

Chapter 23

Genomics Approaches to Dissect the Genetic Basis of Drought Resistance in Durum Wheat

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Abstract A better knowledge of the genetic basis of the mechanisms underlying the adaptive response to drought will be instrumental to more effectively deploy marker-assisted selection (MAS) to improve yield potential while optimizing water-use efficiency. Genomics approaches allow us to identify and clone the genes and QTLs that underlie the adaptive response of durum wheat to drought. Linkage and association mapping have allowed us to identify QTLs for traits that influence drought resistance and yield in durum and bread wheat. Once major genes and QTLs that affect yield under drought conditions are identified, their cloning provides a more direct path for mining and manipulating beneficial alleles. While QTL analysis and cloning addressing natural variation will increasingly shed light on mechanisms of adaptation to drought and other adverse conditions, more emphasis on approaches relying on resequencing, candidate gene identification, ‘omics’ platforms and reverse genetics will accelerate the pace of gene/QTL discovery. Genomic selection provides a valuable option to improve wheat performance under drought conditions without prior knowledge of the relevant QTLs. Modeling crop growth and yield based on the effects of major QTLs offers an additional opportunity to leverage genomics information. Although it is expected that genomics-assisted breeding will enhance the pace of durum wheat improvement, major limiting factors are how to (i) phenotype genetic materials in an accurate, relevant and high-throughput fashion and (ii) more effectively translate the deluge of molecular and phenotypic data into improved cultivars. A multidisciplinary effort will be instrumental to meet these challenges.

Keywords Consensus map • Drought • Genomics • Durum wheat • Marker-assisted selection • Modeling • Phenotyping • QTL • Roots • Yield

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Introduction

Among all abiotic stresses most affected by climate change, drought is the major one curtailing global wheat production. Although conventional breeding has steadily increased crop productivity under drought conditions and across a broad range of environmental constraints, the present rate of increase in wheat productivity is insufficient to meet food security globally. Genomics-assisted crop improvement provides novel opportunities to enhance the yearly rate of increase in wheat yield while advancing our understanding of the genetic and functional basis of the adaptive response to water-limited conditions (Habash et al. 2009; Fleury et al. 2010; Able and Atienza 2014; Tuberosa et al. 2014). This chapter illustrates how genomics approaches have been applied to genetically dissect durum wheat performance under water-scarce conditions and, more in general, how this information might help to mitigate the negative effects of drought on wheat productivity. In view of the genetic and functional similarity shared by durum and bread wheat, a number of relevant examples for the latter have also been considered.

Dissecting the Genetic Basis of Drought Resistance in Durum Wheat

The genetic basis of grain yield and the morpho-physiological traits that determine durum wheat performance under drought involves a myriad of quantitative trait loci (QTLs) of widely different effects, mostly too small to be detected experimentally. One of the reasons accounting for the modest impact of genomics-assisted breeding on the release of drought-tolerant cultivars is that screening conditions adopted under controlled conditions (e.g. growth chamber) usually provide a rather poor surrogate of the dynamics of the drought episodes that crops are exposed in the field (Passioura 2007; Tuberosa 2012). Additionally, the high context-dependency of QTL effects according to the genetic background and environment (Maphosa et al. 2014) further limits the effectiveness of marker-assisted selection (MAS) for improving field performance under drought conditions.

Until the introduction of association mapping, QTL identification has been pursued via linkage mapping based on the evaluation of biparental populations of recombinant inbred lines (RILs). Notably, the availability of maps obtained with different crosses and sharing common polymorphisms allows for the construction of a consensus map (Maccaferri et al. 2014) that in turn enables an even more accurate comparative analysis (e.g. meta-analysis) of QTL positions.

Association mapping (AM) based on sets of unrelated accessions provides additional opportunities to identify the loci (genes and/or QTLs) for target traits. In durum wheat, the evaluation of a panel of elite accessions characterized by high LD (>1 cM) has allowed for a genome-wide search using a limited number of markers (Maccaferri et al. 2005, 2011). Although AM has mostly targeted traits with a

genetic basis less complex than drought tolerance (e.g. resistance to biotic stress), some studies have targeted drought-adaptative traits and grain yield in durum wheat grown under varying water regimes (Sanguineti et al. 2007; Maccaferri et al. 2011; Canè et al. 2014; Graziani et al. 2014).

