

## Genetic and molecular dissection of drought tolerance in wheat and barley

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### Abstract

Drought stress has become a major threat to international food security. Drought resistance is regulated by various small effect loci and polygenes that control morphological and physiological responses to drought. In this review, we summarize the status of mapping studies for the various traits associated with drought tolerance in wheat and barley. To meet the challenges of climate change, there is a need to explore natural diversity in the existing genetic resource pool of wheat and barley as these resources are yet untapped and provide potential sources to develop elite genotypes with improved adaptation to drought stress. Recent advancements in genome mapping and functional genomics technologies have provided powerful tools for molecular dissection of drought tolerance. Deciphering this complex mechanism in crops will accelerate the development of new cultivars with enhanced drought tolerance.

**Keywords:** Drought tolerance, *Triticum aestivum*, *Hordeum vulgare*, QTL mapping

### Introduction

Wheat is the most widely grown crop in the world over more than 220 million hectares of cropland producing 715 million tonnes of food grains with a productivity of 3.2 t/ha (FAO, 2015). The yield of wheat has doubled over the last 30 years due to a combination of advanced agronomic practices and improved germplasm through selective breeding (Lopes *et al.*, 2014). But the global demand for wheat is expected to rise by 60% by 2050, whereas climate change is anticipated to negatively affect the production by 29% in the same vicinities (Dixon *et al.*, 2009). It is estimated that 65 million ha of wheat production area is affected by drought (FAO, 2013). Similarly, barley (*Hordeum vulgare* ssp. *vulgare* L.) is one of the major cereal grains, currently ranking fourth in world production behind maize, rice and wheat. In India, barley is generally cultivated in harsh environments like drought, cold, salinity/alkalinity and marginal lands. It is cultivated on about 0.695 mha area with production of 1.74 mt tonnes and productivity of 2508 kg/ha (Kumar *et al.*, 2014). Barley is rather well-tolerant to drought, salinity and other dehydrative stresses.

An alarming situation in the water-stressed areas is expected to occur worldwide by 2030, which would influence 50 countries collectively harbouring almost three billion people (Graham and Vance, 2003). Drought stress can occur at any growth stage and can affect this productivity to variable degrees depending on the onset time, duration, and intensity of drought effect. Drought is a complex and polygenic trait with strong interactions between loci and genotype  $\times$  environment interactions. Plants use multiple strategies to respond to drought stress and have evolved to adapt to drought via morphological, biochemical and physiological changes through diverse signaling cascades. Hundreds of genes in these pathways controlling the key plant's processes in response to drought stress have been identified by genetic, genomic (at the transcriptomic, proteomic, metabolomic, and epigenetic levels), and transgenic approaches. Barley is characterized by relatively simple genome structure and complete barley genome annotation has been published (The International Barley Genome Sequencing Consortium 2012). Similarly genome sequence drafts of bread wheat and its progenitors have been acquired via shotgun and chromosome-based approaches, and this represents a milestone for wheat

improvement. Currently the survey sequences of all chromosomes, the physical maps of 16 chromosomes, and the reference sequence of 3B have been achieved in bread wheat (Wang *et al.* 2015). Based on these achievements and advances in NGS, high-resolution transcriptome and genotype maps are now available which will increase chances of identification of candidate genes involved in drought tolerance.

Nevertheless, due to climate changes some areas have been predicted to be more subjected to frequent drought. Therefore, efforts to improve drought tolerance in genotypes need to be continued and strengthened. In this direction, molecular approaches offer novel opportunities for the dissection and more targeted manipulation of the genetic and functional basis of drought tolerance in crops like wheat and barley in the changing climatic scenario. Many reviews on drought tolerance have focused on particular molecules, signaling pathways, or crop engineering in plants (Shinozaki *et al.* 2007; Nezhadahmadi *et al.* 2013; Budak *et al.* 2015). In this review we emphasize on the progress of recent mapping studies aimed at detection of quantitative trait loci (QTLs) for the various traits associated with drought tolerance in wheat and barley.

