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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 <i>et al.</i> (2001)
1979–1995	ISWYN	2.75% (70.5 kg ha ⁻¹) yr ⁻¹	Drought prone	Lantican <i>et al.</i> (2001)
1979–1998	ESWYT	0.19% (5.3 kg ha ⁻¹) yr ⁻¹	Low yielding environments	Trethowan <i>et al.</i> (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 <i>et al.</i> (2001)
1991–1997	SAWYTs	0.09% (2.1 kg ha ⁻¹) yr ⁻¹	Low yielding drought prone environments	Trethowan <i>et al.</i> (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 <i>et al.</i> (2012)

cover, which reduces evaporative losses (Spielmeyer *et al.* 2007). Wheat traits associated with reduced evaporative losses and photo-assimilate production such as leaf rolling, flag leaf persistence, stomatal conductance, and canopy temperature should be selected, based on their positive correlation with yield under stress (Kumar *et al.* 2010; Dodig *et al.* 2012). For instance, high stomatal conductance is positively correlated with water stressed yield ($r=0.94$) (Fischer *et al.* 1998) due to increased transpiration which is associated with optimum water uptake from a depth, low canopy temperature and high photo-assimilate production (Blum 2009; Lopes and Reynolds 2010; Kumar *et al.* 2012). The ultimate criteria for genotype selection should, however, be guided by how well the variety integrates its adaptive mechanisms to optimize yields, other than being based on a single trait. Selection based on yield should be supported by proper calculation, utilization and interpretation of various drought indices which evaluate genotypic yield response to water stress (Fernandez 1992).

3.2. Use of rain-out shelter and controlled water application

Artificial simulation of drought through controlled water application and utilization of rain-out shelters play key roles in reducing experimental error in field experiments through improving homogeneity in moisture levels and eliminating confounding effects of untimely rainfall. Several designs of fixed-location and automated moveable rain-out shelters have been documented for utilization in drought tolerance research in major field crops including wheat (Dodig *et al.* 2012). Movable rain-out shelters which only cover the plot only when it is raining, cause the minimum alteration of non target variables such as temperature, which may have confounding effects. Timing of drought induction and water regimes should be guided by the typical drought patterns in

the targeted environments. Also, the whole system should be monitored with standard and well serviced soil moisture sensors which suit the researcher's particular requirements (Su *et al.* 2014). In the past, various researchers employed different water regimes to simulate drought. Table 2 summarizes different water regimes previously adopted on wheat, which may serve as important guidelines for drought tolerance studies.

3.3. Use of high-throughput and automated phenotyping techniques

The slow pace, high costs and inconsistencies associated with trait quantification and data management using traditional phenotyping techniques still limit the progress of drought tolerance improvement. This could, also, have been contributing to the complexities of understanding the genetic and physiological basis of drought tolerance both at the phenotypic and the genomic levels (Xu and Crouch 2008). The utilization of sophisticated, non-destructive, high-throughput phenotyping technologies with automated systems for capturing, storage and statistical analysis of large volumes of data, allows for fast and precise large scale quantification and monitoring of various phenotypic traits (Araus and Cairns 2014). Ground and remote sensing techniques based on near or far-infrared reflectance digital sensors, thermometers, and cameras are reported to precisely measure various phenotypic traits (Zhu *et al.* 2011; Araus and Cairns 2014; Honsdorf *et al.* 2014). These include automated camera systems which are connected to computers for monitoring complex root architectural traits through periodic image capturing (Iyer-Pascuzzo 2010). Some of these tools are graced with image processing and analysis software (Schneider *et al.* 2012). These advanced phenotyping technologies may create local databases for easy management of the vast

Table 2 Previously used water regimes for drought tolerance evaluation in wheat

Water regime (treatments) ¹⁾	Reference
Control: water to 60% field capacity (FC) Stress: water to 20% FC	Majer <i>et al.</i> (2008)
Control: irrigate at 60% FC Stress: irrigate at 40% FC	Omar <i>et al.</i> (2010)
Control: irrigate after 70 mm E _o Stress: irrigate after 140 mm E _o	Golabadi <i>et al.</i> (2011)
Control: moisture content kept at 100% FC Stress level 1: watering done at 35% FC back to 100% Stress level 2: maintain moisture between 25 and 35% FC	Khakwani <i>et al.</i> (2011)
Control: moisture content kept at 100% FC Stress: withhold water for 20 days at booting and after anthesis	Khakwani <i>et al.</i> (2012)
Control: provide normal irrigation Stress: withhold water from tillering to anthesis then stressing up to maturity	Mohamed and Ahmed (2013)

¹⁾E_o, evaporation from a class A pan.

amounts of data that will be generated.

