

Genetic improvement of wheat for dry environments – a trait based approach

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INTRODUCTION

Improving crop performance where there is limited rainfall will remain one of the most challenging long term issues for farmers, researchers, industry and governments globally. This is because there are no easy solutions and the occurrence and severity of drought is like a lottery – totally unpredictable – making breeding progress extremely difficult. There has not been much clarity in the international literature for improving crop performance under drought and this has hampered progress. For example, terms such as ‘drought tolerance’ and ‘drought resistance’ are common, but these are not easily measured and they may be unrelated to productivity per unit area or per unit of water use (Passioura, 2002). Even where there is a focus on productivity, expectations in drought years may be very different. For example, in many semi-arid regions a drought may mean total crop failure and the small amount of biomass available is fed to animals, whereas in milder climates, such as in the UK, it may mean a reduction in grain yield from 9t ha⁻¹ to 7 t ha⁻¹ (Foulkes et al, 2004). This complexity and uncertainty has often resulted in bewilderment and lack of focus and, more than likely, a lack of significant progress in improving yield in water-limited conditions. Although this is not always the case as in some dry regions where limited irrigation water is available to alleviate extreme drought conditions there can be some predictability. This is most evident in India and China. Despite the complexity of drought and the substantial seasonal variability in rainfall, there has been progress in crop improvement (eg Perry and D’Antuono, 1989; McCaig and Clarke, 1995). Farmers have adopted different germplasm or changed species and management practices. Plant breeders have made progress through the last century but this has largely been through better matching phenology to growing season rainfall (Richards, 1991). Breeders have also had some comfort and hope in knowing that in the evolution of land based plants multiple adaptations to drought have evolved that have a genetic basis that may be useful in crop improvement programs (Damania, 1990).

PROGRESS IN WHEAT IMPROVEMENT IN DRY ENVIRONMENTS

Some of the lessons we have learnt about progress in wheat improvement in dry regions can be summarised by the following three factors. Firstly, empirical selection in ‘conventional’ breeding programs in dry regions continues to make progress. Much of this progress cannot be attributed to improved crop growth in dry conditions but to breeding for resistance/tolerance to biotic (eg, nematodes, root diseases) and abiotic (eg, soil

chemical toxicities such as Al, Na, B) factors that reduce growth when soil water is limited. Secondly, yield under drought has been greatly improved by incorporating germplasm that has a high yield potential under favourable conditions. This is most evident in wheat by the importance of CIMMYT germplasm that has been selected under favourable conditions but it has been adopted in dry regions (Laing and Fischer, 1977; Lantican et al, 2002). However, this may also be because the heritability for yield is higher under favourable conditions relative to dry conditions and this will favour genetic progress. Thirdly, phenology has been the single most important trait that has been genetically modified that has contributed to yield improvements in dry regions. The improvement in yield is usually been associated with selecting for earlier flowering time so as to avoid drought and this has resulted in an improved harvest index rather than an increase in biomass production (Perry and D’Antuono, 1989). However, altering the duration of the growing season such as sowing earlier can also have a dramatic impact on increasing grain yield and above-ground biomass and this has been evident where conservation farming practices have been adopted (Anderson et al, 1996).

LACK OF PROGRESS IN WHEAT IMPROVEMENT IN DRY ENVIRONMENTS

There are also some lessons learned associated with lack of progress in breeding for water-limited environments. Some of these are as follows:

1. Yield progress is slow, especially in variable rainfed environments, because genotype x season sources of variation dwarf genotypic variation resulting in a low heritability for yield (Brennan and Byth, 1974).
2. In reviewing progress in all crops for improved performance under drought it is evident that plant water relations are rarely important (Richards, 2006).
3. There is little evidence that landraces or wild relative of wheat, that may have developed important mechanisms for dry environments, have contributed to wheat improvement for dry conditions (Hajjar and Hodgkin, 2007). However, it is expected that landraces will be a rich source of genetic variation for traits of importance.
4. Most traits associated with improved performance under drought are complex in their nature and controlled by many genes each having a small effect (Rebetzke et al, 2007; Rebetzke et al, 2008; Yang et al, 2007). The corollary to this is that GM approaches to improving performance under drought will be hard fought.

5. Traits that are important in one environment may not be important in another where the drought is different (eg crops grown on stored soil water vs current rainfall) (Condon et al, 2002).
6. Little progress is made without a prolonged investment in long term drought research that is connected to wheat breeding programs and the delivery of commercial varieties.
7. Significant advances in performance under drought will come from overcoming biotic limitations such as soil-borne diseases and other abiotic constraints such as soil chemical constraints (Paull et al, 1992; Ogbonnaya et al, 2001).