Notwithstanding the clear advantages of AM as compared to biparental linkage mapping, a major limitation of the former is the high rate of false positives (i.e. Type-I error rate) due to the presence of hidden population structure. Additionally, for highly integrative and functionally complex traits such as yield, particularly under drought conditions, the effectiveness of AM is reduced by the fact that different genotypes may show similar phenotypes due to trait compensation (e.g. yield components), which inevitably undermines the identification of significant marker-trait association. Although the number of studies is clearly too limited to draw more certain conclusions on the validity of AM in identifying QTLs for yield, the results reported by Maccaferri et al. (2008, 2011) in durum wheat suggest that the identification of yield QTLs under different water regimes should also be pursued via biparental mapping. This is particularly true whenever the investigated trait (e.g. yield under drought conditions) is strongly influenced by flowering time, in which case the overwhelming effects on yield of this phenological covariate will overshadow the effects due to the action of yield per se QTLs, hence reducing the possibility of identifying them.

QTLs for Drought-Adaptive Traits

On the discovery side, the past two decades have witnessed remarkable progress in several areas as shown also by the manuscripts in this special issue. The pivotal role of phenotyping in drought-related research is now universally recognized and receiving renewed attention (Tuberosa 2012; Araus and Cairns 2014). This revival in phenotyping has been sparked by the recent availability of new phenotyping technologies and highly automated platforms coupled with a better appreciation of the role of phenotyping in accelerating the response to selection for drought resistance, either through conventional or non-conventional approaches.

Dehydration avoidance and dehydration tolerance are the main mechanisms that contribute to maintain yielding ability under water-limited conditions (Blum 1988). Deep rooting and osmotic adjustment – classified under dehydration avoidance – enable the plant to maintain better hydration while other biochemical and physiological features (e.g. accumulation of molecular protectants, remobilization of stem water-soluble carbohydrates, etc.) classified under dehydration tolerance enable the plant to sustain metabolism even under severely dehydrated conditions. Notably, most genes induced under extreme dehydration have been shown to belong to metabolic pathways with doubtful functional significance under the water-limited field conditions encountered by wheat (Passioura 2007). Conversely, exploitation of naturally occurring variation for yield and/or drought-adaptive traits has allowed for

slow albeit unequivocal progress in wheat performance under drought conditions (Reynolds and Tuberosa 2008).

Given the quantitative nature of abiotic stress tolerance, QTLs have been the main target of studies attempting to identify the loci regulating the adaptive response of crops to environmentally constrained conditions. In very few cases, major QTLs affecting yield and other drought-adaptive traits across a broad range of soil moisture conditions have been identified (Quarrie et al. 2005; Maccaferri et al. 2008).

QTLs for Root Architecture and Size Among the traits that affect the water balance of the plant, roots play a key role in conditions of limited soil moisture (Richards 2008). Roots show a high level of morphological and developmental plasticity, a peculiarity that allows plants to adapt to moisture-limited conditions (de Dorlodot et al. 2007; Den Herder et al. 2010). An example is provided by root aerenchyma and root angle, root features that are receiving increasing attention for their effects on the response to drought and other abiotic stresses (Christopher et al. 2013). Other root features remain much more challenging to investigate, particularly under field conditions, such as in the case of root depth, a trait that has repeatedly shown a key role in crop adaptation to drought conditions when residual moisture at maturity is mainly available in deeper soil layers (Blum 2009, 2011; Watt et al. 2013). In bread wheat, soil coring down to 2 m depth revealed a broad range of genetic variation in deep root traits and showed that root features of high-performing genotypes were superior to those of low-performing genotypes or commercial varieties (Wasson et al. 2014). Since direct measuring of root depth remains an unresolved challenge, large-scale phenotyping for this trait can only be addressed through the use of proxies (e.g. canopy temperature depression) that through aerial remote sensing allow for monitoring the water status of a large number of genotypes in the field (Lopes and Reynolds 2010; Lopes et al. 2014).

In wheat, root metaxylem diameter is another feature that has shown an association with yield under drought conditions (Schoppach et al. 2014). Notably, selection for higher water-use efficiency (WUE) has shown merits in Australian environments where the crop prevalently grows on moisture stored in the soil prior to planting. Under these conditions, a wheat plant using water conservatively is able to complete grain filling with greater amount of water available in the soil. The adoption of this conservative strategy led to the release of two cultivars ('Drysdale' and 'Rees'; Condon et al. 2004) characterized by yield increases of up to 23 % when compared with control cultivars. The final effects of root architecture and size on yield will depend on the distribution of soil moisture and the level of competition for water resources within the plant community.

