

Breeding for Enhanced Drought Resistance in Barley and Wheat – Drought-associated Traits, Genetic Resources and their Potential Utilization in Breeding Programmes

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Abstract

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Drought represents the most devastating abiotic stress factor worldwide. It severely limits plant growth and development as well as agricultural characteristics including the final yield. The aim of this review is to summarise recent results of the breeding of barley (*Hordeum vulgare*) and wheat (*Triticum aestivum*; *T. durum*) for improved resistance to drought stress. First, drought-associated terms and definitions are outlined and plant strategies to cope with drought are presented. A brief overview of plant physiological mechanisms involved in water uptake and release is provided. Photosynthesis-related parameters (CO₂ availability and associated features such as ribulose-1,5-bisphosphate carboxylase/oxygenase activity, ¹³C discrimination activity, water use efficiency) are discussed due to the crucial role of plant leaf stomata in both photosynthesis and water management. The second part describes the present state of research on drought resistance-associated traits in barley and wheat. Different strategies of plant water management aimed at maximising the final yield under various types of drought stress are discussed. Possibilities of the detection, identification and characterization of quantitative trait loci (QTLs) in barley and wheat germplasm are discussed and the future approaches to breeding for enhanced drought resistance as a complex physiological and agronomical trait are outlined.

Keywords: cereals; drought resistance; genetic mapping; genetic materials; plant water regime; QTL analysis

Common wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) represent the most important cereal crops worldwide whose production is severely limited by drought in many production areas. It is estimated that ca 65 million ha of wheat production area are affected by drought (FAO 2013). Recently, several summarising reviews on crop breeding for drought environments have been published (CATTIVELLI *et al.* 2008; FLEURY *et al.* 2010; PASSIOURA & ANGUS 2010). Our review focuses on problems and challenges associated with breeding for an enhanced drought resistance in small-grain cereals, namely barley (*Hordeum vulgare* L.), common wheat (*Triti-*

cum aestivum L.) and durum wheat (*Triticum durum* Desf.). An overview of recent mapping studies aimed at detection of quantitative trait loci (QTLs) associated with drought resistance and drought-affected yield parameters in barley and wheat is provided in the second part of the review.

There are several definitions of drought depending on different points of view. From a meteorological point of view, drought means a lack of precipitation (rain, snow) with respect to average values at a given time period in a given area. From a physiological point of view, drought means an imbalance in the plant water regime resulting in an excessive evapotranspiration by

shoot over water uptake by root (REYNOLDS *et al.* 2005). Therefore, meteorological drought does not always correspond with physiological drought and vice versa, i.e. a plant can have a sufficient water supply due to an exploitation of deep soil water reserves from previous periods by its root system. Moreover, stress factors do not usually affect plants independently but in various combinations under field conditions and the effect of joint stress factor action (for example drought and heat) does not equate the sum of separate stress factor effects (MITTLER 2002, 2006). According to the plant phenological phase affected by drought, three types of drought (water-deficit) stress can occur: (1) pre-flowering water deficit (regions of South America); (2) grain-filling (post-anthesis) water deficit (Mediterranean and Australian regions); (3) continuous water deficit (regions of South Asia) (REYNOLDS *et al.* 2005).

Plants have generally evolved three basic strategies how to cope with a lack of water (LEVITT 1980; CHAVES *et al.* 2003; LARCHER 2003). The first approach lies in a drought escape strategy, i.e. minimizing the effect of adverse drought conditions on a plant. This includes a short life cycle utilizing the soil moisture in the most favourable season and a survival of drought periods in a metabolically inactive stage such as seeds or desiccated vegetative tissues. Escape strategy is also often associated with an early vigour, i.e. an acceleration of plant development. The second approach, drought resistance strategy, means that the plant adapts itself to survive drought in a metabolically active state. Two types of strategies leading to drought resistance can be distinguished – drought avoidance and drought tolerance. Drought avoidance strategy is based on minimizing the tissue dehydration, i.e. maintenance of high water potential in plant cells under limited water supply. Plants try to maximize water uptake by roots and to minimize water release by leaves. Drought tolerance represents an adaptation of plant physiological functions to a limited water supply and a decreased plant cell water potential in order to reach a sustainable balance between water uptake by roots and water release by shoots. This represents the major strategy in poikilohydric plants and resurrection plants. In cereals, drought resistance strategies are mainly based on maintenance of the cell water potential, i.e. drought avoidance.

Plant physiological mechanisms associated with drought resistance

Water transport in the soil–plant–atmosphere continuum represents a passive process from a physical

point of view which is, however, actively regulated by a plant. Physiological traits associated with water regime and drought resistance are described by TUBEROSA (2012). Here, only a brief overview of the most important phenotypic traits affecting plant water uptake and release is given.

Changes in the osmotic potential of cell cytoplasm are sensed by membrane two-component histidine kinases homoeologous to AtHK1 in *Arabidopsis thaliana* (URAO *et al.* 1999). The signal is transferred by phosphorylation (MAPK signalling cascades) and calcium signalling from plasmalemma to nucleus where it induces changes in gene expression. A co-ordinate action of abscisic acid (ABA)-dependent and ABA-independent pathways results in an up-regulation of several genes involved in biosynthesis of novel compounds associated with drought response such as organic osmolytes, proteins, etc. (reviewed in CHAVES *et al.* 2003; YAMAGUCHI-SHINOZAKI & SHINOZAKI 2006). Osmotic adjustment (OA) of root cell cytoplasm represents a high-energy-cost strategy how to ensure water uptake by roots. However, this strategy only seems efficient at relatively low water potential gradients between plant root cells and ambient soil (SERRA & SINCLAIR 2002; LAWLOR 2013). Compatible solute accumulation is species-specific, i.e. a given plant species accumulates preferably only some osmolytes. In barley and wheat, the major low-molecular osmolytes are water-soluble carbohydrates (WSC) such as glucose in durum wheat and sucrose in barley (KAMELI & LÖSEL 1995). High-molecular osmolytes include hydrophilic proteins such as late embryogenesis abundant (LEA) proteins including dehydrins (BATTAGLIA *et al.* 2008; KOSOVÁ *et al.* 2010). OA can be quantified as a difference between osmotic potential (OP) values at two different water treatments, i.e. control and water-stressed conditions (LUDLOW & MUCHOV 1990). Studies on Australian wheat cultivars have revealed a positive effect of OA on final yield (MORGAN 1983; BLUM *et al.* 1999).