### Genetic control of morphological traits

Morphological traits such as leaf rolling, leaf expansion, leaf waxiness, cuticle tolerance, stomatal density and stomatal aperture are frequently used as criteria for drought avoidance (Hu and Xiong, 2014). Stomatal density and stomatal aperture are two of the main factors that determine stomatal conductance and thus photosynthetic ability. Leaf rolling and leaf senescence are traits that are relatively easy to score. In durum wheat, the QTLs for osmotic adjustment and leaf rolling were detected on chromosome 2B, 4A, 5A, and 7B (Peleg *et al.*, 2009). Leaf waxiness or glaucousness has been reported to protect plants against high radiation, reducing canopy temperatures, increasing water use efficiency, and improving yield in barley and wheat in certain environments (Gonzalez and Ayerbe 2010). Mason *et al.* (2010) identified a single QTL for flag leaf glaucousness on chromosome 5A, with the additive allele coming from a heat tolerant parent. A novel QTL for flag leaf glaucousness of large, repeatable effect was detected in six field experiments, on chromosome 3A (*QW.aww-3A*) and accounted for up to 52 percent of genetic variance for this trait in a double haploid (DH) population from cross Kukri and RAC875 (Bennett *et al.*, 2012). Similarly, genetic patterns of the morphological and physiological traits in flag leaf of barley were studied in a DH population (Xwetel, 2008; Liu *et al.*, 2015).

Optimum plant height is required for better yield in wheat, as tall plants are susceptible to lodging and excessively

short plants are often associated with a yield penalty in resource limited areas (Griffiths *et al.*, 2012). Rht genes (*Rht4*, *Rht5*, *Rht8*, *Rht9*, *Rht12* and *Rht13*) that do not confer GA insensitivity, more suitable in reducing final plant height without compromising early plant growth. The GA-sensitive *Rht8* gene on chromosome 2DS is a potential candidate in the development of semi-dwarfing wheat varieties with long-coleoptiles (Rebetzke *et al.*, 2012; Griffiths *et al.*, 2012) (Table 1). Rebetzke *et al.* (2011) identified the *Rht 13* dwarfing gene which reduced peduncle length and plant height to increase the grain number and yield of wheat. Under drought, 154 accessions were studied for plant height dynamic development and observed a total of 46 significant association signals ( $P < 0.01$ ) in 23 markers, with phenotypic variation ranged from 7 to 50% (Zhang *et al.*, 2011). In recent study, the dwarfness and compactness of dwarf mutant of Sumai 3 was controlled by a single dominant gene designated as *Rht23* mapped 4.7 cM distal to SSR marker *Gdm63* and 11.1 cM proximal to *Barc110* on chromosome 5DL (Chen *et al.*, 2015).

A key trait in developing new barley varieties with improved agronomics, including yield, is plant height. In barley, numerous mutants carrying semi-dwarfing genes are known. These semi-dwarfing genes, including semi-brachytic 1 (*uzu1*), semi-dwarf 1 (*sdw1* or *denso*), *breviaristatum-e* (*ari-e*), and short culm 1 (*hcm1*), are mainly used in barley improvement (Wang *et al.*, 2014). The *uzu1*, *sdw1* and *denso* genes are located on chromosome 3H and are very close to each other (Wang *et al.*, 2010) with the *sdw1* gene being allelic to *denso*. Many QTL conferring plant height have been reported and are detected in all 7 chromosomes (von Korff *et al.*, 2006; Pillen *et al.*, 2003) (Table. 2). Major plant height QTL was located on 2H (Pillen *et al.* 2004; von Korff *et al.* 2006), 3H, 4H and 5H (Talamé *et al.* 2004; von Korff *et al.* 2006). Dahleen *et al.* (2012) identified QTL affecting plant height on chromosome 1H at 131 cM, 2H at 65, 81 and 156 cM, 3H at 51 and 120 cM, 4H at 188 cM and 6H at 100 cM. Recently a QTL for plant height has been identified on chromosome 7H reported to be responsible to a semi-dwarfing gene (Yu *et al.*, 2010) and this QTL showed no significant effects on other agronomic traits and yield components and consistently expressed in the six environments (Wang *et al.*, 2014).

