Genomic tools to assist breeding for drought tolerance

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Water deficit or drought stress is a major limitation to crop production globally. Plant breeders have used a wide range of technologies to successfully breed varieties that perform well under the growth conditions for their target environments but they are always seeking new opportunities to enhance rates of genetic gain. Under drought, yield is determined by the integration of variable levels of water deficit across the developmental life of the crop. Genomics technologies were seen as a path to understand the genetic and environmental complexity of drought stress. To be relevant to breeding programs, genomic studies must consider the nature of drought stress in the target environment and use plant material and phenotyping techniques that relate to field conditions.

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The drought environment

The term 'drought stress' hides great complexity and varies greatly between crops and environments. For example, maize yield may fail due to moderate stress whose timing delays anthesis-silking interval beyond a critical threshold [1•]. Wheat on the other hand can show a linear response to water, and this plasticity permits it to be grown under highly unpredictable conditions, including severe moisture stress [2]. While rainfall is probably the least predictable environmental factor in most crop environments, breeding has been very effective at targeting lines to a wide range of water availabilities [3]. Consequently, for most major crops, farmers have access to varieties that perform well under the typical environmental conditions for their region. For wheat, farmers in the UK have varieties that can take advantage of highly favourable production conditions and routinely yield up to 15 t/ha while Australian farmers sow varieties that produce an average of 1.5 t/ha. However, both UK and Australian wheat breeders are seeking improved performance of their varieties under drought. In reality the problem they are trying to tackle is environmental variability rather than drought per se. Below average and unfavourable distribution of rainfall is the core problem. Therefore we need to ask how can we improve the ability of our crops to cope with unusually low rainfall and are the requirements the same for the UK as for the Australian varieties? If genomics tools are to be of value to breeding activities, we need to consider how they can help breeders tackle this question. Importantly, we need to show that these tools can add value over and above what can be achieved using existing breeding and selection techniques.

Genomics applications

Broadly speaking genomics tools offer knowledge and information about single genes, pathways or gene networks, and genome structure and behaviour. This knowledge and information can be deployed in several ways. Where individual genes controlling the trait of interest are known, the gene knowledge can be used to identify, discover and tag individual alleles and to develop and deploy molecular markers to track the desired alleles in breeding programs [4]. Armed with gene knowledge, novel alleles can be sought in diverse germplasm pools, including wild relatives, expression variation can be studied and new alleles, both structural and expression, can be created either through genetic engineering or through the new genome editing techniques.

At the genome structure level, genomics and whole genome analysis can help breeders design optimal recombination strategies and deploy some new breeding techniques, such as genomic selection [5••]. Marker information can also be valuable in genetic dissection to distinguish between traits with an independent genetic basis that could, for example, be combined to achieve cumulative gene action versus trait expression associated with alternate alleles at a given loci that can only be traded-off against each other.

The areas where genomics tools are being applied are where the genetic control of the target trait is clearly defined and, consequently simple, or where information on individual genes is not required and genome structural and predictive models can be used [6]. The area where genomics has struggled to have an impact is also the area where genomics was thought to offer the greatest potential, namely in describing and defining complex traits

where genotype x environment interactions exert a major effect, such as drought tolerance [7]. The limitation may not lie with the genomics technologies but rather with our understanding of the genetic basis of target traits and the interactions with an environment that is in constant flux.

The nature and components of drought stress

First we need to consider the nature of drought stress in more detail. Drought stress is not static; it can occur at any time during the crop growth, it can vary in severity and it frequently occurs in conjunction with other environment stresses, such as heat and salinity [8]. Different tissues or organs of the plant will respond differently to drought stress and the level of stress will fluctuate diurnally, high stress during peak photosynthetic periods and low stress overnight [9]. The nature of a plants' response will also vary greatly depending on whether the plant is entering stress for the first time or after several exposures and whether they are recovering from stress after a rainfall or irrigation event [10].

Drought tolerance can take on several very different forms (Figure 1) including:

- the ability of the plant to access water-determined largely by the architecture and health of the root system [11,12•,13•];
- the efficiency of water use by the plant-usually based on a series of compromises between the ability to access CO_2 for photosynthesis while limiting water loss [14], the allocation of resources (roots versus shoots, carbon storage versus growth) [15];

Figure 1

A conceptual model of drought adaptive traits in wheat (adapted from Reynolds and Tuberosa, 2008); WU, WUE, and HI stand for water uptake, water use efficiency, and harvest index, respectively.

- protection against damage-especially to reproductive growth-resulting from dehydration and heat [16•], including oxidative stress [17].
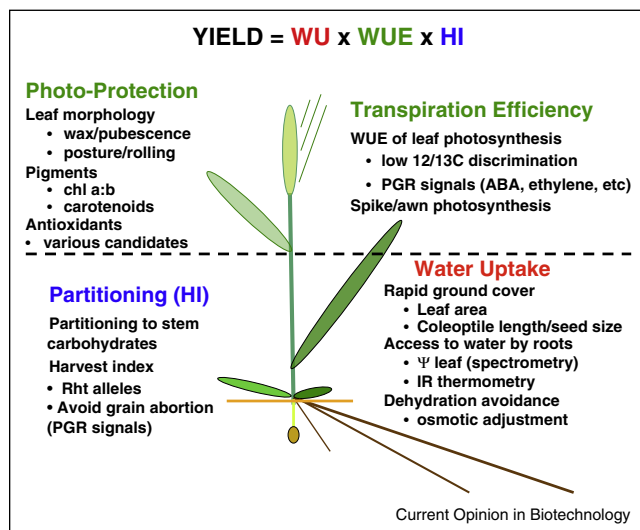
Defect elimination

There are several areas where relatively simple traits, from a genetic perspective, can be directly tackled to enhance the performance of the crop plant under water-limited condition [18]. Perhaps the most important area where this has been shown is related to root function where there are some very effective examples of significant advances through the applications of genomics.

Root health and vigour can dramatically affect the ability of the plant to access water; nematodes, fungi and bacteria can all damage root systems, while nutrient deficiencies (particularly P, Zn and Fe) and toxicities (salt, Al, B) can limit root vigour (for example [19]). In some environments deep roots will help capture moisture [11,12•,20•] while in others, where deep water is absent or even toxic (e.g., saline or acid), strong surface roots may be the best option [21]. In many cases our best option for improving drought tolerance is to tackle these components or associated stresses since these are often under simple genetic control and can be rapidly and reliably phenotyped. For example, incorporating resistance to nematodes [22] or tolerance to toxic levels of boron [23] or salt [24] may offer significant improvements in drought tolerance. This strategy of defect elimination has been widely deployed and resulted in significant improvement in crop performance.

Phenotyping for drought tolerance

Following on from the above discussion, the most important drought tolerance phenotype is yield under conditions where water availability is below expectations for the target environment. How can this trait be measured, or more specifically how do we expose plants to a relevant drought stress and measure the impact of the stress on yield or component physiological, developmental, biochemical or genetic traits [25,20•,26]? While some believe controlled facilities are the only way to achieve scientific precision, abstraction from reality can produced unacceptable levels of artefacts. These errors can be reduced if knowledge of the environmental and biological systems being simulated is used to design phenotyping platforms. Although we lack comprehensive biophysical information about many of the drought environments worldwide, some general rules of thumb can still be applied. For example, drought screens often fail to differentiate between water use efficiency (WUE) and water uptake (WU) as targets for improvement. While both have benefits in the right agronomic context, they are very different phenomena, and require distinct screening protocols.

Another key limitation to controlled facilities is that crop plants normally grow as a community of genetically