Plant water uptake is governed by a water potential gradient between the root hair cell cytoplasm and ambient soil. The soil water potential is dependent on soil water relative content; however, the relationship between soil water content and soil water potential is nonlinear. Under low values of soil water content, the soil water potential decreases exponentially with a decreasing soil water content (LAWLOR 2013). Water uptake into the cells is regulated by aquaporin protein channels located in the plasma membrane of root hair cells (AGRE *et al.* 1993; TYERMAN *et al.* 2002) and can be determined by a lysimetric method. The

application of lysimetric method in sorghum revealed a large genotypic variation in water extraction capacity from the soil profile and can also be used for a gravimetric screening of transpiration efficiency (TE) (VADEZ *et al.* 2008, 2011, 2013; VADEZ 2014). The method can also be applied to other cereals such as wheat and barley.

Plant water release is regulated by evapotranspiration in the shoots. Transpiration represents a passive process governed by a gradient in the water potential between the leaf cell cytoplasm and ambient air. It is affected by plant leaf morphology including epidermal layers such as cuticle and trichomes, and by stomatal density, patchiness and openness. Stomata have a dual role in plants – they serve not only for plant water release, but also for CO₂ uptake. Upon a low CO₂ internal concentration (C_i) in the leaf mesophyll due to the stomatal closure, photosynthesis becomes limited and, moreover, competed by photorespiration due to a dual carboxylase/oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO). The reduced RubisCO carboxylation activity leads to a disbalance between the rate of photosynthetic electron transport processes and carbon assimilation resulting in a photooxidative stress which represents a major concomitant stress to drought in natural environments (MITTLER 2002; CHAVES *et al.* 2003). Plants in arid and semi-arid climates evolved a mechanism of dual CO₂ fixation to overcome restricted CO₂ availability (C4 and Crassulaceae acid metabolism (CAM) plants). However, cereals from the tribe Triticeae are C3 plants which have to cope with the dilemma of a trade-off between CO₂ fixation and transpiration.

In C3 plants, stomatal openness and thus drought stress can be indirectly monitored via RubisCO ¹³C discrimination activity. Carbon isotope discrimination ($\Delta^{13}\text{C}$) is positively correlated with the ratio of internal leaf CO₂ concentration to ambient CO₂ concentration (C_i/C_a) and negatively correlated with TE (FARQUHAR & RICHARDS 1984). Therefore, $\Delta^{13}\text{C}$ can be used as an indirect marker of the severity of drought stress in C3 plants. However, the resulting $\Delta^{13}\text{C}$ in plant tissues seems to be more affected by discrimination at a RubisCO level, i.e. carboxylation efficiency of RubisCO, than at a stomata level, i.e. stomatal conductance and C_i/C_a ratio (FARQUHAR *et al.* 1989).

At the whole canopy level, plant evapotranspiration is affected by temperature. Transpiration results in a decrease in the canopy temperature up to 8°C with respect to ambient temperature, the phenomenon known as canopy temperature depression (CTD).

Thus, the extent of CTD may be used as an indirect marker of the plant transpiration rate. Another important canopy parameter affecting the leaf transpiration rate is leaf area index (LAI; WATSON 1947). The higher the LAI, the higher the transpiration from a given area (LAWLOR 2013). At the canopy level, shading the soil surface resulting in an elimination of soil water evaporation is also important. It can be achieved by thinner, wider leaves and a more prostrate growth habit (RICHARDS *et al.* 2002).

The complex regulatory role of stomata in water release and CO₂ uptake is reflected in plant water use efficiency (WUE). There are several definitions of WUE based on the aims and practical needs of plant biologists, agronomists and others. Basically, WUE can be defined as an amount of water needed for the production of one unit amount of plant dry matter. The parameter WUE thus reflects the ability of a plant to resolve the dilemma between the states of “being hungry” or “being thirsty”, i.e. to retain water or to ensure a sufficient CO₂ supply. From an agronomical point of view WUE means an amount of water needed for the production of one unit amount of crop yield. It has to be kept in mind that agronomists and farmers are interested in crop yield, not in WUE, and that WUE does not always positively correlate with crop yield (TUBEROSA 2012). Several studies have shown that breeding for an enhanced WUE or its component TE means a reduced stomatal transpiration and thus a reduced yield under optimum or mild stress conditions (CONDON *et al.* 2004). An attempt to maximize WUE while maintaining photosynthesis was carried out in common wheat (REBETZKE *et al.* 2002). The breeding effort resulted in lines with a 10% yield increase in very dry scenarios and low-yielding environments (1 to 4 t/ha). However, the yield advantage disappeared at annual rainfall higher than 400 mm. Therefore, other concepts of water utilization parameters are being introduced. Effective use of water (EUW) is defined as maximizing plant water uptake from soil while minimizing plant water release by ways other than stomatal transpiration coupled with CO₂ fixation (BLUM 2009, 2011). According to BLUM (2009, 2011), the crucial aspect of drought resistance in most crop plants lies in drought avoidance, i.e. in the maintenance of sufficient cellular hydration. This aim can be achieved by many ways both at plant individual and canopy levels such as restricting soil water evaporation, elimination of water release via thicker leaf cuticle, etc. A negative relationship between WUE, TE and $\Delta^{13}\text{C}$ has been proposed, which

has led to a prediction of the lower yield potential in low $\Delta^{13}\text{C}$ genotypes (HUBICK & FARQUHAR 1989). However, high WUE or TE can help the crop spare water during critical developmental stages such as grain-filling period (VADEZ *et al.* 2014). Studies from dry environments show that the final yield is highly dependent on water availability and plant ability for its utilisation during these periods, which is, indeed, the most limiting factor (VADEZ *et al.* 2014). For example, every extra millimetre of water extracted from soil during the grain-filling period increased the final yield in wheat by 55 to 59 kg/ha (MANSCHADI *et al.* 2006; KIRKEGAARD *et al.* 2007).

REYNOLDS *et al.* (2005) defined four major groups of physiological mechanisms involved in an enhanced wheat drought resistance:

- (1) Traits associated with plant access to water: root morphology; OA to facilitate water uptake by a plant; seedling vigour (large seed and embryo).
- (2) Early growth in a pre-anthesis period: development of shoot biomass enables plants (canopy) to shade the soil surface, minimizing water loss due to evaporation and shading out weeds that could compete for soil water resources. The development of a sufficiently deep root system enables plants to utilize deep soil moisture and to redistribute water from deeper to shallower parts of the soil profile via hydraulic lift in accordance with a gradient in the soil water potential (JACKSON *et al.* 2000).
- (3) Traits associated with leaf photoprotection and minimizing transpiration: these include traits associated with leaf morphology (pale colour due to reduced chlorophyll; erect leaf posture to minimize the absorption of solar radiation

which could lead to an increased temperature and transpiration; cuticle waxes, trichomes, stomatal density).