### Genetic control of physiological traits related to drought tolerance

3.1 *Canopy temperature*: Canopy temperature (CT) reflects the interactions among plants, soil, atmosphere and has been commonly used in evaluating drought tolerance. Under drought stimulated conditions, wheat with low CT could maintain superiority to wheat with high CT (Reynolds *et al.*, 2009). The genetic studies on canopy temperature also need much attention as till now very few

studies have been carried out. Pinto *et al.* (2010) reported a QTL on the 3B explained 14% of CT variation in Seri/Babax RIL population under drought. Two QTLs related to CT and grain yield traits with 22% variance, have been identified on chromosome 3B of RAC875/Kukri DH population (Bennett *et al.*, 2012). Leaf chlorophyll content can also be used as an indicator of a crop's potential photosynthetic capacity. Kumar *et al.* (2012) identified a QTL for Chl (*QChl.ksu-3B*) and *Fv/Fm* (*QFv/Fm.ksu-3B*) controlling chlorophyll content and quantum efficiency of PS II under stress, on chromosome 3B, in the marker interval *Xbarc68-Xbarc101* and explained 35–40% of the phenotypic variation for each trait.

**3.2 Leaf senescence and stay green:** Leaf senescence is a result of catabolism of chlorophyll, proteins, lipids and nutrient remobilization into developing grains (Vijayalakshimi *et al.*, 2010). The timing of flag leaf senescence (FLS) represents an important determinant of yield under terminal drought conditions due to an increase in cumulative photosynthesis. The winter wheat flag leaf senescence QTL were detected on long arms of chromosomes 2D and 2B under drought stress and irrigated condition, respectively (Verma *et al.*, 2004). FLS revealed a positive correlation with yield and transpiration efficiency under water limited conditions in wheat. Barakat *et al.*, (2013) also identified SSR marker *Xgwm382* for FLS with 73% of phenotypic variation in wheat. Stay-green' in the post-anthesis period is an efficient drought-tolerance trait in crops and can be studied at the physiological level. The genetic basis of the stay green trait has been studied in wheat (Kumar *et al.*, 2010; Joshi *et al.*, 2007). Green leaf duration after heading (GLDAH) has been reported to provide drought and heat tolerance in several crops. Naruoka *et al.*, (2012) identified QTL *QGfd.mst-4A* had an effect on GLDAH under stress conditions in the Conan/Reeder population and a RIL population derived from McNeal/Reeder in wheat. In barley, two QTLs for leaf wilting under drought stress were identified from DH population from a cross between

TX9425 (a Chinese landrace variety with superior drought and salinity tolerance) and a sensitive variety, Franklin. One QTL located on 2H determined 42% of phenotypic variation and was closely linked with a gene controlling ear emergence. Another QTL on 5H was less affected by agronomic traits and a candidate gene for this QTL was identified based on the draft barley genome sequence (Fan *et al.*, 2015).

**3.3 Relative water content:** Relative water content (RWC) measures the percent of water in a leaf relative to full turgor and thus represents the water stress being experienced by the plant. Studies reporting molecular markers associated with plant water status-related traits in cereals are scarce. However, few QTLs for RWC were reported in barley. Teulat *et al.* (2001) mapped six QTL for RWC to chromosomes 2H (1 QTL), 6H (1 QTL), and 7H (4 QTL) in 167 RILs of barley derived from a cross between Tadmor and Er/Apmof. Three of these were detected under well watered conditions and three were detected under stress. In Barley, Diab *et al.* (2004) reported a QTL that affects RWC in vicinity of this gene on chromosome 3H. Therefore, higher expression level of *Hsdr4* under dehydration stress in tolerant rather than sensitive genotypes and its co-localization with drought tolerance QTLs suggests that *Hsdr4* could be a viable candidate gene for drought tolerance.

**3.4 Carbon Isotope discrimination (CID):** Under drought stress, carbon isotope discrimination ( $\Delta^{13}C$ ) is considered to be good predictor of water use efficiency (WUE) and stomatal conductance (Condon *et al.*, 2004) in plants. Commonly, but not always (Turner *et al.*, 2007),  $\Delta^{13}C$  is negatively associated with WUE over period of dry mass accumulation (Condon *et al.*, 2004; Xu *et al.*, 2007). Rizza *et al.* (2012) found a strong relation of CID with WUE in wheat grains harvested in field. Despite the available evidence that CID is heritable trait and is under genetic control, only a few studies have been carried out to dissect the genetic control of this important trait

