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Modern Breeding Strategies for the Identification of Drought Tolerance in Wheat: A Comprehensive Review

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ABSTRACT

The global food supply is under significant threat due to climate change with drought being a major limiting factor in bread wheat production. This review paper is an integrated account of phenotypic and molecular methods for identifying drought tolerance in bread wheat at the importance of a synergistic approach. Traditional phenotypic approaches which use observable traits such as grain yield and physiological indicators are useful for initial screening and field validation but can be time-consuming and subject to environmental factors. In contrast, modern molecular techniques, including Marker-Assisted Selection (MAS), Quantitative Trait Loci (QTL) mapping and functional genomics, provide precise and efficient means for the identification of superior genotypes at the genetic level. By synthesizing findings from recent literature, this review highlights that an integrated approach that combines high-throughput phenotyping with advanced molecular tools is the most effective way to overcome the limitations of single-method screening and advance the development of climate-resilient wheat varieties. Future directions in breeding are likely to make use of pan-genomics and advanced genetic engineering to proactively design crops with greater resilience.

INTRODUCTION

Wheat *(Triticum aestivum* L.) is one of the most popular cereal crops globally and one-third of the world population consumes the wheat grain as primary source of food. It contributes almost one-fifth to food and nutritional security in the world (Sewore et al., 2023; Song et al., 2023), as it serves as a source of dietary calories and protein in almost every part of the world. In addition to its nutritional value, wheat is also important in sustaining livelihoods in the form of providing a substantial contribution to the economy of agricultural use in Asia, Africa and Europe. In 2024-2025, the annual wheat production in Pakistan has declined from 31 million metric tonnes to 28.4 million metric tonnes due to the drought stress caused by climate change (USDA). The most important limiting factor for the production of wheat is drought. It covers about 60 million hectares across the globe (Ihsan et al., 2016). Drought treatments occur when there is depletion of water below what plants need to perform optimally within the plant; this water scarcity deteriorates photosynthesis, cell expansion, and assimilate partitioning (Ahmad et al., 2022). It also interferes with the phenological growth, especially with the sensitive stages that include tillering, anthesis and grain filling stage which are very important in terms of yield components (Golabadi et al., 2010). Terminal drought, which is encountered during reproductive phases, is critically disastrous since it decreases the grain filling period, lowers the grain number, and decreases the kernel weight (Mwadzingeni et al., 2016). At the physiological level, drought stress induces excessive production of reactive oxygen species (ROS), which have deleterious effect of damaging lipids, proteins, and nucleic acids as well as weakening the chloroplast structure and lowering photosynthetic activity in plants (Ahmad et al., 2022). Due to climate change, the severity of droughts is increasing day by day and it requires the development of climate-resilient wheat varieties that perform well under water-limited conditions and give higher yield. Drought tolerance in wheat is a complex, polygenic trait that is environmentally dependent. Many genes, QTL's and molecular pathways help in the survival of wheat under drought stress by developing adaptive mechanisms such as root system architecture and stomatal control (Kirigwi et al., 2007). Due to this complexity, breeders need a multifaceted approach to breed for drought-tolerant genotypes (Anwaar et al., 2020). In order to develop drought-tolerant varieties, breeders first need to understand the traits (leaf rolling, waxiness, cooler canopy, fewer tillers and strong root system) and the genetic mechanisms that give resistance to drought stress. Traditionally, field-based phenotypic screening was a way to identify drought-tolerant wheat genotypes but now an integrated approach has been used to identify the superior genotypes at the early stages, this approach is called Marker-Assisted Selection (MAS). It allows for to identification and comparison of related traits to specific genetic markers (Haque et al., 2020; Pour-Aboughadareh et al., 2020). Introduction of molecular markers like RAPD, SSR, SNP and KASP has revolutionized the aspect of genetic variation in wheat (Gupta et al., 1999; Song et al., 2023). Genetic markers can be utilized to provide insights into the allelic diversity, marker-assisted selection (MAS) as well as yielding the quick identification of QTLs which can be used in breeding for crop improvement of drought-related traits like root-depth level, chlorophyll retention and grain weight. Molecular markers can be utilized across any plant developmental process, hence are effective in overcoming the time-consuming plant breeding process (Gupta et al., 1999). E.g., SSR markers like Xgwm437 (3A) and Xgwm296 (5B) have been seen to be linked with increased yield traits under water stress (Golabadi et al., 2010). In parallel, high density SNP array and GBS-based genotyping methods have provided the opportunity to conduct genome-wide association studies (GWAS), which can identify specific loci that are linked to drought resilience (Song et al., 2023). This review paper aims to give an overview about how modern molecular markers and classical grain yield indices strategies together can accelerate the development of drought tolerant wheat varieties.

