VIRTUAL ISSUE EDITORIAL

Improving crop performance under drought – cross-fertilization of disciplines

Better crop performance in dry environments is imperative for food security in the face of climate change. This has never been as true as in 2017, but the concern has existed for decades. The four InterDrought conferences held since 1995 have addressed issues associated with crop performance under drought with a clear multi-disciplinary approach. During this time *Journal of Experimental Botany* has been at the forefront in publishing the underlying experimental science encompassing the disciplines and scales of organization required in drought research. We hope that the papers highlighted here will be useful to, and instrumental for, broadening interdisciplinary understanding of drought tolerance.

One of the most productive ways of tackling the agricultural challenge of drought is through cross-fertilization between areas of research, in particular crop physiology, agronomy, genetics, breeding, and environmental characterization/modelling. Scientists need to become familiar with multi-scale approaches from cells to crops subjected to water deficit, and this has been a major achievement of the InterDrought network (Box 1). Indeed, drought tolerance involves cellular aspects such as detoxification (Missihoun et al., 2011) and osmotic adjustment (Blum, 2016), but also whole-plant signalling involved in the control of growth and transpiration under water deficit (Tardieu, 2016), the whole-plant control of shoot and root system architectures, and feedbacks between water capture, growth and transpiration at canopy level (Messina et al., 2015). The exploitation of native genetic variability provides invaluable opportunities for improving plant performance based on mechanisms at any of these scales, namely cell, organ, whole-plant and canopy, in particular through progress in phenotyping (Fiorani and Schurr, 2013; see also the special issue ‘Phenotyping in plants’, introduced by Pieruschka and Lawson, 2015) and genomics-assisted breeding (Reynolds and Langridge, 2016).

Improved knowledge of the physiological mechanisms involved in the control of transpiration and growth, and of their genetic make-up, paves the way for manipulating and eventually fine-tuning these controls in order to enhance their efficiency via genetic approaches (Habben et al., 2014), possibly complemented by application of compounds that affect them (Park et al., 2015). While agronomy is currently undergoing a major change in focus based on the widespread use of sensors, robots and imaging techniques resulting in precision agriculture, breeders are taking full advantage of our increasing ability to identify and tailor beneficial alleles able to enhance crop productivity and eventually mitigate the negative effects of drought.

Rapid progress in molecular physiology and genomics applied to drought

Identification of the sources of tolerance and then cross-hybridization to recombine genomic segments form the basis of classical breeding for the development of drought-tolerant cultivars (Rauf et al., 2016). However, the pace of development of improved drought-tolerant cultivars is slow, severely hampering the timely replacement of improved varieties for agriculture.

The controlling mechanisms for plant performance under drought are complex due to the multifaceted interplay between genetic components including genes, transcription factors, microRNAs (miRNAs), hormones, proteins, co-factors, ions and metabolites (reviewed by Janiak et al., 2016; Tardieu, 2016). Advances in cost-effective sequencing and high-throughput genotyping technologies now mean that sequencing/genotyping large amounts of genetic material can be achieved within a limited period of time. These sequencing and genotyping data together with information from multi-environment phenotyping have enabled high-resolution genetic mapping leading to genetic dissection of improved yield under drought. Quantitative trait loci (QTLs) and candidate genes have been identified in various crops including rice (Zhou et al., 2010), wheat (Maccferri et al., 2016), maize (Millet et al., 2016) and chickpea (Jaganathan et al., 2015; Kale et al., 2015). Although gene editing has shown great potential as a powerful tool for improving any trait for which sequence variation is available (Bortesi et al., 2015), this technology has yet to contribute to an appreciable improvement in drought tolerance in crop plants.

In addition to genetic studies conducted at the DNA level, efforts have also been made in candidate gene discovery through RNA deep sequencing (Chang et al., 2016; Garg et al., 2016; Shankar et al., 2016) and microarray analysis.
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(Mishra et al., 2016). For example, whole-genome transcriptome-profiling studies have identified a large number of transcripts encoding members of various gene families reported to play an important role in abiotic stress tolerance, including AP2/EREBP, bLHL, MYB, and auxin-related families (Chang et al., 2016; Garg et al., 2016). Similarly, transcriptome analysis has identified the molecular mechanism underlying the high degree of plasticity of the water-deficit response in maize (Opitz et al., 2016). Furthermore, induced expression of various transcription factors (e.g. MYB) have favourable effects under drought in maize (Casaretto et al., 2016) and Arabidopsis (Scarpeci et al., 2016).

Various studies have reported a role of miRNAs in abiotic stress tolerance (Shriram et al., 2016), as in the case of drought-induced expression of Hv-miR827 in barley (Ferdous et al., 2016). Likewise, up- or down-regulation of different miRNAs was found to be associated with improved performance in rice (Chung et al., 2016) and barley (Hackenberg et al., 2015) subjected to water deficit. Hormones also play an important role in the regulation of drought acclimation/adaptation (Li et al., 2016; Tardieu, 2016; Visentin et al., 2016). For instance, recent studies suggest a role for cytokinins in barley (Pospíšilová et al., 2016), Arabidopsis (Nguyen et al., 2016), tomato (Farber et al., 2016) and rice (Talla et al., 2016), and for strigolactones in tomato (Visentin et al., 2016). These mechanisms have a crucial role for phenotypic plasticity. Indeed, the latter is a key trait for dealing with complex G×E interactions, as shown by Sadras et al. (2016), who explored the genetic control of phenotypic plasticity in chickpea. A systems-based approach which allows the integration of ‘omic’ technologies...
using computer-assisted theoretical and molecular biology would therefore help capture a global view of the complex mechanisms involved in the phenotypic plasticity associated with drought responses (Hussain et al., 2016).