- (4) Traits associated with WUE: low $\Delta^{13}\text{C}$, high harvest index (HI).

Plant drought resistance mechanisms have a significant impact on characteristics associated with plant growth and final yield. These characteristics are also assessed in genetic mapping studies aimed at an investigation of drought resistance in wheat and barley. An overview of phenotypic characteristics associated with drought resistance at root, shoot, whole plant and canopy levels as well as drought-affected yield characteristics are given in Table 1. Novel high-throughput phenotyping platforms (HTPPs) utilising robotics and remote sensing approaches are emerging for sampling the sets of phenotypic data in large mapping populations. An overview of modern phenotyping methods which can be utilized in the assessment of drought-associated characteristics is given in ARAUS and CAIRNS (2014).

Genetic determination of drought resistance in barley and wheat

Drought resistance represents a complex quantitative trait determined by a multitude of genes and QTLs which depend on the composition of a given population, plant growth stage, environmental conditions and other factors. Agronomic yield under drought-stressed conditions is affected by both constitutive QTLs, i.e. QTLs affecting yield irrespective of environmental conditions, and drought-responsive QTLs, i.e. QTLs affecting yield only under drought conditions (COLLINS *et al.* 2008). Cereals including

Table 1. An overview of phenotypic traits assessed in genetic mapping studies with respect to drought resistance and drought-affected yield in barley (*Hordeum vulgare*) and common wheat (*Triticum aestivum*)

Drought-affected traits	Examples of evaluated traits
Plant root level	Root morphology, root length, OA
Plant shoot level	$\Delta^{13}\text{C}$, g_s , RWC, TE, WSC
Whole plant level	GrH, OA, EUW, WUE
Canopy level	CTD, LAI
Plant growth and development	FLS, HD, NFT, PH, TN
Yield-associated characteristics	EP, GE, KW, NGE, TGW

CTD – canopy temperature depression; EP – ears per plant; EUW – effective use of water; FLS – flag leaf senescence; GE – grains per ear; GrH – growth habit (erect – prostrate); g_s – stomatal conductance; HD – heading date; KW – kernel weight; LAI – leaf area index; NFT – number of fertile tillers; NGE – number of grains per ear; PH – plant height; OA – osmotic adjustment; RWC – relative water content; TE – transpiration efficiency; TGW – thousand grain weight; TN – number of tillers per plant; WSC – water-soluble carbohydrates; WUE – water use efficiency; $\Delta^{13}\text{C}$ – ^{13}C discrimination

barley and wheat reveal large genotypic variability as well as the effect of genotype \times environment ($G \times E$) interactions in several traits ($\Delta^{13}C$, OA, TE, WUE; characteristics associated with the timing of flowering) affecting the resulting drought resistance.

Barley (*Hordeum vulgare*) is rather well-tolerant to drought, salinity and other dehydrative stresses. It is characterized by a relatively simple genome structure possessing only a diploid set of chromosomes (7 basic chromosomes of *Triticeae*, H genome). Recently, a complete barley genome annotation has been published (The International Barley Genome Sequencing Consortium 2012). Common wheat (*Triticum aestivum*) is an allohexaploid species with three genome sets (A, B and D genomes) whose genome sequencing represents a great challenge and is currently in progress (www.wheatgenome.org). The availability of the complete genome sequence will increase our chances to identify candidate genes underlying drought resistance-associated QTLs determined in the mapping populations derived from a cross between contrasting genotypes.

Both barley and common wheat have a very large and diverse genotype pool including several landraces adapted to arid and semi-arid climates. Both species had been domesticated in the area called Fertile Crescent, a region ranging from Israel and Jordan to Syria, southeastern Turkey and Iraq, about 10 000 years ago (ARAUS *et al.* 2007). Domestication of barley and wheat represented an event associated with a significant reduction in allelic diversity including traits (QTLs) underlying an enhanced resistance to abiotic and biotic stress factors (POWELL *et al.* 1997). Wild progenitors and relatives of cultivated wheat and barley, wild barley (*Hordeum vulgare* ssp. *spontaneum*), einkorn wheat (*Triticum monococcum*), wild emmer (*Triticum dicoccum* ssp. *dicoccoides*) and others represent important sources of QTLs underlying an enhanced resistance to several stressors, especially abiotic stressors with a strong dehydrative component such as drought, heat, salinity, as well as pathogens such as powdery mildew, leaf rust (NEVO 1992), Fusarium head blight (reviewed in KOSOVÁ *et al.* 2009) and others.

The major aims in breeding for an enhanced drought resistance and yield under drought-stressed conditions lie first in the knowledge of the target environment, i.e. soil characteristics with respect to water regime (soil depth, particle size, chemical composition, retention and infiltration capacity), timing and severity of drought stress with respect to the crop life cycle. The knowledge of the target

environment is necessary to construct a crop ideotype and to design the optimum breeding strategy for maximizing drought resistance and the final yield. Then, identification of crucial phenotypic traits and their quantitative values is necessary. Selection of the most suitable genetic resources and identification of QTLs underlying desirable phenotypic traits should follow as the next step. Transfer of the proposed QTL underlying drought resistance-associated traits has to be followed by evaluation of the effect of the transferred QTL on plant phenotype. Genetic interactions with other QTLs and $G \times E$ interactions have to be considered (reviewed in TARDIEU & TUBEROSA 2010).

Overview of studies on mapping drought-associated QTLs in barley and wheat

QTL mapping studies in barley

Studies utilizing barley landraces adapted to arid and semi-arid environments. An overview of genetic mapping studies aimed at drought resistance-associated QTL detection in barley (*Hordeum vulgare* ssp., *vulgare*; *H. vulgare* ssp. *spontaneum*), common wheat (*Triticum aestivum*) and durum wheat (*T. durum*) is provided in Table 2.

