulators of stress-related genes, including those for drought (Marshall *et al.* 2012).

Studies with microRNA technology may lead to a more precise identification of candidate genes with more profound effects on drought-affected traits, and these genes may be used for subsequent transgenic research towards improving drought resistance in crops (Sunkar *et al.* 2008; Ding *et al.* 2013). Moreover, the availability of many candidate genes that are involved in various pathways may enable a systems biology approach for improving drought resistance (Bohnert *et al.* 2006). However, transgenic approaches for the development of drought-resistant crops have had limited success to date. In a recent special issue of *Nature* on genetically modified (GM) crops (Anon 2013), it was reported that the GM market is dominated by herbicide- and insect-resistant cultivars, and there was no mention of drought-resistant crops. Attempts have been made to review and understand the reasons for this slow progress with drought-resistance breeding using GM approaches (e.g. Deikman *et al.* 2012). One of the reasons is likely to be the very high cost of development and delivery of a GM cultivar (Shakya *et al.* 2012). Nevertheless, some progress is being made. The introduction of cold shock protein genes by genetic modification improved abiotic stress resistance, including drought resistance, in rice and maize in the field (Castiglioni *et al.* 2008), and increased yields of maize in the

drought year of 2012 in the Western Plains Region of the United States of America (Monsanto 2014).

Translation of the outputs of genomic studies to the field is essential (Xu and Crouch 2008; Varshney and Tuberosa 2013). Although molecular mapping approaches have been extensively employed in the last 15–20 years for detecting major QTLs for various drought-adaptive traits and yield under drought (Maccaferri *et al.* 2008; Fleury *et al.* 2010; Landi *et al.* 2010; Cakir *et al.* 2011; Kholová *et al.* 2012; Henry *et al.* 2014), only a minute fraction of these QTLs have entered the breeding pipeline (Mishra *et al.* 2013; Steele *et al.* 2013; Uga *et al.* 2013; Henry *et al.* 2014). Additionally, linkage mapping studies have limited power in detecting minor QTLs for complex traits such as drought resistance. More recently, association mapping (Courtois *et al.* 2013; Varshney *et al.* 2014) and nested association mapping provide additional opportunities in view of the lower linkage disequilibrium and the higher diversity explored in conjunction with the development of ultrahigh-throughput Single Nucleotide Polymorphism (SNP) markers and the use of next-generation sequencing (Varshney *et al.* 2014). Progress in high-throughput precision phenotyping is now enabling a more precise detection of QTLs for ‘hard-to-phenotype’ complex traits, an issue that is particularly relevant for the selection of drought-resistant genotypes (Walter *et al.* 2012), even more so for the fine mapping and eventually the cloning of major QTLs for drought-adaptive traits (Mishra *et al.* 2013; Uga *et al.* 2013). These mapping approaches have already provided closely linked markers for complex traits such as stay-green (Borrell *et al.* 2014) and root architecture (Landi *et al.* 2010; Courtois *et al.* 2013; Steele *et al.* 2013; Uga *et al.* 2013).

Other procedures such as RNAi, TILLING and eco-TILLING are now routinely used for functional studies of the genes that are putatively involved in the adaptive response to drought. Modern mapping methods have identified a large number of QTLs for various drought-related traits (escape, avoidance and tolerance), and a cluster or ‘hotspot’ of QTLs or transcription factors (or both) have been or are being used through marker-assisted breeding to improve the drought resistance of chickpea (Varshney *et al.* 2012, 2014; Thudi *et al.* 2014), rice (Mishra *et al.* 2013; Steele *et al.* 2013), millet (Yadav *et al.* 2011) and maize (Cooper *et al.* 2014). More recently, the adoption of genomic selection has provided novel opportunities for the selection of traits with low heritability that are controlled by many QTLs with small effects (Heffner *et al.* 2009). This notwithstanding, a more widespread application of genomic selection is limited because of its poor predictive ability for yield.