Table 1. List of QTLs for various traits associated with drought tolerance in wheat

| Trait                   | Chromosome                                 | References                             |
|-------------------------|--|--|
| Coleoptile length       | 4BS, 4DS                                   | Rebetzke <i>et al.</i> (2007)          |
|                         | 3AS, 6AS                                   | Spielmeyer <i>et al.</i> (2007)        |
|                         | 4DS, 5AL                                   | Wang <i>et al.</i> (2009)              |
|                         | 1B, 4DS, 4DL, 5AS, 5B                      | Yu <i>et al.</i> (2010)                |
|                         | 1AS, 2B, 4A, 5A,6B                         | Rebetzke <i>et al.</i> (2014)          |
| CT                      | 1A, 2A, 2B, 3A, 3B, 4B, 5A, 5B, 6A, 6B, 6D | Diab <i>et al.</i> (2008)              |
|                         | 1B, 2B, 3B, 4A, 5A                         | Olivares-Villegas <i>et al.</i> (2008) |
| Flag leaf rolling index | 1A, 2A, 2B, 4B, 5A, 5B, 6A, 6B, 7A, 7B     | Peleg <i>et al.</i> (2009)             |

|   |  |                                       |
|---|--|---------------------------------------|
| FLS                                     | 2B   | Verma <i>et al.</i> (2004)            |
|   | 2D   | Barakat <i>et al.</i> (2013)          |
| NDVI                                    | 1B,2A, 2B, 3B, 4A, 7A  | Olivares-Villegas <i>etal.</i> (2008) |
|   | 1B, 2B, 3B, 4A, 7A   | Pinto <i>et al.</i> (2010)            |
| ABA                                     | 5A   | Quarrie <i>et al.</i> (1994)          |
|   | 3B, 4A, 5A   | Barakat <i>et al.</i> (2015)          |
| CHL                                     | 1A, 1B, 2A, 2B, 3A, 3B, 4B, 5A, 5B, 6A, 6B, 6D, 7A, 7B         | Diab <i>et al.</i> (2008)             |
|   | 1D, 4B   | Olivares-Villegas <i>etal.</i> (2008) |
|   | 1A, 1B, 2B, 4A, 5A, 5B, 6A, 7A                                 | Peleg <i>et al.</i> (2009)            |
| CID                                     | 2A, 2B, 3A, 3B, 4B, 5A, 5B, 6A, 6B, 6D, 7A, 7B                 | Diab <i>et al.</i> (2008)             |
|   | 1B, 2B, 3B, 4A, 4B, 5A, 6D, 7A, 7B                             | Rebetzke <i>et al.</i> (2008a)        |
|   | 1A, 2B, 3B, 5A, 7A and 7B                                      | Wu <i>et al.</i> (2011)               |
| WSC                                     | 1A, 1B, 1D, 2A, 2B, 2D, 3A, 3B, 4B, 4D, 5A, 5B, 6B, 6D, 7A, 7D | Rebetzke <i>et al.</i> (2008b)        |
|   | 1A, 1D, 2A, 2D, 3B, 4A, 6B, 7B, 7D                             | Yang <i>et al.</i> (2007)             |
| Plant height                            | 2D, 4B, 4D, 5B, 7A, 7B   | McCartney <i>et al.</i> (2005)        |
|   | 3A   | Dilbirligi <i>et al.</i> (2006)       |
|   | 2B, 2D, 3B, 4B, 6A   | Marza <i>et al.</i> (2006)            |
|   | 1B, 4B, 4D   | Rebetzke <i>et al.</i> (2008a)        |
|   | 1B, 2A, 2D, 4D,5B  | Wang <i>et al.</i> (2010)             |
|   | 4D,6A  | Li <i>et al.</i> (2015)               |
| Phenology (anthesis, heading, maturity) | 3B, 4A, 4D   | McCartney <i>et al.</i> (2005)        |
|   | 1B, 3A, 3B, 5B, 6B, 6D   | Marza <i>et al.</i> (2006)            |
|   | 2D, 4A, 7A   | Rebetzke <i>et al.</i> (2008a)        |
| Grain number (GM <sup>2</sup> )         | 1D, 2B   | Mathews <i>et al.</i> (2008)          |
|   | 3A   | Dilbirligi <i>et al.</i> (2006)       |
|   | 1A, 1B, 2B,2D, 3B, 4B,6A                                       | Marza <i>et al.</i> (2006)            |
|   | 4A, 4B   | Kirigwi <i>et al.</i> (2007)          |
|   | 1B, 4A, 5A   | Olivares-Villegas <i>etal.</i> (2008) |
| Grain wt. (TGW)                         | 2A, 4A, 4B, 4D, 6D   | McCartney <i>et al.</i> (2005)        |
|   | 3A   | Dilbirligi <i>et al.</i> ( 2006)      |
|   | 1B, 2B, 2D, 3B, 5A, 6B   | Marza <i>et al.</i> (2006),           |
|   | 2A, 4A, 5B, 6A, 7A   | Yang <i>et al.</i> (2007)             |
|   | 4A   | Kirigwi <i>et al.</i> (2007)          |
|   | 3B, 4A, 4B   | Pinto <i>et al.</i> (2010)            |
|   | 1A, 4A, 4B, 7A, 7D   | Nezhad <i>et al.</i> (2012)           |
|   | 1D, 2A, 6A   | Sun <i>et al.</i> (2008)              |
|   | 6B   | Quarrie <i>et al.</i> (2005)          |