In many studies of drought-associated QTLs in barley, mapping populations derived from the cultivar Tadmor are used. Tadmor represents a black-seeded barley cultivar selected by International Center for Agricultural Research in the Dry Areas (ICARDA) from a Syrian landrace Arabi Aswad. It represents a very drought- and salt-tolerant genotype suitable as a genetic source for an incorporation of beneficial alleles and QTLs into elite modern barley cultivars (TEULAT *et al.* 1998). A set of 167 F8 recombinant inbred lines (RILs) derived from a cross between Tadmor and Er/Apm (a genotype originating from the Mediterranean basin, but adapted only to specific dry environments) has been investigated for drought-associated QTLs under different environments (diverse field locations across the Mediterranean basin; growth chamber experiments) by several authors (TEULAT *et al.* 1998, 2001a, b, 2002, 2003; DIAB *et al.* 2004). The studies were focused on determination of QTLs associated with drought-related traits (OA, OP, osmotic potential at full turgor OP_{100} , relative water content (RWC), relative water content at full turgor RWC_{100} , WSC, water-soluble carbohydrates at full turgor WSC_{100} , $\Delta^{13}C$). The detected QTLs differed in their stability across environments as well as the length of mapping interval and the effect

Table 2. An overview of genetic mapping studies in barley (*Hordeum vulgare*), wild barley (*H. vulgare* ssp. *spontaneum*), common wheat (*Triticum aestivum*) and durum wheat (*T. durum*) aimed at determination of major QTLs affecting drought-associated traits and the final yield characteristics

Mapping population, location, treatment	Identified QTLs trait – chromosome	Reference
Barley (<i>Hordeum vulgare</i> ssp. <i>vulgare</i>)		
A set of 167 F ₈ RILs Tadmor × Er/Apm Controlled conditions: stress (14% field water capacity) and control (100% field water capacity)	stress: RWC – 6H (<i>Dhn4</i>), 7H (<i>Acl3</i>); OP – 2H, 6H, 7H (<i>Acl3</i>); OP ₁₀₀ – 5H, 6H; control: RWC – 7H; OP ₁₀₀ – 6H; stress vs control: 6H	TEULAT <i>et al.</i> (1998)
Controlled conditions: stress (14% field water capacity) and control (100% field water capacity)	additional QTLs to TEULAT <i>et al.</i> (1998): stress: RWC – 1H; OP – 4H, 5H; OP ₁₀₀ – 2H, 4H, 5H; WSC – 2H; control: RWC – 2H, 7H; OP – 1H, 5H; OP ₁₀₀ – 1H, 5H; WSC ₁₀₀ – 4H, 5H	TEULAT <i>et al.</i> (2001a)
Field conditions – Mediterranean environments: Montpellier 1995 (France) M95; Granada 1996 (Spain) G96; Mauguio 1997 (France) – rainfed M97 _{rain} and irrigated M97 _{ir} ; Montpellier 1999 – rainfed M99 _{rain} and irrigated M99 _{ir}	DAB: M95 – 4H; M99 _{ir} – 6H GY: M95 – 4H, 7H; M99 _{ir} – 5H HD: G96 – 1H, 3H; M97 _{rain} – 2H; M99 _{rain} – 3H; M99 _{ir} – 3H, 6H, 7H HI: M97 _{rain} – 3H, 5H; M99 _{rain} – 7H; M99 _{ir} – 4H NFT: M95 – 3H; M97 _{rain} – 4H; M97 _{ir} – 6H NGE: M95 – 4H; G96 – 3H; M97 _{ir} – 3H, 4H PH: M95 – 3H, 6H, 7H; G96 – 2H, 3H, 6H; M97 _{rain} – 3H, 6H; M97 _{ir} – 2H, 3H, 4H, 5H, 6H; M99 _{rain} – 3H, 6H; M99 _{ir} – 6H TGW: M95 – 3H, 6H; G96 – 5H, 6H; M97 _{rain} – 4H, 6H; M97 _{ir} – 5H, 6H; M99 _{rain} – 1H, 2H, 4H, 6H; M99 _{ir} – 5H, 6H	TEULAT <i>et al.</i> (2001b)
Field conditions – Mediterranean environments: Granada 1996 (Spain) G96; Montpellier 1999 – rainfed M99 _{rain} and irrigated M99 _{ir}	Δ ¹³ C: all environments: 2H, 3H, 6H, 7H; M99 _{rain} vs M99 _{ir} : 1H, 5H, 6H	TEULAT <i>et al.</i> (2002)
Field conditions – Mediterranean environments: Montpellier 1999 – rainfed M99 _{rain} and irrigated M99 _{ir} ; Meknès, Morocco 2000/2001; Le Kef, Tunisia 2001	RWC: 6HL	TEULAT <i>et al.</i> (2003)
Controlled conditions: rainfed (14% field water capacity) and irrigated conditions (100% field water capacity)	OA: 3H, 5H; OP: 2H, 3H, 4H, 5H; RWC: 3H, 5H, 7H; WSC: 2H, 3H, 4H, 5H, 7H	DIAB <i>et al.</i> (2004)
Field conditions: Kfardane (Lebanon), Tel Hadya (Syria) – mild drought; Breda (Syria), Terbol (Lebanon) – severe drought	GY: 1HL (<i>Ppd-H2</i> ; <i>HVA1</i>)	VON KORFF <i>et al.</i> (2008)
Crosses between <i>H. vulgare</i> ssp. <i>vulgare</i> and <i>H. vulgare</i> ssp. <i>spontaneum</i>		
494 RILs of Arta × <i>H. spontaneum</i> 41-1 Field conditions: Tel Hadya (Th) and Breda (Br; Syria) – 1996/97 and 1997/98 – variants Br97, Br98, Th97, Th98	BY: 1H; Br97, Th97, Th98 – 3H (<i>btr</i> locus) CD: Th97 – 2H, 5H; Th98 – 4H, 5H, 6H; both – 5H, 7H Col: Th97 – 2H, 3H HD: Br97 – 4H, 7H; Th97 – 2H, 3H, 7H; both – 5H GrH: Th97 and Th98 – 1H, 6H GrV: 6H GY: 3H, 7H KW: Th97 – 1H, 2H, 3H, 7H PC: Br97 – 5H; Th97 – 3H, 6H PH: all environments – 1H, 3H; Br97,98 – 4H TN: Br97 – 1H, 2H, 3H, 4H	BAUM <i>et al.</i> (2003)