3.4. Applications of biochemical markers to improve drought tolerance

Drought stress triggers the expression of many genes influencing the metabolism of several bio-chemicals including key enzymes, transcription factors, hormones, amino acids, and carbohydrates (Yang *et al.* 2010). Notable among these include the phytohormone abscisic acid (ABA), proline, tryptophan, late embryogenesis abundant (LEA) proteins, trehalose, raffinose, mannitol, glycine-betaine, and superoxide dismutase (Sivamani *et al.* 2000; Hameed *et al.* 2011; Nio *et al.* 2011). These bio-molecules are involved in dehydration avoidance or dehydration tolerance events such as osmotic adjustment, membrane stabilization, anti-oxidation, scavenging of reactive oxygen species (ROS), and gene regulation, among other functions (Ashraf 2010; Yang *et al.* 2010). However, the specific drought responsive mechanisms and functions of the majority of these metabolites are still ambiguous. This necessitates further studies to reveal their roles to allow for informed manipulation of the genetic diversity existing in the expression of their respective genes under stress. Yield benefits from biochemical accumulations should be considered in breeding programs because osmotic adjustment seems to use energy to accumulate photo-assimilates in other plant organs to ensure survival at the expense of grain yield.

Application of knowledge gained on signaling and metabolism of these drought-related bio-chemicals has mainly been mediated through transgenics derived from other crop species beyond the *Triticum* genome. For instance, improved water use efficiency, biomass accumulation and root weight occurred among water stressed transgenic wheat lines expressing the barley (*Hordeum vulgare* L.) gene, *HVA1*, encoding for some late embryogenesis abundant proteins that work as osmo-protectants (Sivamani *et al.* 2000). On the other hand, a proline inducing gene (*P5CS*) boosted drought tolerance of transgenic lines in a response that was possibly due to proline's antioxidant protection of cells from oxidative damage by oxygen free radicals (Vendruscolo *et al.* 2007). Also, a mannitol biosynthesis (*mtlD*) gene from *Escherichia coli* increased drought tolerance in wheat by acting as an osmo-protectant (Abebe *et al.* 2003). The potential contribution of the various genes to drought tolerance improvement may be overstated because most evaluations are carried out on seedling plants under artificial conditions. However, this may not represent the performances of the trans-genes through all growth stages of wheat under field conditions. Intensive screening of the diverse wheat germplasm based on biochemical accumulation could enhance the introgression of the genes involved

using conventional breeding techniques.

3.5. QTLs/genes controlling drought tolerance

Application of marker technologies eliminates confounding effects of the environment during selection, especially when considering polygenic traits like drought tolerance and allows for indirect selection of traits independent of the stage of plant development. Several molecular markers have been used, of which, sequence-based DNA markers, notably single nucleotide polymorphisms (SNPs), are gaining popularity and are expected to advance the dissection of complex traits on complex genomes due to their high linkage with heritable variation (Gupta *et al.* 2011; Berkman *et al.* 2012). Thus far, several phenotypic drought-responsive traits on wheat have been correlated with molecular markers allowing precise mapping of their respective QTLs on chromosomes (Ibrahim *et al.* 2012; Ahmad *et al.* 2014). However, QTL identification for tracing drought tolerance remains a challenge due to the large number of genes influencing the trait, instability of some QTLs, the large size of the wheat genome, and epistatic QTL interactions, among other constraints (Ashraf 2010; Kumar *et al.* 2010; Sharma 2013). Further, the full benefits of molecular markers in selecting for quantitative traits will remain a challenge as most marker techniques are just qualitative measures indicating the presence of a gene with no further information on; whether the gene is expressed or not, the levels of its expression and its impact on the complex trait, and the presence and expression of other genes influencing it. There is, therefore, a need to integrate molecular tools with precise high-throughput phenotyping and biochemical analysis to confirm the consistency of molecular markers.

Detection of QTLs containing the genes conferring quantitative traits including drought tolerance have revolutionized the selection process towards marker assisted and genomic selection (Mir *et al.* 2012). To date, several putative QTLs for drought tolerance related traits have been mapped in wheat, particularly on the A and B genomes where most of relevant QTLs seem to be localized on chromosomes 2B, 3A, 4A, 4B, 7A, and 7B, as presented in Table 3. However, there are no QTLs detected for grain quality under drought stress in wheat, yet Balla *et al.* (2011) pointed out that drought stress and high temperature caused dough quality deterioration. The utilization of the abundant QTLs identified so far through marker assisted selection (MAS), candidate gene detection, and QTLs introgression or pyramiding for drought tolerance improvement in wheat has not been reported as utilized in practice. Also, the utilization of above mentioned markers seem to be reliable for detecting QTLs with major phenotypic effects (Kumar *et al.* 2012), yet drought tolerance is a function of many QTLs of major and minor effects. Further,

cloning of these QTLs is necessary for the determination of their molecular modes of action so that effective selection can be carried out based on their breeding values. Statistical analysis is also a requisite to determine epistatic QTL interactions and complex QTL by environment interactions to account for the error variances due to the environment (Kumar *et al.* 2010). These limitations may be resolved through the use of advanced sequence-based techniques to improve the consistency of detecting QTLs, including those with minor effects as outlined below.