Phenotypic Strategies for Screening Drought Tolerance

Morphological and Yield-Related Traits

Traditionally, breeders have focused on the different traits responsible for high yield, such as plant height, productive tillers, canopy temperature and grain yield but the architecture of root-system is an important morphological trait that gives tolerance to drought. In water-limited conditions, wheat plants with deeper root system allows the plant to store water in deep layers and withstand the water stress. Phenotypic traits such as days to heading, days to maturity and grain yield per plant are used to measure the genetic differences among the bread wheat genotypes when they are under drought stress (Belete et al., 2021). Combining the morphological traits and physiological indicators helps to breed for drought-tolerant genotypes with improved efficiencies (Khadka et al., 2020). By Combining morphological traits with yield can be effectively used to screen for drought tolerance in wheat (Semahegn et al., 2020). Combining the traits like tillers per plant, plant height and spike length along with grain yield per plant is an effective approach for screening drought-resistant wheat genotypes (Poudel et al., 2020). Phenological markers such as days to heading and days to maturity have been used to assess how different wheat genotypes show differences for drought resistance among them (El-Esawi et al., 2022). Characterization of Egyptian wheat land races and commercial cultivars revealed that waxy coating on the flag leaf and culm and ear in some landraces is a key adaptive trait during drought stress. These landraces were characterized based on morphological and agronomic features (Gharib et al., 2020). Different wheat genotypes were screened and identified under drought stress as tolerant, moderately tolerant and susceptible (Haque et al., 2020). A Large number of bread wheat genotypes were evaluated under water-limited and well-watered conditions, highlighting the importance of morphological and physiological traits (Sewore et al., 2023). Selection of wheat genotypes for morphological and physiological traits or the yield components under drought stress during the final stages of wheat is of great importance for breeding resistant cultivars (Bapela et al., 2022). Under drought stress, shorter grain-filling duration and higher thousand-grain weight are indicators of high-yielding plants. Whereas, days to heading and days to maturity are negatively associated with the yield (Yashavanthakumar et al., 2021). In durum wheat, drought-susceptible cultivars showed a reduction in plant height, grain yield and spike length, whereas drought-tolerant cultivars were high yielding and gave a high harvest index. It shows how drought impacts morpho-physiological and agronomic traits in plants (Pour-Aboughadareh et al., 2020). 14 bread wheat genotypes were screened using different yield-attributes such as productive tillers, 1000-grain weight, biological yield etc. These traits were considered important in the phenotypic evaluation of drought-resistant cultivars (Wasaya et al., 2021). Genetic pattern of important phenological traits that were easily observable, under drought stress further helped to screen for drought tolerance in wheat (Ishaaq et al., 2022).

Phenotypic selection fundamentally relies on output components like Grain Yield (GY), Thousand-Grain Weight (TGW), and Biological Yield (BY), all of which are severely reduced by terminal drought (Anwaar et al., 2020; Pour-Aboughadareh et al., 2020). To standardize comparative assessment between non-stress (Yp) and drought stress (Ys) environments, breeders utilize various Drought Tolerance Indices (DTIs) (Yadav & Bhatnagar, 2001). The Stress Tolerance Index (STI) is particularly effective as a selection metric, identifying genotypes superior under both environmental conditions (Fernandez, 1993; Sio-Se Mardeh et al., 2006). Complementarily, the Stress Susceptibility Index (SSI) helps identify genotypes that minimize yield loss relative to their non-stress potential, classifying those with values less than one as tolerant (Anwaar et al., 2020; Fischer & Maurer, 1978). Studies consistently confirm that STI, Geometric Mean Productivity (GMP), and Mean Productivity (MP) are reliable selection metrics showing strong positive correlations with yield in both environments (Ahmed et al., 2020; Anwaar et al., 2020). For example, highly tolerant lines (e.g., GA-02 and Faisalabad-83) were shown to have favorable DTI scores and low grain yield loss, in contrast to sensitive lines like Chenab-00, which showed up to 31.7%