Table 2 to be continued

Mapping population, location, treatment	Identified QTLs trait – chromosome	Reference
123 DH lines derived from BC ₁ F ₂ plants of Barke × <i>H. spontaneum</i> 11508 Field conditions: Cadriano (Italy), Meknès (Morocco), Le Kef (Tunisia) – 2000/01	EL: 7H GrH: 1HL, 3HL, 6HL GY: 2H, 5H HD: 3H, 7H KW: 7H PH: 3H	TALAMÈ <i>et al.</i> (2004)
Common wheat (<i>Triticum aestivum</i>)		
48 DH lines from F ₁ of Beaver × Soissons Field conditions: Gleadthorpe, UK –1999/2000 (control) and 2000/01 (drought)	FLS: 2B, 2D	VERMA <i>et al.</i> (2004)
95 DH lines from F ₁ of Chinese Spring × SQ1 Field conditions: Norwich, UK (1994, 1997, 1998); Zajecar, Serbia (1999,2000); Almaty, Kazakhstan (1998, 1999, 2000); Zaragoza, Spain (1998, 1999) – rainfed vs irrigated treatments per each location and season	yield components: EP: 1AS, 1BL, 2BS, 3DL, 4AL, 4BS, 4BL, 5AL, 5DL GE: 1AS, 1BL, 2BS, 4AL, 4AS, 4BS, 4BL, 5AL, 5BS, 5BL, 5DS, 5DL, 7AL, 7BS, 7BL TGW: 1BL, 3DL, 4AL, 4AS, 4BL, 4DL, 5AL, 5BL, 5DL, 6BL, 7BS	QUARRIE <i>et al.</i> (2005)
	GE: 7AL, 7BL	QUARRIE <i>et al.</i> (2006)
Dharwar Dry × Sitta – Obregon, Sonora, Mexico; growing seasons 1998–99 and 1999–2000	GY: 4AL (<i>Xwmc89</i>)	KIRIGWI <i>et al.</i> (2007)
460 RILs from F ₁ of Chuan-Mai18 (Chinese semi-dwarf wheat carrying dwarfing gene <i>Rht8</i>) × Vigour18	Seedling growth traits: leaf width, coleoptile length – 6A	SPIELMEYER <i>et al.</i> (2007)
192 RILs from a reciprocal cross between Seri M 82 × Babax – north-eastern Australia 2002-2006	GY: 1D GY: 7A WSC: 6D	MATHEWS <i>et al.</i> (2008) MCINTYRE <i>et al.</i> (2010)
161 to 190 DH lines from F ₁ of Cranbrook × Halberd, Sunco × Tasman, CD87 × Katepwa	Δ ¹³ C: 1BL, 2BS, 3BS, 4AS, 4BS, 5AS, 7AS, 7BS	REBETZKE <i>et al.</i> (2008)
Durum wheat (<i>Triticum durum</i>)		
249 RILs from F ₇ of Kofa × Svevo – Mediterranean countries (Italy, Lebanon, Morocco, Spain, Syria, Tunisia) 2004/2005	16 growth environments (10 rainfed and 6 irrigated) GY: 2BL, 3BS HD: 2AS, 2BL, 7BS PH: 1BS, 3AL, 7AS	MACCAFERRI <i>et al.</i> (2008)
152 RILs from F ₆ of durum wheat Langdon × wild emmer (<i>T. turgidum</i> ssp. <i>dicoccoides</i>) accession G18-16 - Israel 2004/2005	Col: 1A, 1B, 2B, 4A, 5A, 5B GY: 2B, 4A, 4B, 5A, 7B HD: 1B, 2B, 3A, 4B, 5A, 7B HI: 1B, 2A, 2B, 5A, 5B, 6A, 6B OA: 2A, 2B, 3A, 3B, 5A, 5B, 6B Δ ¹³ C: 1A, 2A, 4A, 5A, 5B, 6A, 6B	PELEG <i>et al.</i> (2009)

BY – biological yield; CD – cold damage; Col – total chlorophyll content; DAB – dry aerial biomass per plant; DH – double haploid line; EL – ear length; EP – number of ears per plant; FLS – flag leaf senescence; GE – grains per ear; GrH – growth habit of plants (erect vs prostrate); GrV – growth vigour; GY – grain yield per plant; HD – heading date; HI – harvest index; KW – kernel weight; NFT – number of fertile tillers; NGE – number of grains per ear; OP – osmotic potential; OP₁₀₀ – osmotic potential at full turgor; PC – protein content; PH – plant height; RIL – recombinant inbred line; RWC – relative water content; TGW – thousand grain weight; TN – tiller number; WSC – water-soluble carbohydrates; WSC₁₀₀ – water-soluble carbohydrates at full turgor; Δ¹³C – ¹³C discrimination

of G × E interactions. Several additive and epistatic effects were detected between the QTLs. Several QTLs were also associated with multiple traits. Some

QTLs colocalized with known candidate genes. For example, the QTL region on the long arm of 6H chromosome for OA coincided with *Dhn4* locus

and explained 17.7% of the phenotypic variation (TEULAT *et al.* 1998, 2003). QTLs for OP and RWC co-segregated with specific loci with known candidate genes such as chromosome 7H *Acl3* locus coding for barley acyl carrier protein III (HANSEN & VON WETTSTEIN-KNOWLES 1991). This protein encodes a cofactor of plant fatty acid synthetase involved in the *de novo* synthesis of fatty acyl chain, especially in chloroplasts, and revealing an effect on the membrane fluidity. Other QTLs were detected in the vicinity of *Ss1B*, *Dhn4* and *KG1348* loci coding for sucrose synthase, dehydrin 4 and thionin. *Dhn4* reveals an allelic variation in the copy number of hydrophilic ϕ segments and the resulting molecular weight (CAMPBELL & CLOSE 1997; CHOI *et al.* 1999); this variation could exhibit a quantitative effect on OA. In the study of TEULAT *et al.* (2001b), a QTL for thousand grain weight (TGW) was mapped on the long arm of chromosome 5H near the *Dhn1* locus. The most stable QTLs detected across multiple environments included the QTL on chromosomes 3H and 6H affecting plant height (PH) and TGW. Several overlaps were detected between QTLs for different traits. For example, a total of eight QTLs affecting grain $\Delta^{13}\text{C}$ were identified by TEULAT *et al.* (2002), revealing overlaps with QTLs for water status and yield-associated characteristics such as a QTL for TGW mapped near EBmac0684 on chromosome 2H, QTL for PH close to BCD266 on chromosome 2H, QTLs controlling HD on chromosomes 3H and 5H located near Bmag0013 and Bmag0223, respectively, as well as ca 13 areas on chromosome 7H where QTLs controlling RWC and OP were mapped. A large region on chromosome 2H between BCD1069 and Bmag0125 collocated with QTLs affecting OA, a region on chromosome 4H collocated with QTL described for WSC₁₀₀, the QTL mapped on the long arm of chromosome 1H collocated with QTLs for OP and OP₁₀₀, and finally, two regions on chromosomes 7H (nearby ac13) and 2H (between O7.1 and Bmag0125) collocated with QTLs for RWC, OA and agronomic traits. The region on chromosome 2H between O7.1 and Bmag0125 contained overlapping QTLs for $\Delta^{13}\text{C}$, OA and WSC indicating an important role of this region in genetic determination of carbohydrate metabolism (TEULAT *et al.* 2002).