Finally, the very best varieties already approach the yield potential in a water-limited environment when best agronomic management practices are adopted (Sadras and Angus, 2006). This would imply that although advances will continue they will be modest and there will be no miracles.

A TRAIT BASED APPROACH TO WHEAT IMPROVEMENT FOR WATER LIMITED ENVIRONMENTS

The approach to wheat improvement for dry conditions taken at CSIRO in Australia has been to first understand the physiological and agronomic limitations to drought performance in temperate cereals and then to search for breeding solutions. The reasons for this approach have been outlined before (Richards et al, 2002). It offers a more targeted approach to crop improvement and one which may identify new sources of genetic variation that are not currently found in breeding programs. It complements empirical breeding but it also relies on empirical breeding in the final stages of elite line selection. In addition, as $G \times E$ for yield is generally very high in variable rainfed environments, resulting in a low heritability for yield, then a physiological approach may identify traits with high heritability and low $G \times E$. An additional attraction is that physiological traits may be cheaper and easier to select for than yield itself. They can often be conducted out of season and they lend themselves to marker assisted selection. In turn this can lead to gene discovery and an understanding of the molecular and physiological basis of yield formation in cereals.

A major challenge with this approach is to prioritise traits to use in breeding as the literature has an abundance of traits associated with performance in dry conditions. However, the dissection of yield under water-limited conditions into three components proposed by Passioura (1977) was a major breakthrough that simplified this. Passioura proposed that when water is limited, grain yield is a function of (i) the amount of water the crop transpires from current rainfall and from water in the soil, (ii) how efficiently the plant exchanges carbon dioxide for water to produce dry matter and (iii) the proportion of the dry matter that finishes up in the grain (ie the harvest index). Passioura has argued that improving any one of these should improve grain yield. Knowledge of which of these components may be

limiting in a target region and which traits may show genetic variation enables a group of 'best bet' traits to be identified for genetic improvement. Table 1 summarises a set of 'best bet' or priority traits and how each is expected to increase yield. Also shown in the Table are key references that establish the importance of the trait or important genetic variation found for the trait.

A number of important factors emerge from this analysis. These are as follows:

1. All traits are in general complex and controlled by multiple genes. Even where major genes are involved such as for flowering time, crop establishment and tiller reduction, minor genes are often required to fine tune the expression of the trait.
2. A good understanding of each trait has resulted in the development of selection methods that are fast and effective. A good example of this is when it became clear that early leaf area growth (early vigour) of wheat was poor in contrast to barley and that the main drivers of vigour were the two complex traits embryo size and specific leaf area. Then a simple surrogate for these (leaf width of the second leaf) was developed that was both fast and had a high heritability and resulted in effective selection for vigour (López-Castañeda et al 1996). Effective selection methods for other complex traits, such as carbon isotope discrimination, stem carbohydrate storage and remobilisation, have also been developed whilst maintaining a high heritability for the trait. The importance of fast and accurate phenotyping is essential for progress and this also underpins the development of useful molecular markers.
3. Most traits are associated with growth processes or the allocation of carbon rather than with plant-water relations.
4. Studies conducted on large populations that vary for some of these traits so as to identify QTLs that may be useful in selection have shown that many of the QTL co-locate with regions associated with plant height and flowering time (Rebetzke et al, 2008). Thus any variation in flowering time or height is likely to confound studies on key traits associated with yield under drought. Ways must therefore be sought to minimise these effects and it is important that the measurement of flowering time and height always accompany the measurement of key traits.

CHALLENGES AHEAD

Above-ground traits, apart from reproductive organs, have received more attention than below ground traits for obvious reasons. More attention should now be given to factors responsible for genetic variation in root system traits as this is likely to be as rewarding as above-ground traits have been. This is going to be challenging mostly because of the difficulty in effectively measuring roots in real soils and understanding where the main limitations to root growth are in field soils. It will be complicated by soil type, cropping history, chemical and soil physical factors. We

are going to need to use our ingenuity to develop effective selection criteria for root systems. A good example of this is to use stomatal aperture traits which are non-destructive such as canopy temperature depression, stomatal conductance or carbon isotope discrimination, all of which can be measured on the above-ground plant quickly and effectively, and provide some indirect measure of how effective roots are in accessing water deep in the soil; eg, Olivares-Villegas et al, 2007 . Other methods becoming available to monitor root growth involve similar non-destructive methods where plants are grown in special tubes that are permeable to infra-red radiation. Improved destructive methods for use in the field are also being developed using hydraulic coring methods and DNA detection methods.