A most challenging aspect is to define the most desirable root ideotype able to optimize yield according to the prevailing dynamics of soil moisture profile but also accounting for the concurrent presence of gradients in the soil profile for other abiotic factors (e.g. salinity, toxic elements, high pH, etc.) that may impair plant growth. Therefore, each root ideotype should be established based upon the prevailing soil features in the target environment, a good understanding of the root architectural features that limit water uptake, and the metabolic cost required to develop

and functionally sustain the root system. Along this line, loci that affect root growth under particular abiotic (e.g. boron toxicity) and biotic (e.g. nematode resistance) constraints are interesting targets for MAS aimed at improving drought resistance through a more vigorous root system of wheat grown in problematic soils.

QTLs for Carbohydrate Accumulation and Relocation In wheat, the accumulation of carbohydrates and their relocation to the ear are key factors for optimizing yield under adverse environmental conditions (Blum 1998; Reynolds et al. 2009). In bread wheat, QTLs for stem reserve, water-soluble carbohydrates (WSC) remobilization and leaf senescence have been reported across well-watered and water-stressed conditions (Snape et al. 2007; Rebetzke et al. 2008; Bennett et al. 2012; Zhang et al. 2015). Although these studies showed an important role for WSC in assuring stable yield and grain size, Rebetzke et al. (2008) concluded that the small effects of many independent WSC QTLs may limit their direct use for MAS. A combined QTL analysis for yield of several wheat populations evaluated across different environments and seasons enabled Snape et al. (2007) to identify QTLs showing stable and differential expression across irrigated and non-irrigated conditions. Variation for stem water-soluble carbohydrate reserves was associated with the chr. 1RS arm of the 1BL/1RS translocated (from rye to wheat) chromosome, and was positively associated with yield under both irrigated and rainfed conditions, thus contributing to general adaptability (Snape et al. 2007). The beneficial role of this translocation on wheat performance under drought-stressed conditions has already been reported (Ehdaie et al. 2003).

QTLs for Other Traits of Interest for the Control of Water Balance Measurement of traits such as stomatal conductance, canopy temperature and leaf rolling provides indications of water extraction patterns and the water status of the plant. Therefore, measuring these traits together with soil moisture may help in selecting deep-rooted germplasm in environments where water is available at depth (Blum 1988; Reynolds et al. 2009). Stomatal conductance integrates important environmental and metabolic cues and allows the plant to modulate and optimize its transpiration and WUE (Brennan et al. 2007). A study conducted on a series of successful bread wheat cultivars released from 1962 to 1988 showed a strong and positive correlation between stomatal conductance and grain yield ($r=0.94$; Fischer et al. 1998), suggesting that the more modern cultivars extract more water from the soil. These results indicate the possibility of raising the yield potential using stomatal conductance as proxie and suggest the value of identifying the relevant QTLs. Canopy temperature is an integrative trait that reports on the water balance at the leaf and whole-plant level, thus providing a proxie of the capacity of the plant to extract soil moisture (Blum 1988, 2009; Reynolds and Tuberosa 2008). Canopy temperature depression (CTD) is mainly useful in hot and dry environments, with measurements preferably made on recently irrigated crops in cloudless and windless days at high vapour pressure deficits (Blum 1988; Reynolds et al. 2009). Under these circumstances, CTD can be a good predictor of grain yield in bread wheat (r varying from 0.6 to 0.8; Reynolds et al. 2009), where yield progress has been associated with cooler

canopies, hence higher transpiration (Fischer et al. 1998). Genetic gains in yield have also been reported in response to direct selection for CTD (Reynolds et al. 2009).