|            |                                    |                                     |
|------------|------------------------------------|-------------------------------------|
| Grain size | 1A, 1B, 2A, 2B, 3B, 4A, 4B, 6A     | Sun <i>et al.</i> (2008)            |
| Yield      | 2A, 2B, 4D                         | McCartney <i>et al.</i> (2005)      |
|            | 1D, 4A, 4B, 5A, 5B, 6D, 7A         | Quarrie <i>et al.</i> (2005)        |
|            | 3A                                 | Dilbirligi <i>et al.</i> (2006)     |
|            | 1A, 1B, 2B, 4A, 4B, 5A, 6A, 6B, 7A | Marza <i>et al.</i> (2006)          |
|            | 4A                                 | Kirigwi <i>et al.</i> (2007)        |
|            | 4D, 6A                             | Snape <i>et al.</i> (2007)          |
|            | 1D, 4B, 5A, 6B, 6D                 | Mathews <i>et al.</i> (2008),       |
|            | 2B, 4A, 4B, 5A, 7B                 | Peleg <i>et al.</i> (2009)          |
|            | 1B, 3B, 4A                         | Pinto <i>et al.</i> (2010)          |
|            | 2B, 2D, 3A, 3B, 4B, 5A,            | Czyczyło-Mysza <i>et al.</i> (2011) |
|            | 5D, 6B                             | Kadam <i>et al.</i> (2012)          |
|            | 4B                                 | Edae <i>et al.</i> (2014)           |
|            | 2D, 5B                             |                                     |

Table 2. List of QTLs for various traits associated with drought tolerance in barley

| Trait             | Chromosome              | References                       |
|-------------------|-------------------------|----------------------------------|
| Growth habit      | 1H, 2H, 4H and 5H       | Naz <i>et al.</i> (2014)         |
| Plant height      | 2H, 3H, and 7H          | Baum <i>et al.</i> (2003)        |
|                   | 2H                      | Pillen <i>et al.</i> (2004)      |
|                   | 2H, 3H, 4H, 5H          | von Korff <i>et al.</i> (2006)   |
| Days to heading   | All 7 chromosomes       | Baum <i>et al.</i> (2003)        |
|                   | 7H and 2H               | Mohammadi <i>et al.</i> (2005)   |
| Days to maturity  | 2H, 5H, 6H, 7H          | Mohammadi <i>et al.</i> (2005)   |
| RWC               | 1H 2H, 4H, 5H, 6H, 7H   | Teulat <i>et al.</i> (2001)      |
|                   | 5H, 7H                  | Diab (2004)                      |
|                   | 1H, 2H, 6H              | Chen <i>et al.</i> (2010)        |
|                   | 2H, 3H, 4H              | Arifuzzaman <i>et al.</i> (2014) |
| Osmotic potential | 7H, 6H.                 | Teulat <i>et al.</i> (2001)      |
|                   | 3H, 4H                  | Diab (2004)                      |
| Flaf leaf         | 2H                      | Liu <i>et al.</i> (2015)         |
| Root length       | 2H, 5H, 6H              | Chen <i>et al.</i> (2010)        |
|                   | 2H, 3H, 5H              | Sayed <i>et al.</i> (2011)       |
|                   | 1H, 4H, 5H              | Naz <i>et al.</i> (2014)         |
|                   | 2H, 3H, 5H              | Arifuzzaman <i>et al.</i> (2014) |
| Root dry weight   | 1H, 2H, 3H, 4H, 5H, 7H. | Arifuzzaman <i>et al.</i> (2014) |
| Root volume       | 1H, 2H, 5H, 6H, 7H      | Naz <i>et al.</i> (2014)         |
| Root shoot ratio  | 1H, 3H, 5H, 7H.         | Arifuzzaman <i>et al.</i> (2014) |
| Number of grain   | 2H, 4H, 7H              | Mohammadi and Baum (2008)        |
|                   | 2H, 4H                  | Meharavan <i>et al.</i> (2014)   |