QTLs for yield and yield components in dry versus mild Mediterranean conditions were mapped on 1HL in the vicinity of the flowering regulating gene *Ppd-H1* and dehydration stress-related *Lea* gene *HVA1* indicating an important role of the timing of flowering and accumulation of dehydration-induced

LEA proteins in barley drought resistance under severe Mediterranean environments (VON KORFF *et al.* 2008).

Studies utilizing wild barley (*Hordeum vulgare* ssp. *spontaneum*). The population of RILs derived from a cross of Arta \times *Hordeum vulgare* ssp. *spontaneum* line 41-1 was investigated by BAUM *et al.* (2003). Drought-associated traits were evaluated at two ICARDA research stations Tel Hadya and Breda in Syria. Mapped QTLs for drought resistance associated traits were identified for plant morphological and developmental traits (growth habit GrH, growth vigour GrV, heading date HD, PH, tiller number TN), yield associated traits (biological yield BY, grain yield GY, TGW) and stress resistance-associated traits (cold damage; Table 2). Some of the identified QTLs showed also pleiotropic effects on multiple important agronomic traits, e.g. the QTL on 3HS coinciding with *btr* (non-brittle rachis) locus and revealing also a pleiotropic effect on other traits such as HD, BY and GY. Advanced backcross QTL (AB-QTL) analysis was used to obtain a population of 123 double haploid (DH) lines derived from BC₁F₂ plants derived from a cross between Barke, a European two-rowed barley cultivar, and wild barley line HOR11508 (TALAMÈ *et al.* 2004). The DH lines were tested in environments with different water availability in Italy, Morocco and Tunisia, and 80 putative QTLs associated with one or more out of the 7 analysed traits (GrH – erect or prostrate, HD, PH, ear length, ear extrusion, GY, kernel weight KW) were identified. The allele increasing the value of the trait was contributed by *H. spontaneum* in 42 QTLs. For example, the alleles increasing GY at six regions on chromosomes 2H, 3H, 5H and 7H were contributed by *H. spontaneum* and two of these QTLs (QTLs associated with Bmac0093 on chromosome 2H and Bmac0684 on chromosome 5H) were detected in all three environments and revealed the highest additive effects.

QTL mapping studies in wheat

Advancement in utilization of several types of molecular markers (RFLP, AFLP, SSR) has enabled researchers to study QTLs affecting yield and its components, i.e. ears per plant (EP), grains per ear (GE) and TGW, respectively, also in common wheat (*Triticum aestivum*) known for its large, allohexaploid genome. The common wheat genome, especially the D genome, reveals a relatively low level of polymorphism due to its young origin. Therefore, the researchers needed to cross distant wheat genotypes

in order to obtain high-density genetic maps (RÖDER *et al.* 1998; MESSMER *et al.* 1999).

QUARRIE *et al.* (2005) carried out a large QTL mapping study on the population of 95 DH lines derived from F1 plants of Chinese Spring \times SQ1 (a high ABA-expressing breeding line) cross. QTL analysis was performed based on the data from 24 site \times treatment \times year combinations, including nutrient, drought and salt stress factors (locations: Norwich, the UK; Zajecar, Serbia; Almaty, Kazakhstan; Zaragoza, Spain). Seventeen clusters of yield-affecting QTLs were mapped to the wheat genome, two of which were mapped to group 1 chromosomes, one to group 2, one to group 3, five to group 4, four to group 5, one to group 6 and three to group 7. The strongest yield-affecting QTLs were mapped to chromosomes 7AL and 7BL, mainly due to their effect on the number of grains per ear (NGE). Comparative mapping using a collinearity between wheat and rice genomes has identified candidate genes *AINTEGUMENTA* and G-protein subunit affecting the lateral cell division at 7AL locus (QUARRIE *et al.* 2006). Three of the yield-affecting QTLs were coincident with the positions of the dwarfing gene *Rht-B1* on 4BS and with vernalisation genes *Vrn-A1* on 5AL and *Vrn-D1* on 5DL. Two additional yield-affecting QTLs were identified on chromosomes 1D and 5A in drought-stressed environments.

In a mapping population derived from Mexican wheat cultivars, a region on chromosome 4AL associated with SSR locus *Xwmc89* was found to have a significant effect on GY and yield-associated components (grain fill rate, spike density, biomass production, drought susceptibility index DSI; KIRIGWI *et al.* 2007). Further studies have revealed a strong dependence of yield-associated QTL on QTLs associated with anthesis (date of flowering) and further characteristics such as grain number and grain size (MATHEWS *et al.* 2008; MCINTYRE *et al.* 2010).

Carbon isotope discrimination ($\Delta^{13}\text{C}$) significantly affects wheat yield in dry environments. Genetic analysis of three wheat mapping populations with respect to $\Delta^{13}\text{C}$ has revealed a relatively high number of QTLs affecting $\Delta^{13}\text{C}$ revealing stability across different genetic materials and environments. Some of these QTL were associated with a variation in HD and PH confirming an association between $\Delta^{13}\text{C}$ and GY. However, small effects of the individual QTLs may reduce the utilization of $\Delta^{13}\text{C}$ in breeding programmes (REBETZKE *et al.* 2008).

Shading the soil early during plant development helps young plants spare water. Greater seedling

leaf area and longer coleoptiles represent the major determinants of early vigour, wheat ability to form a closed canopy early enough to diminish water losses by the soil surface evaporation. A QTL on chromosome 6A was determined in the breeding population derived from a cross between Chinese semi-dwarf wheat Chuan-Mai 18 and tall breeding line Vigour 18 by SPIELMEYER *et al.* (2007). This QTL was associated with SSR marker NW3106 and accounted for up to 8% of the variation in coleoptile length and 14% of seedling leaf width.

The timing of flag leaf senescence (FLS) represents an important determinant of yield under terminal drought conditions due to an increase in cumulative photosynthesis. VERMA *et al.* (2004) investigated QTLs involved in the regulation of FLS in a population of 48 DH lines derived from a cross between Beaver, a photoperiod-sensitive variety, and Soissons, a photoperiod-insensitive variety. The major QTLs involved in the regulation of FLS were mapped on chromosomes 2B and 2D. The dynamics of FLS was evaluated as a percentage of green flag leaf area remaining in 14 days and 35 days after anthesis. Flag leaf senescence revealed a positive correlation with yield under variable environments.