QTLs for Yield Under Different Water Regimes As global climate change intensifies, the identification of loci with consistent per se effects on yield (i.e. not loci for flowering time) across a broad range of soil moisture regimes becomes increasingly important to raise yield potential (Maccaferri et al. 2008; Pinto et al. 2010; Reynolds et al. 2011; Turner et al. 2014). Major QTLs for grain yield and its components across a broad range of soil moisture regimes have all been reported in bread wheat (Quarrie et al. 2005; Kirigwi et al. 2007; Snape et al. 2007) with only one notable exception in durum wheat where Maccaferri et al. (2008) searched for QTLs for grain yield in RILs evaluated in 16 environments with a broad range in grain yield values (from 0.56 to 5.88 t ha⁻¹), mainly consequent to different soil moisture availability. Two major QTLs on chr. 2BL and 3BS (*QYld.idw-2B* and *QYld.idw-3B*, respectively) showed highly significant and consistent effects in eight and seven environments, respectively. In both cases, an extensive overlap was observed between the LOD profiles for grain yield and plant height, but not with those for heading date, thus indicating that the effects of these two QTLs on yield were not due to escape from drought, a well-known factor in determining yield under terminal drought stress conditions that typically characterize Mediterranean environments (Araus et al. 2008). Accordingly, this population was originally chosen because it had shown limited variability in flowering time. For plant height and grain yield, a strong epistasis between *QYld.idw-2B* and *QYld.idw-3B* was detected across several environments, with the parental combinations providing the higher performance. These two QTLs evidenced significant additive and epistatic effects also on ear peduncle length and kernel weight (Graziani et al. 2014). As a prerequisite to positional cloning, progeny derived from the cross of isogenic lines have been evaluated for fine mapping of both QTLs (Maccaferri et al. unpublished).

Improving Drought Resistance via Marker-Assisted Selection

Several factors limit the possibility of obtaining reliable QTL data and, most importantly, their deployment in breeding programs through MAS (Tuberosa et al. 2007). Among such factors, the environment dependence of QTL expression is of utmost importance in order to obtain reproducible data and effectively assess the value of a particular QTL. This aspect is particularly relevant for stress tolerance traits since the effect of the same QTL can markedly differ according to the prevailing environmental conditions (Collins et al. 2008). Although many studies have described QTLs that influence tolerance to drought, MAS has so far contributed marginally to the release of drought-resistant cultivars. Improving crop performance under water-limiting conditions via MAS may also require considering QTLs for tolerance to abiotic (e.g. high boron) and biotic (e.g. nematodes) factors that impair root growth and functions. A common feature of cereal responses to drought near flowering and

during early stages of seed growth is a reduction of reproductive fertility due to partial sterility and/or early abortion. This loss of fertility has been attributed to different factors acting alone and more likely on reproductive fertility. The QTL approach attempts to dissect out the genetic and physiological components affecting source-sink relationships under abiotic stress and to what extent these may influence yield (Miralles and Slafer 2007). Major QTLs for seed weight and grain yield at different moisture conditions have been identified in durum wheat (Maccaferri et al. 2008) and are being introgressed in different genetic backgrounds. In bread wheat, Fleury et al. (2010) have implemented a strategy where a specific environment is targeted and appropriate germplasm adapted to the chosen environment is selected, based on extensive definition of the morpho-physiological and molecular mechanisms of tolerance of the parents. This information was then used to create structured populations and develop models for QTL analysis, MAS and positional cloning.

Future Perspectives

Increasing attention has been devoted to the use of crop modeling for elucidating the genetic basis of genotype \times management \times environment ($G \times M \times E$) interaction at the level of the entire genotype and, more recently, at the level of single loci (Ludwig and Asseng 2010; Richards et al. 2010; Tardieu and Tuberosa 2010; van Eeuwijk et al. 2010; Parent and Tardieu 2014). The objective is to predict, via modeling, yield differences among genotypes grown under different environmental conditions (Cooper et al. 2009; Tardieu and Tuberosa 2010). The benefits accrued by modeling studies are expected to increase as the complexity of the genetic control of traits increases provided it is possible to account for the effects of genetic interactions for predicting trait variation (Cooper et al. 2009). Ultimately, modeling aims to predict the best combinations of QTL alleles able to optimize yield. The main underlying assumption of the modelling approach is that yield and other functionally complex traits can be analyzed and improved by dissecting it into simpler processes, and then by re-assembling such processes to reconstruct via modelling higher order of plant functionality and ultimately yield itself. Models have been used to generate an index of the climatic environment (e.g. of drought stress) for breeding program trials. In wheat grown in northern Australia, this has shown that mid-season drought generates large genotype by environment interaction (Chapman 2008).