Exploitation of genetic resources based on association mapping and genomic selection

Root features play a pivotal role in crop performance under water deficit, as well as in optimizing use of the available water resources (Messina et al., 2015). In the past, roots have received limited experimental attention due to difficulties in phenotyping, particularly under field conditions. However, recent technical advances in root phenotyping and the utilization of high-throughput platforms have led to the publication of an impressive number of papers.

Particular attention has been devoted to the characterization of root mutants and the dissection of the genetic makeup governing root system architecture (RSA) and its effects on crop performance under different water regimes. The work of Jiang et al. (2016) highlights the role of strigolactones in the hormonal landscape that shapes RSA through the modulation of lateral root development via a tight interplay with auxins and cytokinins. Additional physiological work in Arabidopsis by Kircher and Schopfe (2016) supports the existence of periodic priming signals influencing lateral root formation along the growing root (see also the Insight article by Scheres and Laskowski, 2016). A valuable example of how to leverage molecular knowledge on lateral root growth to enhance the field performance of a drought-stressed crop is presented by Li et al. (2016). In rice, overexpression of transcription factor gene MORE ROOT (TaMOR) from wheat results in more roots and higher grain yield. TaMOR, a plant-specific transcription factor belonging to the ASYMMETRIC LEAVES2/LATERAL ORGAN BOUNDARIES (AS2/LOB) protein family, is highly conserved in wheat and its wild relatives. Notably, TaMOR-D-overexpressing lines had larger root systems in Arabidopsis and rice, and produced a higher grain yield per plant. Therefore, TaMOR offers an opportunity to improve root architecture and increase yield in crops.

Among crops, cereals have a particularly complex and plastic root system whose components play different adaptive roles according to the growth stage and prevailing soil conditions (Hochholdinger, 2016). In maize, the QTL study of Gao and Lynch (2016) shows that a reduced crown root number is associated with greater root depth and improved water acquisition from drying soil. Previous studies have shown that major QTLs for RSA influence yield in maize grown under different water regimes (Landi et al., 2007, 2010). Similar results have also been reported in rice (Price et al., 2002; Uga et al., 2011) and chickpea (Varshney et al., 2013).

From an agronomic standpoint, the work of Lilley and Kirkegaard (2016) shows the importance of the time-space interplay between root depth and water capture as related to soil depth and annual resetting of soil water. This modelling study shows that capturing more water from deeper soil layers is not always the best option. Additionally, the simulation shows a greater impact of earlier sowing than modified root systems on water uptake, indicating that crop sequence must be managed tactically to optimize overall system benefits.

‘Whole-plant mechanisms’ which affect yield may differ between environments

Causal relationships between potential mechanisms and plant behaviour under drought are often far from straightforward or unidirectional due to multiple feedbacks at different timescales (Tardieu and Parent, 2017). For instance, it is well-known that early-flowering genotypes tend to escape drought compared with later genotypes, because flowering time and physiological maturity occur earlier in the season when the soil water reserve is not depleted. This is at the expense of potential biomass accumulation because of a shorter period in which photosynthesis can occur over the plant’s life cycle. Kazan and Lyons (2016) show that evolution may well have resulted in elaborate mechanisms in Arabidopsis plants subjected to water deficit which fine-tune the escape strategy and avoid its negative trade-offs. In particular, earliness is correlated with differences in the case of drought in late or early-maturing accessions via differential expression of genes involved in the floral transition. This results in interesting feedback loops between floral transition, water uptake and growth. Another interesting example arises from the study of Christopher et al. (2016) (see also the Insight article by Rebetzke et al., 2016b). Stay-green is often considered as a trait per se that confers drought tolerance. Christopher et al. considered the relationship between yield and different stay-green traits in eight contrasting environments. They found marked differences in relationships in well-watered conditions, and in water deficit occurring during either flowering or grain filling. Hence, indicators of stay-green have an effect on yield that is dependent on context. This may well be a general case for most traits involved in drought tolerance (Tardieu, 2012).

Similarly, there has been a long-standing debate about the effects of awns on yield, particularly under water deficit. Rebetzke et al. (2016a) propose a Solomon-like judgment: the presence or absence of awns has opposite effects on grain number and grain size, resulting in no major effect on yield (see also the Insight article by Guo and Schnurbusch, 2016). Indeed, the allocation of assimilates to awns decreases floret fertility, but favours grain filling particularly in dry environments. However, the respective effects on grain number and grain yield may have amplitudes that are context-dependent.

Hence, Blum (2016) states that drought tolerance needs to be re-defined in a better way by distinguishing the environment as sensed by plants (stress), the early plant reactions (strain) that trigger signalling processes and, eventually, acclimation processes. It is noteworthy that evolutionary geneticists usually reserve the term ‘adaptation’ for the selection of these acclimation processes over generations. As stated by Maron et al. (2016), fine-tuning concepts have large consequences for annotating so-called stress-resistance genes with
markedly different effects in time and scales of organization (Tardieu and Parent, 2017). The latter considerations may considerably complicate early screening for drought tolerance based on root and shoot (Avramova et al., 2016).

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