reduction in GY (Anwaar et al., 2020). These key selection criteria are summarized below (Table 1)

Table 1

Key Drought Tolerance Indices for Wheat Screening

Index	Abbreviation	Calculation basis	Primary Selection Goal	Reference
Stress Tolerance Index	STI	$(Yp \times Ys)/MYP^2$	Superior yield across both stress and non-stress environments	(Fernandez, 1993)
Stress Susceptibility Index	SSI	$(1 - Ys/Yp)/SI$	Minimize yield reduction in stress environment ($SSI < 1$ indicates tolerance)	(Fischer & Maurer, 1978)
Geometric Mean Productivity	GMP	$\sqrt{(Yp \times Ys)}$	High-yielding stability across variable environments	(Anwaar et al., 2020)
Mean Productivity	MP	$(Yp + Ys)/2$	High average performance across tested conditions	(Ahmed et al., 2020)

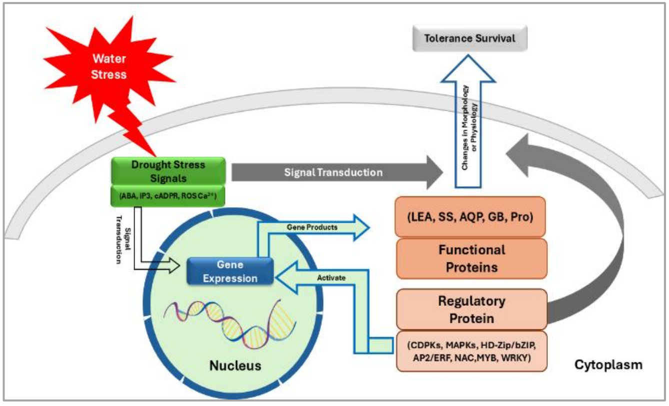
Furthermore, advanced statistical methods like Principal Component Analysis (PCA) are often integrated to effectively classify and cluster superior genotypes for tolerance, capturing up to 79.02% of the total phenotypic variation under drought stress (Ahmed et al., 2020; Pantha et al., 2025; Semahegn et al., 2020). In addition to yield, key morphological traits such as Days to Heading (DTH) and Days to Maturity (DTM) are crucial for drought escape, often exhibiting a negative correlation with yield under stress (Ishaaq et al., 2022; Poudel et al., 2020; Yashavanthakumar et al., 2021). Other critical physical traits include glaucousness (a protective waxy coating) observed in adaptive landraces (Gharib et al., 2020), and the depth and extent of the root system architecture, an essential mechanism for dehydration avoidance (Bapela et al., 2022; Yao et al., 2025).

Physiological and Biochemical Indicators

Physiological and biochemical traits provide the cellular and functional rationale behind the observed yield differences (Ahmed et al., 2020). A key adaptive mechanism is the accumulation of osmo-protectants: drought-tolerant plants exhibit significantly elevated levels of proline (increased by 159%) and total soluble sugars (increased by 122%) in moisture-deficient environments, acting to stabilize cellular structure and maintain turgor (Ahmed et al., 2020; Kavi Kishor & Sreenivasulu, 2014). This response is genetically regulated, demonstrated by the finding that overexpressing the DREB transcription factor *TaDREB3-AI* enhances tolerance by significantly increasing proline concentration and reducing cellular damage (Niu et al., 2020). Cellular integrity is assessed via the Leaf Membrane Stability Index (LMSI) (Ahmed et al., 2020; Chowdhury et al., 2021) and the management of reactive oxygen species (ROS) homeostasis through enhanced antioxidant enzyme activities (e.g., SOD, CAT, POD) (Bhanbhro et al., 2024; Niu et al., 2020). Stomatal Conductance (gsw) is another highly heritable trait that strongly predicts yield under stress (Aminian et al., 2010; Pantha et al., 2025).