Significant attention to GM approaches for improving performance under drought will continue. Many of these have been misdirected in the past and even when studies on all species are taken into account, there are few examples which show promise in dry areas, that are likely to be effective in the spectrum of variable environments normally encountered in semi-arid regions and particularly those which provide economic returns to farmers. The best examples so far would be the studies by Bahieldin et al (2005), Wang et al (2005) and Hu et al (2006). Only the former was conducted with wheat and it appears not to have been independently tested or pursued further. Our expectations of GM traits for water-limited environments should not be too high for a number of reasons (and this also applies to traits improved through conventional breeding). One is that our current elite varieties are close to the biological limit for yield in dry environments, and second, most traits are complex and are controlled by multiple genes. However, there is no doubt that considerable genetic progress is still possible.

More studies are required to understand the physiology and genetics of yield formation in the absence of water limitations. An increase in yield potential is likely to have impact in many water-limited environments as well as in the absence of water stress. The best example is with the green revolution dwarfing genes which have been hugely important in dry environments. Wheat varieties in Australia, which is among the driest wheat growing regions globally, are now dominated by the semi-dwarf genes *Rht-B1b* and *Rht-D1b*. This is because they enhance yield over tall wheats in environments where yield exceeds about 1.5 t ha⁻¹ (Laing and Fischer, 1977). Another example could be the enhanced yield associated with the *Lr19* translocation from *Thinopyrum ponticum* which gives enhanced yields in both favourable and moderately dry environments (Reynolds et al, 2001).

The final challenge of importance is more a political and institutional one rather than a scientific one and that is to assemble stable teams of interactive scientists that not only include breeders, physiologists and molecular biologists but also agronomists and soil biologists. This

could even extend to modellers and pathologists. All must be closely connected to farmers and the team must be maintained over a long time period. The weakness in scientific skills at the present time is more associated with field based scientists and effective phenotyping. Molecular technologies have flourished and the bottleneck is now with effective phenotyping to better use and apply the molecular technologies and the validation of physiological traits and molecular tools in field grown crops.

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Table 1. Priority traits in wheat for water-limited environments

Yield component	Trait	Universal trait or environment specific ^a	Selection method ^b	Reference
1. Increase crop water use	Extended phenology	Env. specific	P	Gomez-Machperson & Richards, 1995
	Improved early establishment	Universal	P, M	Richards, 1992; Rebetzke et al, 1999; Ellis et al, 2005; Rebetzke et al, 2006b
	Improved above-ground crop vigour	Env. specific	P	Liang & Richards, 1994; López-Casteñeda et al, 1996; Rebetzke & Richards, 1999; Rebetzke & Richards, 2000; Richards & Lukacs, 2002.
	Improved early root vigour	Universal	P, M	Richards et al, 2007
	Increased root depth	Universal	M	Richards et al, 2007; Manschadi, 2006; Hurd, 1976
	Stay green	Env. specific	P, M	Christopher, 2008
2. Increase transpiration efficiency	Stomatal conductance	Env. specific	P	Richards et al, 1986; Condon et al, 1990; Rebetzke et al, 2003; Olivares-Villegas, 2007; Rebetzke et al, 2006a
	Photosynthetic capacity	Universal	GM	Farquhar & Richards, 1984; Condon et al, 1990.
	Maximised crop growth in winter	Env. specific	P, M	Gomez-Machperson & Richards, 1995; Richards, 1991.
	Reduced wasteful respiration and exudate from roots	Universal	P, M, GM	
3. Increase harvest index	Maximised stem carbohydrate storage and remobilisation	Universal	P, M	López-Casteñeda & Richards, 1994; van Herwaarden et al, 1998; Ruuska et al, 2006
	Reduced wasteful tillering	Universal	P, M	Duggan et al, 2005; Spielmeyer & Richards, 2004; Richards, 1988.
	Increased axial resistance in seminar roots	Env. specific	P, M	Passioura, 1972; Richards & Passioura, 1989.
	Increased floret fertility	Universal	P, M	
	Extended rooting depth (see increased root depth above)	Universal	M	

^a This is an assessment as to whether the trait is expected to be important in all water-limited environments (*Universal*) or to specific environments (*Env. specific*).

^b This shows whether molecular markers (*M*) have been identified to assist selection, whether direct phenotyping is effective (*P*) or whether GM traits are likely to be effective.