3.6. Applications of next generation sequencing (NGS) and genome engineering technologies

Most traditional marker techniques do not detect some se-

quences including those within low-copy genomic regions, non-coding regions, transposable elements, and less prolific repeats that may, however, play crucial roles in regulating some key phenotypic traits (Elshire *et al.* 2011; Edwards *et al.* 2013). These problems can be mitigated through the employment of NGS techniques including the Illumina and Roche/454 technologies to achieve a wider *de novo* genome sequencing and gene expression analysis under stress (Berkman *et al.* 2012). The advent of NGS techniques has given birth to robust, cost, labor, and time effective genotyping by sequencing (GBS) approaches that are expected to aid the analysis of the structurally complex wheat genome through elimination of ascertainment biases and the need for prior genome sequence information associated with traditional techniques (Elshire *et al.* 2011; Poland *et al.* 2012).

Table 3 Putative quantitative trait loci (QTL) regions identified for drought tolerance related traits in wheat either under stressed conditions only or under both stressed and optimal conditions

Chromosome	Traits associated with the putative QTL	Mapping populations	Reference
2A	Relative water content, awn length, grain weight, coleoptiles length, shoot length, and extrusion length	Core collection	Ahmad <i>et al.</i> (2014)
1B, 4A, 4B, 7A, 7D	Thousand-grain weight	Core collection	Nezhad <i>et al.</i> (2012)
1A, 1D, 2B, 3A, 3B, 4B, 4D, 5B, 6A	Potential quantum efficiency of photosystem (PS) II, chlorophyll content, flag leaf temperature, and grain yield	Recombinant inbred lines (RILs) derived from a cross between cultivars C306 and HUUW206	Kumar <i>et al.</i> (2012)
1D, 2A, 2B, 2D, 3A, 4A, 4B, 5B, 5D, 6D, 7A, 7D	Root diameter, volume, surface area, crossings, forks, and tips	Advanced backcross population derived from a spring wheat cultivar Devon and a synthetic hexaploid accession Syn084	Ibrahim <i>et al.</i> (2012)
1D, 2B, 3A, 3B, 4A, 4B, 5A, 5B, 6A, 6D, 7A, 7B	Grain yield and yield	RILs from a cross between common wheat cultivars Dharwar Dry and Sitta	Alexander <i>et al.</i> (2012)
3BL	Grain yield	Doubled haploid (DH) population from a cross between line RAC875 and variety Kukri	Bennett <i>et al.</i> (2012)
1B, 2B, 3B, 5B, 7B, 7A	Grain weight, grain weight spike ⁻¹ , grain number spike ⁻¹ , spikes m ⁻² , spike weight, spike harvest index, and harvest index	RILs obtained from a cross between genotypes Oste-Gata and Massara-1	Golabadi <i>et al.</i> (2011)
All except 1D and 6A	Grain yield, number of grains per ear and chlorophyll <i>a</i> fluorescence	DH lines derived from genotypes Chinese Spring and SQ1	Czyczyło-Mysza <i>et al.</i> (2011)
All except 2A, 2D, 3D, 5D, 6D, and 7D	Agronomic, phenological and physiological traits	RILs derived from a cross between variety Seri M82 and a fixed line Babax	Pinto <i>et al.</i> (2010)
1A, 3D, 7B	Stay green	RILs derived from a crosses between a stay green cultivar Chirya 3 and a non-stay green synthetic Sonalika	Kumar <i>et al.</i> (2010)
2B, 4A, 5A, 7B	Crop productivity, morpho-physiological and phenological traits	RILs derived from a cross between durum wheat cultivar Langdon and a wild emmer accession G18-16	Peleg <i>et al.</i> (2009)
1B, 1D, 2B, 3A, 4A, 4B, 4D, 5A, 5B, 6A, 6B, 7A, 7B	Yield, anthesis and height	RILs derived from a cross between elite spring bread wheats, Seri M 82 and Babax	Mathews <i>et al.</i> (2008)
6A	Coleoptiles, seedling vigour and plant height	RILs derived from a cross between a Chinese semi-dwarf wheat Chuanmai 18 and a tall breeding line Vigour 18	Spielmeier <i>et al.</i> (2007)

Therefore, NGS technologies, including GBS and some transcriptomic approaches, should be considered because they can contribute to the elucidation of gene expression, variety screening, single nucleotide polymorphism (SNP) marker detection, exposition of QTLs, and the discovery of candidate genes controlling drought tolerance in wheat (Berkman *et al.* 2012; Edwards *et al.* 2013). These technologies generate vast amounts of genomic data in real time. However, this requires investments and expertise in bioinformatics for management of the data. Given reduction in costs of NGS, genes involved in drought tolerance will soon be cloned to generate gene-derived markers and to enable their effective usage in breeding for drought tolerance in wheat.