In durum wheat (*Triticum durum*), an extensive mapping study was carried out by MACCAFERRI *et al.* (2008) on a population of 249 RILs derived from a cross between cultivars Kofa and Svevo. The lines were grown in 16 environments characterised by large differences in water availability. Sixteen QTLs affecting GY were detected, out of which two major QTLs on chromosomes 2BL and 3BS showed significant effects in 8 and 7 environments, respectively. Plant height associated QTLs were identified on chromosomes 1BS, 3AL and 7AS. Heading date associated QTLs were detected on chromosomes 2AS, 2BL and 7BS. Moreover, an overlap for GY and PH QTLs was detected on 2BL and 3BS revealing a significant epistatic effect on these traits across several environments. In a population of 152 RILs derived from a cross between durum wheat cv. Langdon and wild emmer (*Triticum turgidum* ssp. *dicoccoides*), a total of 110 QTLs were mapped by PELEG *et al.* (2009) for 11 growth and yield-related traits under drought. Major QTLs affecting yield were mapped to chromosomes 2B, 4A, 5A and 7B and were associated with QTLs for drought resistance-related traits such as $\Delta^{13}\text{C}$ and OA indicating a significant effect of these traits on the final yield under drought. A high synteny between A and B genomes was also observed.

Breeding approaches to improve drought resistance in barley and wheat

Breeding programs aimed at an improvement of wheat and barley resistance to drought are established at institutions focused on dryland agriculture such as ICARDA, International Crops Research Institute for Semi-arid Tropics (ICRISAT), International Maize and Wheat Improvement Center (CIMMYT), etc. Wide crossing approaches using interspecific and intergeneric hybridisation represent a promising way of stress resistance enhancement based on the exploitation of secondary and tertiary gene pools, respectively. Wild relatives and landraces are used in wheat breeding programmes carried out at CIMMYT. Alleles associated with an enhanced stress resistance which were lost due to the bottleneck of domestication can be thus introduced into modern germplasm. Interspecific hybridisation includes the techniques associated with preparation and exploitation of resynthesized wheat lines. Wild relatives of wheat, wild emmer with genome AB, and *Aegilops tauschii* with genome D, were employed to construct synthetic or resynthesized hexaploid wheat. The resynthesized hexaploid wheats are then used in crosses with elite breeding wheat cultivars in order to introduce novel alleles into the relatively poor genetic background of these materials. Four lines derived from the crosses between synthetic hexaploid wheat and elite materials (d67.2/p66.270/*Ae. squarrosa* (320)/3/Cunningham; Croc_1/*Ae. squarrosa* (210)//2*Excalibur; Croc_1/*Ae. squarrosa* (224)//Opata; Sokoll) were employed in the study of REYNOLDS *et al.* (2007) and used for comparison of their ability to adapt themselves to drought with respect to their elite parents (Cunningham, Excalibur). The crosses between resynthesized hexaploid wheats and elite materials, the so-called synthetic derived (SYN-DER) lines, in comparison with their recurrent parents (REC-PAR), revealed a better adaptation of their root system to drought. However, this was not associated with simply a larger overall investment in root dry weight, but rather with an increased partitioning of root biomass to deeper soil profiles (between 60 and 120 cm) and an increased ability to extract moisture from these depths. The studied SYN-DER lines also revealed with respect to REC-PAR a relatively higher biomass under drought combined with a relatively high level of WSC, increased WUE and TE which resulted in a higher GY. Around 800 different synthetic hexaploids have been produced by CIMMYT to date, out of which 95 lines are further used in breeding programs globally (REYNOLDS *et al.* 2005).

Intergeneric hybridisation tries to exploit stress resistance-associated traits also from wild related genera such as *Thinopyrum* (*Th. elongatum*, *Th. ponticum*). Crossing with wheat leads to production of amphiploids and formation of lines with alien chromosome additions, substitutions, translocations or introgressions. An introgression of chromosome 4D from *Aegilops tauschii* in durum wheat cv. Langdon via homologous recombination leading to the substitution of durum wheat chromosome 4A by *Ae. tauschii* chromosome 4D and an improved salinity resistance can be given as an example (DVOŘÁK & GORHAM 1992).

Another strategy of the introduction of new alleles into elite breeding germplasm lies in utilization of landraces grown in harsh environments. Prior to breeding, prescreening tests are usually carried out to select the most promising genotypes. Comparison of selected landraces and modern cultivars of durum wheat from the Mediterranean region has revealed significant differences in many traits between the two groups. Modern cultivars exhibited higher yields under both rainfed and irrigated conditions, higher grain weight by about 2 mg, and four more grains per spike on average than landraces. In contrast, landraces flowered on average 1 day later and were about 20 cm taller than their modern counterparts (ARAUS *et al.* 2007). However, the utilisation of wild germplasm such as landraces and secondary and tertiary gene pools for the improvement of stress resistance in modern cultivars represents a controversial process. Besides desirable drought resistance-related alleles, other alleles with adverse effects on important agronomic characteristics such as grain quality and yield parameters can be introduced into elite breeding materials. Advanced backcross QTL analysis represents a promising approach to transfer valuable QTLs from an unadapted germplasm into elite breeding lines (TANKSLEY & NELSON 1996).

Besides bi-parental crosses, multi-parental crossing approaches such as backcross nested association mapping (BCNAM) approach are becoming utilised in the breeding programmes in some cereal crops (sorghum) and may also be used in wheat and barley breeding in the future (sorghum joint breeding project of ICRISAT-Mali and Agropolis; www.generationcp.org/sorghum-bcnam-project-2). Doubled haploids as a homozygous genetic material in breeding represent a valuable source for breeding programmes aimed at an improvement of complex traits such as drought resistance due to a significant elimination of G × E interactions (REYNOLDS *et al.* 2005). “Smart crossing”

of carefully selected germplasm based on a cooperation of breeders, modellers and plant biologists can be used to accumulate desirable alleles underlying multiple phenotypic traits to achieve a superior enhancement in drought resistance (REYNOLDS *et al.* 2005).

Marker-assisted selection (MAS) utilizes knowledge of the position of drought-associated QTLs gained via genetic mapping studies. However, in the case of abiotic stress factors such as drought, most QTLs depend both on a given genetic background and a given environment. Thus, first of all, the identification of stable QTLs is necessary for breeders (COLLINS *et al.* 2008). Association of drought-related QTLs with molecular markers or even candidate genes enables the breeders to detect the presence or absence of a given QTL in selected plant material during breeding. Utilisation of MAS approaches also enables QTL pyramiding, i.e. an introduction of multiple QTLs associated with different drought-related phenotypic traits into one plant material to improve multiple drought- and yield-associated traits. QTL pyramiding can be utilised to produce an elite genetic material encompassing suitable alleles from diverse genetic resources in one breeding material. The strategy of QTL pyramiding has been effective in genes underlying resistance to pathogens, i.e. traits determined by a few genes with major effects. In the case of multigenic traits, utilisation of this approach is more complicated due to a large number of QTLs affecting the resulting trait and often complicated genetic interactions (additive, dominant, overdominant, epistatic effects) between the individual QTLs (reviewed in TUBEROSA & SALVI 2006).