|                         |                                   |                                   |
|-------------------------|-----------------------------------|-----------------------------------|
| Number of kernels/spike | 2H, 3H, 4H, 6H                    | Arifuzzaman <i>et al.</i> (2014)  |
|                         | 1H, 5H                            | Pillen <i>et al.</i> (2003; 2004) |
| Grain filling period    | 1H, 3H, 5H, 7H                    | Mohammadi <i>et al.</i> (2005)    |
| Grain yield             | AB-QTL.                           | Pillen <i>et al.</i> (2003)       |
|                         | All chromosomes except 3H and 5H. | Saal <i>et al.</i> (2011)         |
|                         | 2H, 3H                            | von Korff <i>et al.</i> (2006).   |
|                         | 2H                                | Meharavan <i>et al.</i> (2014)    |
|                         | 2H, 3H, 6H                        | Arifuzzaman <i>et al.</i> (2014)  |
| Harvest Index           | 4H, 5H, 7H                        | Pillen <i>et al.</i> (2003)       |
|                         | 2H, 3H, 5H.                       | Pillen <i>et al.</i> (2004)       |
|                         | All seven chromosomes,            | von korff <i>et al.</i> (2006)    |
|                         | 3H                                | Wang <i>et al.</i> (2010)         |

CT-canopy temperature, FLS- flag leaf senescence, CID-carbon isotope discrimination, NDVI-Normalized difference vegetation index, RWC-relative water content, Fv/Fm-Chlorophyll fluorescence, WSC-water soluble carbohydrates, ABA-Abscisic acid.

(Rebetzke *et al.*, 2008a; Peleg *et al.*, 2009, Wu *et al.*, 2011). In wheat-barley 4H (4D) disomic substitution lines, the genes located on the 4H chromosome of barley were able to increase the water use efficiency of the wheat substitution line, which is suitable for improving wheat drought tolerance through intergeneric crossing (Molnar *et al.*, 2007). There is a need to study this trait in more efficient manner to identify major and independent QTL for CID for marker-assisted indirect selection for improving WUE and grain yield under water-limited environments.

**3.6 Abscisic acid:** The role of abscisic acid (ABA) accumulation in stomatal regulation under drought has been demonstrated by many researchers (Giday *et al.*, 2014; Reddy *et al.*, 2014). ABA hormone concentration rises rapidly in plant tissues in response to drought and this in turn leads to expression of ABA dependent stress-related genes. Several studies have been conducted for screening plants for ABA concentration under drought conditions and QTL for it have mapped in wheat (Quarrie *et al.*, 1994) and is influenced by genotype and the target environment. Examination of a series of chromosome substitution lines of the high-ABA genotype 'Ciano 67' into the low-ABA recipient 'Chinese Spring' showed that chromosome 5A carries gene(s) that have a major influence on ABA accumulation in a drought (Quarrie *et al.*, 1994). Identification of QTL for ABA responsiveness at a seedling stage associated with an ABA-regulated gene expression in common wheat has been reported by Kobayashi *et al.* (2010). A molecular mapping of loci associated with ABA accumulation in triticale anthers in response to a low temperature stress has been reported by ur *et al.* (2012). Recently, Barakat *et al.* (2015) reported the significant groups of QTLs for ABA content in the regions

of chromosome 3B, 4A and 5A mostly near to *barc164*, *wmc96*, and *Tap9* markers in wheat.

**3.7 Remobilization of water-soluble carbohydrates (WSC):** Remobilization of WSC from the stem and leaves can mitigate the negative effects on grain filling caused by post-anthesis drought tolerance (Reynolds *et al.*, 2007; Rebetzke *et al.*, 2008b). QTLs for stem-reserve remobilization have been reported in bread wheat (Salem *et al.*, 2007; Snape *et al.*, 2007; Yang *et al.*, 2007). Rebetzke *et al.* (2008b) phenotyped three wheat mapping populations for WSC concentration (WSC-C) and for WSC mass per unit area (WSC-A). Polygenic control, predominance of additive component of genetic variance with moderate to high broad/narrow sense heritability for WSC has been reported in wheat (Snape *et al.* 2007). In Barley, the region on chromosome 2H between O7.1 and Bmag0125 contained overlapping QTLs for  $\Delta^{13}C$ , OA (Osmotic adjustment) and WSC indicating an important role of this region in genetic determination of carbohydrate metabolism (Teulat *et al.* 2002).