Figure 1

Response mechanism of wheat to Drought stress



Screening for this trait allows for the classification of adaptive strategies: isohydric (water-saving) genotypes rapidly reduce gsw (up to 74% reduction in *T. urartu*) to conserve water, a survival strategy (Martínez-Vilalta & Garcia-Forner, 2017; Pantha et al., 2025), while anisohydric (risk-taking) genotypes maintain stomatal openness longer to maximize carbon fixation. Furthermore, a critical advancement is the physiological and genetic recognition of the Tolerance vs. Recovery Dichotomy, which reveals that Drought Tolerance (TT) (endurance) and Drought Recovery (RT) (regrowth potential) are phenotypically uncorrelated and controlled by distinct genetic mechanisms, requiring separate screening strategies (Sallam et al., 2022). These key adaptive traits define genotypic resilience.

Table 2

Key Phenotypic and Physiological Adaptive Trait Mechanisms

Trait Type	Key Trait	Measurement /Response	Adaptive Strategy	References
Osmotic/ Biochemical	Proline / Soluble Sugars	Accumulate significantly (up to 159%) under stress	Osmotic Adjustment	(Ahmed et al., 2020)
Cellular Integrity	LMSI, MDA, Antioxidants	LMSI maintained; MDA/ROS reduced by SOD/CAT	Cellular Defense / Membrane Stability	(Bhanbhro et al., 2024)
Water Use	Stomatal Conductance (gsw)	Differential reduction (e.g., 74% in *T. urartu*)	Water Conservation (Isohydric/Anisohydric)	(Pantha et al., 2025)
Resilience Capacity	Recovery Traits (RT)	Regrowth biomass/survival rate after re-watering	Long-term survival	(Sallam et al., 2022)

Drought Tolerance Indices

Various mathematical indices are used for the selection of genotypes under stress and non-stress conditions. Among other indices, the Stress Tolerance Index (STI) is a very common indices used to analyze the performance of wheat genotypes under normal conditions as well as under stress conditions (Anwaar et al., 2020; Sio-Se Mardeh et al., 2006). These indices offer a quantitative basis for the selection of those genotypes that perform well under water-limited conditions. For the calculation, it requires the grain yield of plants under a set of regular and normal growing conditions (Yp) and under stress conditions (Ys) (Rosielle & Hamblin, 1981).

Stress Susceptibility Index (ISS) is another indices used for the assessment of those genotypes that are under drought stress and still perform better to give normal yield as compared to the non-stress conditions (Anwaar et al., 2020). Drought Tolerance Efficiency and Drought Susceptibility Index were used to select and categorize genotypes, whereas stress susceptibility index was used to identify drought-tolerant genotypes of durum wheat. some other indices such as Mean Productivity(MP) and GMP, give a better indication of tolerant genotypes (Haque et al., 2020; Pour-Aboughadareh et al., 2020). These methods have been applied to irrigation systems as well to identify drought resistance (Mansour et al., 2020). Wheat genotypes were evaluated using phonological, growth and physiological indices combined, and along with the Principal Component Analysis (PCA) to evaluate and select superior genotypes (Chowdhury et al., 2021; Semahegn et al., 2020). In drought stress conditions and irrigated conditions, stable and high-yielding genotypes were identified by observing the morphological traits of plants along with yield-related traits (Poudel et al., 2020).

