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REVIEW

Breeding wheat for drought tolerance: Progress and technologies

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Abstract

Recurrent drought associated with climate change is among the principal constraints to global productivity of wheat (*Triticum aestivum* (L.) and *T. turgidum* (L.)). Numerous efforts to mitigate drought through breeding resilient varieties are underway across the world. Progress is, however, hampered because drought tolerance is a complex trait that is controlled by many genes and its full expression is affected by the environment. Furthermore, wheat has a structurally intricate and large genome. Consequently, breeding for drought tolerance requires the integration of various knowledge systems and methodologies from multiple disciplines in plant sciences. This review summarizes the progress made in dry land wheat improvement, advances in knowledge, complementary methodologies, and perspectives towards breeding for drought tolerance in the crop to create a coherent overview. Phenotypic, biochemical and genomics-assisted selection methodologies are discussed as leading research components used to exploit genetic variation. Advances in phenomic and genomic technologies are highlighted as options to circumvent existing bottlenecks in phenotypic and genomic selection, and gene transfer. The prospects of further integration of these technologies with other omics technologies are also provided.

Keywords: drought tolerance, genomic selection, genotyping, phenotyping, wheat

1. Introduction

Global wheat production in the major production regions is being threatened by recurrent drought that is predicted to increase with climate change (Li *et al*. 2009). Drought tolerant wheat varieties are the ultimate means of safeguarding the crop against adverse effects of drought. However, drought tolerance is a complex trait that is controlled by numerous genes, each with minor effects (Bernardo 2008). Some of the genes are located as quantitative trait loci (QTL) exhibiting additive and non-additive gene effects. Due to its polygenic inheritance and genotype by environment interaction, drought tolerance typically has low heritability (Blum 2010; Khakwani *et al*. 2012). Despite these challenges, determination of the genetic diversity existing within and between wheat populations remains the basis for elucidation of the genetic structure and for improvement of quantitative traits, including drought tolerance. In wheat, greater genetic variability can be explored with germplasm from its centers of origin and diversity (Dvorak *et al*. 2011). Besides cultivated wheat varieties and breeding stocks, extensive variability for drought tolerance remains within wild relatives and landraces (Nevo and Chen 2010; Dodig *et al*. 2012). Manipulation of this diversity to improve drought tolerance among cultivars may be achieved through genetic

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modification or selection for adaptive mechanisms; including drought escape, dehydration avoidance and dehydration tolerance (Blum 2010).

Genomics-assisted selection has not yet contributed much to the improvement of drought tolerance in wheat. This may be attributed to the polygenic nature of the trait, and the structural complexity and large size of the crop's genome, which is approximately 17 Gigabase base pairs (Gbp) (Paux *et al*. 2006; Berkman *et al*. 2012). Also, lack of standardized phenotyping techniques could be limiting the application of genomic tools in drought tolerance improvement. Therefore, advanced phenotyping and genotyping technologies may offer prospects towards precise genomic characterization, genomic selection, molecular marker discovery, QTL mapping, and candidate genes discovery. The state of knowledge and complementary methodologies towards breeding for drought tolerance in wheat are often presented disjointedly across various disciplines of plant sciences. The objective of the current review is to provide an up-to-date, comprehensive summary of the advances in breeding for drought tolerance which may pinpoint future research directions to improve drought tolerance in wheat. The review is guided by, but not limited to, the following research questions: (1) What is the current progress in drought tolerance improvement in wheat? and (2) what are the best selection methods and technologies for enhancing drought tolerance improvement in wheat?

2. Breeding progress for water limited environments

The International Maize and Wheat Improvement Center (CIMMYT) has contributed to the worldwide adoption of modern wheat varieties that are adapted to marginal environments through multi-environmental testing and collaboration with national breeding programmes (Manes *et al*. 2012). The wheat yield progress under marginal conditions, obtained from CIMMYT's international yield trial data for overlapping periods between 1964 and 2010 is presented in Table 1 (Lantican *et al*. 2001; Trethowan *et al*. 2002; Manes *et al*. 2012).

The rates of yield increase are still too low to catch up with the projected 70% rise in wheat demand by 2050 (CIMMYT 2014). However, increasing dry land wheat productivity is a potential option of meeting this growing demand, since yields under optimum conditions may be approaching a ceiling. Much of the yield progress reported under low yielding environments has been based on evaluations under several biotic and abiotic constraints including drought. Moreover, much of the documented yield increase was partly a result of spillover benefits from selection for yield improvement under optimum conditions. Development of candidate genotypes at target growing environments and drought conditions, and minimizing confounding effects of other stresses in the breeding programs, will enhance selection for drought tolerance. Though CIMMYT data represent international yield trends, there is still a need to compile a comprehensive documentary of the progress observed by national breeding programs to provide a clear map of where to acquire new innovations and germplasm.

3. Selection methods and technologies for drought tolerance

3.1. Phenotyping wheat for drought tolerance using phenotypic traits

Knowledge of phenotypic traits contributing to improved yields under stress is fundamental to the understanding of the complex physiological and genetic mechanisms of wheat adaptability (Reynolds *et al*. 2005). Important target traits include: reduced plant height, which is associated with high harvest index (Slafer *et al*. 2005); reduced number of days to anthesis and maturity, which enable the crop to evade terminal drought stress (Blum 2010); and root architectural traits such as even distribution and root length density, which enable effective water uptake (Manschadi *et al*. 2006; Ehdaie *et al*. 2012). Also, seedling traits associated with vigorous seedling establishment, such as coleoptiles length, can increase adaptation to drought through early ground

Table 1 Rates of yield increase observed from International Maize and Wheat Improvement Center (CIMMYT)'s international spring wheat yield nursery (ISWYN), elite spring wheat yield trial (ESWYT), and semi-arid wheat yield trials (SAWYT) programs from 1964 to 2010 under marginal conditions

Years	Program	Rate of yield increase	Target environment	Reference
1964–1978	ISWYN	1.54% (32.4 kg ha^{-1}) yr^{-1} from about 2.3 to 4.3 t ha^{-1}	Drought prone	Lantican *et al*. (2001)
1979–1995	ISWYN	2.75% (70.5 kg ha^{-1}) yr^{-1}	Drought prone	Lantican *et al*. (2001)
1979–1998	ESWYT	0.19% (5.3 kg ha^{-1}) yr^{-1}	Low yielding environments	Trethowan *et al*. (2002)
1979–1999	ESWYT	3.48% (87.7 kg ha^{-1}) yr^{-1} from about 2.3 to 3.5 t ha^{-1}	Drought prone	Lantican *et al*. (2001)
1991–1997	SAWYTs	0.09% (2.1 kg ha^{-1}) yr^{-1}	Low yielding drought prone environments	Trethowan *et al*. (2002)
1994–2010	SAWYTs	0.7% (37 kg ha^{-1}) yr^{-1}, from about 2.07–2.7 t ha^{-1}	Low yielding environments	Manes *et al*. (2012)