### Genetic control of root traits related to drought tolerance

Many researchers observed the relevance of various root traits such as greater root length density, root surface area and root dry matter in improving WUE (Bengough *et al.*, 2011; Comas *et al.*, 2013; Chapagain *et al.* 2014). Scientists are starting to see roots as central to their efforts to produce crops with a better yield (Narayanan *et al.*, 2014). Research is more focused to develop low-cost high-throughput phenotyping methods to facilitate selection for desirable root architectural traits in wheat (Richard *et al.*, 2015). In comparison to other cereals, little attention has been paid to genetic analysis of root traits in wheat under reproductive stage drought (Fleury *et al.*, 2010). Most of

the studies for identification of QTLs for root traits were carried out at seedling stage (Swamy *et al.*, 2011; Bai *et al.*, 2013; Christopher *et al.*, 2013; Cane *et al.*, 2014). Deeper roots, especially the seminal roots are considered important for wheat growth under drought (Sanguineti *et al.* 2007; Ren *et al.* 2011). The main drawback to the study of root features and their use as selection criteria relates to the difficulty of phenotyping field-grown plants (Richards, 2008). Recently, Uga *et al.*, (2013) cloned and characterized the QTL Deeper rooting 1 (*DRO 1*), which controls root growth angle in rice. *DRO1* is the first root QTL that has been cloned in crops, and this work further confirmed that RSA (root system architecture) can contribute significantly to drought tolerance. Wild barley diversity exhibits great variation in root system architecture that is helpful in adaptation to drought conditions (Naz *et al.*, 2012). QTL analysis under normal and water stress condition in introgression lines of cross ISR42-8 (exotic) with Scarlett (cultivated) revealed 15 chromosomal regions where the exotic QTL alleles (ISR42-8) showed strong positive correlations among the root related traits for root traits like root dry weight (RDW), root volume (RV) and root length (RL).

### Genetics of yield contributing traits

In case of wheat, most QTLs for drought tolerance have been identified through yield and yield component measurements under water limited conditions (Quarrie *et al.*, 2006; Maccaferri *et al.*, 2008; Mathews *et al.*, 2008; McIntyre *et al.*, 2009; von Korff *et al.*, 2008; Barakat *et al.*, 2013, Maphosa *et al.*, 2014; Zhang *et al.*, 2013). Although yield is the most relevant trait to breeders, it is very difficult to describe accurately with respect to water use and to identify candidate regions for positional cloning. El-Feki (2010) reported the most stable yield QTL on chromosome 5A from a study conducted under contrasting moisture levels in Colorado. With association analysis, kernel number QTL were detected on chromosomes 4A and 6B, with the former showing consistency across test environments (Neumann *et al.*, 2011). Golabadi *et al.* (2011) identified *Xcfd22-7B* and *Xcfa2114-6A* markers for harvest index and TGW, *Xgwm181-3B*, *Xwmc405-7B* and *Xgwm148-3B* for spike harvest index and marker *Xwmc166-7B* for grain weight per spike showed 20% of the phenotypic variation in durum wheat and mapped QTLs associated with them explained up to 49.5% of the phenotypic variation under drought and non drought stress environment.

In Barley, Forster *et al.* (2004) reported that the wild parental line contributed a number of positive alleles for yield, with major effects due to QTLs that clustered around major genes controlling flowering time, plant stature and ear type. The most favorable effects of the exotic germplasm on yield were found under drought conditions in Tunisia and Morocco (Talamé *et al.*, 2004). Mehravaran

*et al.* (2014) identified 40 QTLs out of which 9 QTLs in normal condition, 18 QTL in stress condition and 13 QTL in the mean of these two conditions in barley. Recently, a high-throughput phenotyping and genome wide SNP markers were combined for detecting significant marker trait associations (MTAs) in introgressed barley lines (Honsdorf *et al.*, 2014). A genome-wide association study performed across 185 cultivated and 38 wild accessions led to the discovery of a few QTLs related to drought tolerance in barley (Varshney *et al.*, 2012).