With only a few exceptions as listed above, the vast majority of loci that affect crop yield per se have a rather small effect, particularly under drought conditions. Therefore combining the favorable alleles by MAS to achieve a significant improvement quickly becomes impractical and would excessively constrain the potential for achieving yield gain due to the action of other loci. In this case, MAS for mapped QTLs (Randhawa et al. 2013) can be replaced by genome-wide selection (Bernardo 2010; Storlie and Charmet 2013). Nowadays, genome selection is facilitated by the

availability of large numbers of markers, particularly Single Nucleotide Polymorphisms (SNPs; Wang et al. 2014) that are amenable to high-throughput profiling at very low cost.

Conclusions

The release of cultivars better adapted to a broader range of environmental conditions will become an increasingly important goal of breeding projects worldwide. Compared to conventional breeding practices, the contribution in this direction of molecular breeding has somehow fallen short of expectations (Blum 2014; Tuberosa et al. 2014). Nonetheless, genomics approaches and sequence-based breeding will expedite the dissection of the genetic basis of abiotic stress tolerance while providing unprecedented opportunities to tap into wild relatives of wheat. To what extent this will actually impact the release of improved cultivars will largely depend on a more complete and comprehensive understanding of the adaptive response of crops to abiotic stress and our capacity to integrate this information into breeding programs via modeling or other approaches such as genomic selection. In view of the complexity of yield, particularly under drought, we foresee that genomic selection will provide the most effective way to raise the yield potential to the levels required to keep up with the fast-increasing demand in food worldwide. However, MAS will remain a valid option for major loci (genes and/or QTLs) as long as their effects will be sufficiently predictable and economically viable (Tuberosa and Pozniak 2014). Additionally, QTL cloning will become a more routine activity thanks to a more widespread utilization of high-throughput, accurate phenotyping (Tuberosa 2012), sequencing and the identification of suitable candidate genes via ‘omics’ profiling. Ultimately, reducing wheat vulnerability to drought will require a multidisciplinary and integrated approach that will eventually allow breeders to more effectively select drought-resistant cultivars.

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References

- Able J, Atienza S (2014) Durum wheat for the future: challenges, research and prospects in the 21st century. *Crop Pasture Sci* 65:124
- Araus JL, Cairns JE (2014) Field high-throughput phenotyping: the new crop breeding frontier. *Trends Plant Sci* 19:52–61
- Araus JL, Slafer GA, Royo C et al (2008) Breeding for yield potential and stress adaptation in cereals. *Critical Rev Plant Sci* 27:377–412