Publication of the whole genome sequencing results will facilitate the search for candidate genes underlying QTLs identified in genetic mapping studies aimed at the search for drought resistance-related alleles. Candidate gene identification could then open the way to direct transfer of a desirable allele via modern molecular approaches (e.g. cisgenesis) without a risk of concomitant transfer of several adverse alleles from an unadapted germplasm (SCHOUTEN *et al.* 2006; JACOBSEN & SCHOUTEN 2007).

Breeding for an improved drought resistance still remains a great challenge due to a complex nature of the trait. In cereals, drought resistance is usually based upon a drought avoidance strategy, i.e. achieving a balance between plant water uptake and release aimed at the maintenance of a high cellular water potential to retain plant growth under adverse environmental conditions. There are many ways how to achieve this aim. Selection of the most suitable breeding strategies

depends on both the plant developmental phase and the severity of environmental conditions. Under a severe lack of water, the most efficient way of water utilization lies in a “conservative strategy”, i.e. maximizing WUE as observed in low $\Delta^{13}\text{C}$ cereals such as Australian wheat cultivars Drysdale and Rees (REBETZKE *et al.* 2002). However, under mild stress conditions or under artificial irrigation, maximizing WUE could lead to yield penalty due to restricted stomatal transpiration and CO_2 fixation. Strategies based on maximizing EUW, i.e. maximizing plant water uptake without reducing water release via stomatal transpiration as observed in high $\Delta^{13}\text{C}$ cereals, seem to represent a more efficient way with respect to the final yield than conservative strategies based on maximizing WUE (ARAUS *et al.* 2002; CONDON *et al.* 2004). However, total water use and cumulative photosynthesis over the whole crop life cycle seem to represent more relevant criteria with respect to the final yield than WUE or TE (VADEZ *et al.* 2014). The plant developmental phase when drought stress occurs also affects the target traits for breeding programmes. When drought affects young plants, breeding for an early vigour leading to early canopy closure and elimination of soil water evaporation represents an efficient strategy leading to drought avoidance. On the other hand, when drought affects plants during the grain filling period, a “stay-green” phenotype resulting in a delay of FLS represents an efficient strategy leading to an increase in cumulative photosynthesis and in the final yield (BORRELL *et al.* 2001). An overview of various scenarios for different environmental conditions was given in TARDIEU and TUBEROSA (2010) and TARDIEU (2012).

It can be concluded that no universal strategy can be suggested for breeding for an enhanced drought resistance in cereals since the individual strategies are often mutually exclusive, i.e. the given genetic material cannot adopt all of them. As the most crucial example, the “trade-off” principle between water conservation and biomass accumulation as expressed in terms of WUE and EUW can be given (TARDIEU 2012; VADEZ *et al.* 2013). Therefore, knowledge of the environment (a season when drought occurs and the severity of the drought stress) appears to be crucial in the selection of the most suitable breeding strategy. Moreover, the effect of an introduced QTL is also dependent on the given phenotypic context. The effect of a certain QTL affecting a given trait, e.g. ABA content or stomatal conductance, is dependent on many other QTLs, e.g. QTLs affecting root length, which can significantly differ between diverse genetic backgrounds (COLLINS *et al.* 2008).

CONCLUSION

Drought remains the most severe abiotic stress factor for a global cereal production in the 21st century. Drought resistance represents a polygenic trait with multiple components associated with plant water status, cellular metabolism, growth and developmental characteristics affecting the final crop yield whose values depend on many interacting genetic and environmental factors. Intensive genetic mapping programmes aimed at detection and further characterization of stable QTLs affecting key yield characteristics under a broad range of environments have already been launched.

The key steps in the breeding programmes aimed at an improvement of drought resistance in small-grain cereals (barley, wheat) can be described as follows:

First, improvement of agricultural practices, i.e. improvement of crop management (date of sowing, fertilization) and soil characteristics (soil retention and infiltration capacity) leading to enhanced water utilization by the crop has to be considered.

Approaches aimed at genetic improvement of the crop with respect to drought resistance should first consider the knowledge of the target environment and identification of key phenotypic traits and strategies aimed at maximizing crop yield in the given environment.

Further steps should include: (1) modelling of crop ideotype encompassing all key phenotypic traits affecting the resulting drought resistance and the final yield under the given environment; (2) search for the most suitable genetic resources possessing QTLs which can contribute to the improvement of key phenotypic traits of the target plant material; (3) transfer of the selected QTLs from genetic resources via MAS or QTL pyramiding, development of multiple crosses between the locally adapted germplasm and parent possessing the drought-adaptive mechanism (e.g. BCNAM, this also allows the identification of QTLs in “multiple RILs populations”); (4) identification of candidate gene(s) and desirable alleles underlying drought resistance-associated QTLs; this will be hopefully enabled by the knowledge of barley (and in the near future also common wheat) genome sequence; (5) candidate gene transfer can be achieved by genetic engineering techniques (e.g. cisgenesis); (6) the resulting progenies possessing transferred QTL have to be tested for the effects of the transferred QTL on the resulting phenotype. Genetic interactions of the transferred QTL with respect to the novel genetic background have also to be investigated. Testing has to be cheap and rapid, otherwise it is of no use for breeders.

This is an ideal situation; however, the investigation of drought resistance brings several obstacles which may complicate the breeding effort. The first obstacle lies in the complexity of studied traits and drought resistance strategies and their dependence on timing and severity of drought stress. The second obstacle lies in the complexity of $G \times E$ interactions. The third obstacle lies in the successful introgression of a stable drought resistance-associated QTL into elite breeding germplasm and testing its effect in a new genetic background under the field conditions. Moreover, interactions between multiple stress factors in the field conditions have to be taken into account (MITTLER 2002, 2006). However, a rapid progress in novel genetic mapping and breeding approaches (marker-assisted recurrent selection MARS, MAS, RILs, BCNAM) together with increasing knowledge of wheat and barley genome structure, candidate genes underlying QTLs detected in the mapping studies and their mutual genetic interactions can represent a source of optimism for the breeders focused on drought resistance improvement in wheat and barley.

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