### Genomic resources for improving drought tolerance in wheat

Both wheat and barley have a very large and diverse genotype pool including several landraces adapted to arid and semi-arid climates. Since considerable variation for drought resistance exists in wild relatives of wheat including *Aegilops geniculata*, *A. tauschii*, *Triticum urartu*, *T. boeoticum*, *T. dicoccoides* and land races (Valkoun, 2001; Reynolds *et al.*, 2005), wide crossing may be used to introduce stress-adaptive genes in modern wheat cultivars (Reynolds *et al.*, 2005). In the recent past, wide crossing contributed to drought adaptation of wheat germplasm. A large number of available synthetic hexaploid wheats containing complete D-genome of *Ae. tauschii* (goat grass) also carry significant novel genetic variation for tolerance to abiotic stress including drought (Valkoun 2001). Crosses between elite wheat cultivars and synthetic wheat have resulted in lines with improved drought adaptation (Trethowan *et al.*, 2005). Wild barley has often been considered a promising resource for the improvement of water stress tolerance as it is adapted to a wide range of environments and offers the prospect of a goldmine of untapped genetic reserves (Ellis *et al.*, 2000). Wild barley (*H. Spontaneum*) can be used to introgress many exotic alleles into cultivated barley that are associated with adaptation to specific environments with different abiotic stress conditions. The *Hordeum spontaneum* showed variation for important agronomic traits such as seminal root morphology, earliness, biomass, grain yield, plant height under drought, and drought tolerance (Ellis, 2002). This vast potential store of genetic resources is yet largely unexploited.

### Global research initiatives on development of drought tolerant wheat and barley germplasm

Many programs aimed for improvement of wheat and barley resistance to drought are being carried out at well established institutes such as International Maize and Wheat Improvement Center (CIMMYT), International Crops Research Institute for Semi-arid Tropics (ICRISAT), International Center for Agricultural Research in Dry Areas (ICARDA) etc. At CIMMYT, important advances have been made in population development with a narrow range of variation for phenology in both biparental

populations and diverse panel of association mapping e.g. Wheat Association Mapping Initiative (WAMI). CIMMYT's wheat germplasm bank holds more than 114,000 accessions, including parental and advanced breeding lines, cultivars and landraces, and more than 13,000 wild relatives from various regions of the world (Monneveux *et al.*, 2012). Around 800 different synthetic hexaploids have been produced by CIMMYT, out of which 95 lines are further used in breeding programs globally (Reynolds *et al.*, 2005). An International Wheat Genome Sequencing Consortium (IWGSC) has been established to coordinate the efforts to obtain a high quality reference sequence of the wheat genome needed to pave the way for faster and more effective genomics based breeding and creation of improved wheat varieties (IWGSC, 2014). Similarly, ICARDA's barley genotypes are being evaluated in nurseries, yield trials and breeding for a range of traits: yield, drought and cold tolerance, earliness, plant height, disease resistance and grain quality aimed to improve yield and resistance to biotic and abiotic stresses in feed forage and food types. Recently reported, the draft genome of Tibetan hullless barley provides a robust framework to better understand *Poaceae* evolution and a substantial basis for functional genomics of crop species with a large genome. The expansion of stress-related gene families in Tibetan hullless barley implies that it could be considered as an invaluable gene resource aiding stress tolerance improvement in *Triticeae* crops (Zheng *et al.*, 2015).

### Concluding remarks

Number of QTLs for key morpho-physiological characters and yield associated traits under water limited conditions have been identified and mapped in wheat and barley. There is a need to first identify the key phenotypic traits affecting the drought resistance and then aimed at strategies for maximizing crop yield at targeted environment. Several attempts have been made so far to use these major QTLs to develop drought tolerant varieties. However, only few of them can be repeatedly detected mainly due to the influence of genetic background and the environment. Therefore, genetic interactions of the transferred QTL with respect to target genetic background have to be investigated. The precise and high-throughput phenotyping especially under field condition is essential for proper genetic analysis of drought tolerance in wheat and barley. With the recent advances in sequencing technologies, genome sequence of bread wheat is almost complete by the efforts of ITMI (The International Triticeae Mapping Initiative) and which will facilitate the search of candidate genes underlying QTLs identified for the traits in the genetic mapping studies and would lead to better marker development, genome analysis and large scale profiling experiments. Root architecture, which plays an important role in crop

growth under water limited environments and stomatal movement should be focused more for studying the drought tolerance mechanism.

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