- Bennett D, Reynolds M, Mullan D et al (2012) Detection of two major grain yield QTL in bread wheat (*Triticum aestivum* L.) under heat, drought and high yield potential environments. *Theor Appl Genet* 125:1473–1485
- Bernardo R (2010) Genomewide selection with minimal crossing in self-pollinated crops. *Crop Sci* 50:624–627
- Blum A (1988) Plant breeding for stress environments. CRC Press, Boca Raton
- Blum A (1998) Improving wheat grain filling under stress by stem reserve mobilisation. *Euphytica* 100:77–83
- Blum A (2009) Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. *Field Crop Res* 112:119–123
- Blum A (2011) Drought resistance – is it really a complex trait? *Funct Plant Biol* 38:753–757
- Blum A (2014) Genomics for drought resistance – getting down to earth. *Funct Plant Biol* 41:1191–1198
- Brennan JP, Condon AG, van Ginkel M et al (2007) An economic assessment of the use of physiological selection for stomatal aperture-related traits in the CIMMYT wheat breeding programme. *J Agric Sci* 145:187–194
- Canè MA, Maccaferri M, Nazemi G et al (2014) Association mapping for root architectural traits in durum wheat seedlings as related to agronomic performance. *Mol Breed* 34:1629–1645
- Chapman SC (2008) Use of crop models to understand genotype by environment interactions for drought in real-world and simulated plant breeding trials. *Euphytica* 161:195–208
- Christopher J, Christopher M, Jennings R et al (2013) QTL for root angle and number in a population developed from bread wheats (*Triticum aestivum*) with contrasting adaptation to water-limited environments. *Theor Appl Genet* 126:1563–1574
- Collins NC, Tardieu F, Tuberosa R (2008) Quantitative trait loci and crop performance under abiotic stress: where do we stand? *Plant Physiol* 147:469–486
- Condon AG, Richards RA, Rebetzke GJ et al (2004) Breeding for high water-use efficiency. *J Exp Bot* 55:2447–2460
- Cooper M, van Eeuwijk FA, Hammer GL et al (2009) Modeling QTL for complex traits: detection and context for plant breeding. *Curr Opin Plant Biol* 12:231–240
- de Dorlodot S, Forster B, Pages L et al (2007) Root system architecture: opportunities and constraints for genetic improvement of crops. *Trends Plant Sci* 12:474–481
- Den Herder G, Van Isterdael G, Beeckman T et al (2010) The roots of a new green revolution. *Trends Plant Sci* 15:600–607
- Ehdaie B, Whitkus RW, Waines JG (2003) Root biomass, water-use efficiency, and performance of wheat-rye translocations of chromosomes 1 and 2 in spring bread wheat ‘Pavon’. *Crop Sci* 43:710–717
- Fischer RA, Rees D, Sayre KD et al (1998) Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Sci* 38:1467–1475
- Fleury D, Jefferies S, Kuchel H et al (2010) Genetic and genomic tools to improve drought tolerance in wheat. *J Exp Bot* 61:3211–3222
- Graziani M, Maccaferri M, Royo C et al (2014) QTL dissection of yield components and morphophysiological traits in a durum wheat elite population tested in contrasting thermo-pluviometric conditions. *Crop Pasture Sci* 65:80–95
- Habash DZ, Kehel Z, Nachit M (2009) Genomic approaches for designing durum wheat ready for climate change with a focus on drought. *J Exp Bot* 60:2805–2815
- Kirigwi FM, Van Ginkel M, Nrown-Guedira G et al (2007) Markers associated with a QTL for grain yield in wheat under drought. *Mol Breed* 20:401–413
- Lopes MS, Reynolds MP (2010) Partitioning of assimilates to deeper roots is associated with cooler canopies and increased yield under drought in wheat. *Funct Plant Biol* 37:147–156
- Lopes MS, Rebetzke GJ, Reynolds M (2014) Integration of phenotyping and genetic platforms for a better understanding of wheat performance under drought. *J Exp Bot* 65:6167–6177
- Ludwig F, Asseng S (2010) Potential benefits of early vigor and changes in phenology in wheat to adapt to warmer and drier climates. *Agric Syst* 103:127–136