When these achievements in genomics are viewed from a breeding standpoint, the gap between knowledge and its application towards the delivery of drought-resistant varieties still exists and requires further action (Reynolds and Tuberosa 2008; Xu and Crouch 2008). Cooper *et al.* (2014) demonstrated that the gap can be narrowed and described the development of drought-resistant maize hybrids that yielded 9% (0.5 t/ha) more grain than conventional hybrids in the US corn belt in the 2012 drought with no yield penalty in adequate rainfall environments. As in other successful breeding programs, this multipronged approach involved (i) the use of precision phenotyping in managed-stress nurseries, (ii) genomics and

other molecular technologies to dissect the genetic architecture of drought-adaptive traits and to develop high-throughput markers, (iii) field evaluation at a large number of sites in target environments, and (iv) the use of crop growth models to evaluate the integrated effects of multiple traits for their combined effects and to guide the development and evaluation of the drought-resistant hybrids (Cooper *et al.* 2014). This requires the coordination of very large teams of scientists and technicians, as well as considerable investment in personnel and equipment, which would be affordable primarily for the private sector or public-private partnerships. Consequently, it is not surprising that with the exception of orphan crops, crop breeding is rapidly moving out of universities and national programs into the private sector. The success obtained by these very large-scale programs raises the question of how best to support the capacity and innovative ideas of small teams of breeders in order to contribute to breeding crops with improved drought resistance while recognising that there is no 'silver bullet' for improving crop tolerance to drought. We conclude that it remains a responsibility for the InterDrought conferences to address the requirements not only of the large breeding companies, but also the small-scale research programs, especially in developing and emerging economies where the demand for food is fast increasing and farmers must cope with the increasing risk of global climate change and water scarcity.

Finally, the conference was briefly reminded by one speaker that in drought-prone environments, crop production from a farmer's perspective is an economic decision, and farmers optimise their risks and opportunities across a cropping season or cycle rather than trying to achieve the maximum production from an individual crop. This applies to both subsistence and commercial farmers with different socioeconomic implications. Accordingly, this optimisation may well imply that the best strategy to improve drought resistance is to aim for increased yields in good seasons, and minimise costs and target yield in drought-stressed seasons.

Recommendations

1. Climate change with warmer temperatures and longer and more frequent droughts emphasises the need for crop improvement for hot and dry environments, and also makes it imperative to define target environments and appropriate traits for future drought and climate scenarios, not just the current ones.
2. The political and social imperative of food security inevitably means greater focus on and resources from governments and private enterprise for research on crop breeding and agronomic management, and delivery to the farmer.
3. In some countries, significant gains in yields in water-limited environments have derived from changes in agronomic practices. In many parts of the world, there are still significant opportunities to increase yields by adopting agronomic practices that reduce water loss from the soil and make it available to the crop for reproductive development. In certain cases, simple inventive solutions and a simple clear message have been very effective in improving crop yields in farmers' fields in water-limited environments.
4. Although steady progress has been made in breeding and selection for drought resistance, the present genetic gains are insufficient to ensure food security and there is an urgent need to enhance such gains under drought and heat stress conditions. Even though the individual's intellectual and knowledge base remains very important and instrumental for accelerating yield gains, integrative and interdisciplinary approaches offer new solutions for next-generation breeding for drought resistance and adaptation to drought. It is crucial that such teams integrate breeding, physiology, crop modelling, genomics and crop management expertise, spanning the distance between laboratory and field.
5. Large teams with a range of expertise have been commercially successful, but there is still an opportunity for small teams to make significant steps in improving the drought performance of crops, particularly with minor crops or orphan crops that have limited appeal for private companies but have large social significance, particularly in developing and emerging countries. In these cases, links with the international agricultural research centres within the Consultative Group for International Agricultural Research will be especially beneficial.
6. The importance of teamwork cannot be overstated if the gap between genomics and breeding is to be bridged. The collaboration is not only a question of breeders drawing results from molecular biologists, but, more importantly for breeders and physiologists, one of influencing how genomics are performed in a way that is relevant to the target environment so that it will maximise future delivery to farmers. Such collaboration will also help to develop better knowledge of the molecular and functional basis of the drought-adaptive responses of crops.
7. Finally, papers presented at InterDrought-IV demonstrated that significant progress is being made both in agronomic management and breeding of cultivars for drought-prone environments. Importantly, progress has also been achieved in better understanding the molecular and genetic basis of the response of plants at both the cellular and crop levels. Furthermore, coordination between agronomists, soil scientists, physiologists, modellers, plant breeders, geneticists and molecular biologists is ensuring that the modern tools of genomics are being applied to develop new cultivars of drought-resistant cultivars for water-limited environments. Nevertheless, further research is needed to ensure that the progress continues and even increases to meet the nutritional demands of the world's increasing population in the face of climate change. The crop management tools and new cultivars for drought-prone areas need to be delivered to and adopted by farmers. Without such adoption, food security will continue to be a major impediment to a stable and peaceful society.

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