Rapid genetic gains could be realized through the use of genome engineering technique, as a promising option for improving drought tolerance through gene pyramiding, gene stacking and gene transfer of cloned genes. Genes involved in drought stress tolerance within other species that are cross-incompatible with wheat means that a transgenic approach is the only option available to utilize such genes (Valliyodan and Nguyen 2006). This approach manipulates signaling molecules including transcription factors such as the dehydration-responsive element binding factors (DREB1 and DREB2) that bind to the dehydration-responsive element (DRE); ABA-responsive element binding factor (AREB) that binds to the ABA-responsive element (ABRE); and several protein kinases involved in the expression of several genes under stress (Shinozaki and Yamaguchi-Shinozaki 2007). Important regulatory genes, those encoding proteins involved in the biosynthesis and accumulation of stress related bio-chemicals, and genes involved in post transcriptional modification of ribonucleic acid (RNA) and proteins in response to water stress have been widely reported in the literature (Umezawa *et al.* 2006; Valliyodan and Nguyen 2006; Shinozaki and Yamaguchi-Shinozaki 2007; Ashraf 2010; Yang *et al.* 2010; Deikman *et al.* 2012). Yield benefits should, however, be considered since some drought regulators trigger several genetic responses to drought stress, including some which cause yield reductions (Blum 2010; Rong *et al.* 2014). Despite the existence of numerous potentially useful genes, the technology has not contributed to the release of drought tolerant wheat cultivars. This requires knowledge on the genetic and molecular bases of trans-genes and favorable environments for multi-location field testing of transgenic plants.

3.7. Integration of transcriptomic, proteomic, metabolomic, and phenomic approaches in drought tolerance improvement in wheat

Future progress in breeding for drought tolerance in wheat

could be enhanced by integrating transcriptomic, proteomic, metabolomic and phenomic approaches to further unfold drought-responsive genes and signaling pathways. Lack of a genome sequence, poor genomic resources (Fleury *et al.* 2010), and failure to integrate such approaches may hinder further understanding of the flow of genetic information influencing drought tolerance in wheat. Advances in sequence based gene expression analysis through the use of NGS techniques could shade more light on the regulatory mechanisms and networks of this polygenic trait (Poland *et al.* 2012; Edwards *et al.* 2013). Gene expression analysis and genome-wide transcript profiling under managed stress could increase knowledge on the functions and levels of expression of thousands of drought-responsive genes. To date, several classes of genes have been confirmed to be up- or down-regulated by drought stress to enable dehydration avoidance or tolerance in various plant species including wheat (Hu and Xiong 2014; Langridge and Reynolds 2015).

Proteomic, metabolomic and phenomic approaches can now quantify the levels of expression of the entire set of proteins, metabolites or phenolics under stress. Recent studies combining both transcriptomics and proteomics on wheat, showed genotypic differences in the expression of defence genes, dehydration induced transcripts associated with metabolism of carbohydrate and phyto-hormones, coupled with a rise in bio-chemicals like ABA under stress (Reddy *et al.* 2014; Yin *et al.* 2014). This envisions the application of genome wide association mapping analysis using the vast amounts of data from various OMICs analyses. Consequently, researchers can model drought co-expression networks using all gene nodes co-influencing the same biological process to further characterize the multiple signaling pathways influencing the performance of the crop under drought stress (Yin *et al.* 2014). Additionally, this could improve further understanding of the genetic and morpho-physiological bases of drought tolerance in wheat, enabling identification of putative QTL/gene sequences influencing drought tolerance, and ultimately allowing the realisation of significant genetic gains from selection.

4. Conclusion and future prospects

Recurrent drought associated with climate change limits global wheat production and supply. Achievements made in drought tolerance improvement are minimal, relative to investments and breeding efforts put in by various crop science disciplines working in isolation. Thus, significant progress will be achieved if breeders and other interdisciplinary experts work together with a common goal of timely production of drought tolerant and high yielding wheat cultivars. Recent technologies such as high-throughput phenotyping, NGS and genetic engineering should be uti-

lized for drought tolerance improvement in wheat. It should, also, be noted that drought does not occur independent from other abiotic stresses and is normally associated with heat stress (Jha *et al.* 2014). Therefore, future studies should target improving prevailing stresses concurrently, to achieve improved grain yield and quality of wheat under water limited conditions.

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