- Maccaferri M, Sanguineti MC, Noli E et al (2005) Population structure and long-range linkage disequilibrium in a durum wheat elite collection. *Mol Breed* 15:271–289
- Maccaferri M, Sanguineti MC, Corneti S et al (2008) Quantitative trait loci for grain yield and adaptation of durum wheat (*Triticum durum* desf.) across a wide range of water availability. *Genetics* 178:489–511
- Maccaferri M, Sanguineti MC, Demontis A et al (2011) Association mapping in durum wheat grown across a broad range of water regimes. *J Exp Bot* 62:409–438
- Maccaferri M, Ricci A, Salvi S et al (2014) A high-density SNP-based consensus map of tetraploid wheat as a bridge to integrate durum and bread wheat genomics and breeding. *Plant Biotechnol J*. doi:[10.1111/pbi.12288](https://doi.org/10.1111/pbi.12288)
- Maphosa L, Langridge P, Taylor H et al (2014) Genetic control of grain yield and grain physical characteristics in a bread wheat population grown under a range of environmental conditions. *Theor Appl Genet* 127:1607–1624
- Miralles DJ, Slafer GA (2007) Sink limitations to yield in wheat: how could it be reduced? *J Agric Sci* 145:139–149
- Parent B, Tardieu F (2014) Can current crop models be used in the phenotyping era for predicting the genetic variability of yield of plants subjected to drought or high temperature? *J Exp Bot* 65:6179–6189
- Passioura J (2007) The drought environment: physical, biological and agricultural perspectives. *J Exp Bot* 58:113–117
- Pinto RS, Reynolds MP, Mathew KL et al (2010) Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. *Theor Appl Genet* 121:1001–1021
- Quarrie SA, Steed A, Calestani C et al (2005) A high-density genetic map of hexaploid wheat (*Triticum aestivum* L.) from the cross Chinese spring × SQ1 and its use to compare QTLs for grain yield across a range of environments. *Theor Appl Genet* 110:865–880
- Randhawa HS, Asif M, Pozniak C et al (2013) Application of molecular markers to wheat breeding in Canada. *Plant Breed* 132:458–471
- Rebetzke GJ, van Herwaarden AF, Jenkins C et al (2008) Quantitative trait loci for water-soluble carbohydrates and associations with agronomic traits in wheat. *Aust J Agric Res* 59:891–905
- Reynolds M, Bonnett D, Chapman SC et al (2011) Raising yield potential of wheat. I. Overview of a consortium approach and breeding strategies. *J Exp Bot* 62(2):439–452
- Reynolds M, Tuberosa R (2008) Translational research impacting on crop productivity in drought-prone environments. *Curr Opin Plant Biol* 11:171–179
- Reynolds M, Foulkes MJ, Slafer GA et al (2009) Raising yield potential in wheat. *J Exp Bot* 60:1899–1918
- Richards RA (2008) Genetic opportunities to improve cereal root systems for dryland agriculture. *Plant Prod Sci* 11:12–16
- Richards RA, Rebetzke GJ, Watt M et al (2010) Breeding for improved water productivity in temperate cereals: phenotyping, quantitative trait loci, markers and the selection environment. *Funct Plant Biol* 37:85–97
- Sanguineti MC, Li S, Maccaferri M et al (2007) Genetic dissection of seminal root architecture in elite durum wheat germplasm. *Ann Appl Biol* 151:291–305
- Schoppach R, Wauthelet D, Jeanguenin L et al (2014) Conservative water use under high evaporative demand associated with smaller root metaxylem and limited trans-membrane water transport in wheat. *Funct Plant Biol* 41:257–269
- Snape JW, Foulkes MJ, Simmonds J et al (2007) Dissecting gene × environmental effects on wheat yields via QTL and physiological analysis. *Euphytica* 154:401–408
- Storlie E, Charmet G (2013) Genomic selection accuracy using historical data generated in a wheat breeding program. *Plant Genome*. doi:[10.3835/plantgenome2013.01.0001](https://doi.org/10.3835/plantgenome2013.01.0001)
- Tardieu F, Tuberosa R (2010) Dissection and modelling of abiotic stress tolerance in plants. *Curr Opin Plant Biol* 13:206–212

- Tuberosa R (2012) Phenotyping for drought tolerance of crops in the genomics era. *Front Physiol* 3:347
- Tuberosa R, Pozniak C (2014) Durum wheat genomics comes of age. *Mol Breed* 34:1527–1530
- Tuberosa R, Giuliani S, Parry MAJ et al (2007) Improving water use efficiency in Mediterranean agriculture: what limits the adoption of new technologies? *Ann Appl Biol* 150:157–162
- Tuberosa R, Turner N, Cakir M (2014) Two decades of InterDrought conferences: are we bridging the genotype-to-phenotype gap? *J Exp Bot* 65:6137–6139
- Turner NC, Blum A, Cakir M et al (2014) Strategies to increase yield and yield stability of crops under drought – are we making progress? *Funct Plant Biol* 41:1199–1206
- van Eeuwijk FA, Bink MCAM, Chenu K et al (2010) Detection and use of QTL for complex traits in multiple environments. *Curr Opi Plant Biol* 13:193–205
- Wasson AP, Rebetzke GJ, Kirkegaard JA et al (2014) Soil coring at multiple field environments can directly quantify variation in deep root traits to select wheat genotypes for breeding. *J Exp Bot*. doi:[10.1093/jxb/eru250](https://doi.org/10.1093/jxb/eru250)
- Wang S, Wong D, Forrest K et al (2014) Characterization of polyploid wheat genomic diversity using a high-density 90,000 SNP array. *Plant Biotechnol J* 12:787–796
- Watt M, Moosavi S, Cunningham SC et al (2013) A rapid, controlled-environment seedling root screen for wheat correlates well with rooting depths at vegetative, but not reproductive, stages at two field sites. *Ann Bot* 112:447–455. doi:[10.1093/aob/mct122](https://doi.org/10.1093/aob/mct122)
- Zhang J, Xu Y, Chen W et al (2015) A wheat *1-FEH w3* variant underlies enzyme activity for stem WSC remobilization to grain under drought. *New Phytol* 205:293–305