Molecular Strategies for Screening Drought Tolerance

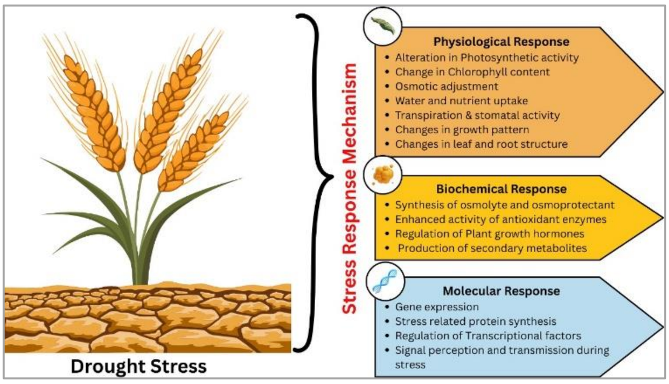
Marker-Assisted Selection (MAS)

In early ages, traditional field-based screening was done to select for desirable traits in plants but this approach has been replaced by more efficient and an early methods to identify superior genotypes, which is called Marker Assisted Selection. It is a very valuable tool used by current plant breeders that allows them to select for desirable traits indirectly. Breeders select these traits on the basis of the presence of genetic markers associated with those traits. There are different gel-based markers used for selecting superior traits, such as Random Amplified Polymorphic DNA (RAPD), Inter Simple Sequence Repeats (ISSR) and high-throughput markers. ISSR markers were used to identify the differences among the bread-wheat genotypes for drought tolerance traits, and population structure of the genotypes was also determined (Belete et al., 2021). In durum wheat, some microsatellite markers were found to be linked with yield components (Golabadi et al., 2010). Greater differences among the wheat genotypes for drought tolerance were observed by using 13 short sequence repeats (SSR). These markers helped to identify drought-tolerant genotypes and drought-sensitive genotypes. It was found to be an efficient integrated approach to use such markers that were associated with those morphological traits controlling drought stress (Haque et al., 2020). Sequence tagged site (STA), Genotype by sequencing (GBS), Single nucleotide polymorphism (SNP) arrays, competitive Allele Specific PCR (KASP) and Simple sequence repeats (SSR) were highlighted in a summarized overview of molecular markers (Song et al., 2023). Wheat genotypes under drought stress were analyzed using RAPD and ISSR markers to see the genetic differences present in the wheat genotypes for drought tolerance and the markers that were linked with those morphological and physiological traits that controlled the grain-yield of plant to give stable yield under stress. For the selection of superior genotypes at the molecular level, Single Marker Analysis was carried out to find markers linked with grains per spike and grain-yield per plant, contributing to resistance against drought stress. (Khaled et al., 2015). Six Egyptian wheat genotypes were analyzed and differentiated under water-limited conditions and normal irrigated conditions. RAPD markers helped to identify those genotypes that were drought-tolerant and drought-susceptible based on their performance under both conditions (Mansour et al., 2020).

In a marker-assisted breeding program, Random Amplified Polymorphic DNA (RAPD) primers were used and seven markers were found that were linked with drought tolerance. By using these primers and markers, genotypes that can withstand water deficit, and genotypes that are unable to stand the drought stress could be differentiated from each other in a marker-assisted breeding program (Ameen & M, 2013). RAPD and ISSR markers are cost-effective methods used in breeding programs. These markers were used to analyze bread-wheat genotypes for genetic variation. RAPD and ISSR markers are helpful toward improving the yield of plants and their compatibility to give stable performance under stress conditions (Nazarzadeh et al., 2020). These markers are valuable to differentiate wheat genotypes according to their genetic makeup and to assess genetic diversity and polygenic association among wheat genotypes (El-Esawi et al., 2022). Useful SNPs linked with TaSnRK2.4 and TaSnRK2.9 genes were found after developing and validating assays. These genes are known to play a role against abiotic stress faced by plants. In Pakistani wheat germplasm, these markers were unable to identify genetic diversity for the TaSnRK2.4 gene, whereas TaSnRK2.9 was found to be highly polymorphic. Due to high polymorphism in TaSnRK2.9, it could be used as a marker for selection of the desired trait (Rauf et al., 2024).

Figure 2

Morpho physio and molecular responses to drought stress in wheat



Quantitative Trait LocI (QTL) Mapping

Drought is a quantitative trait which is controlled by many genes. Each gene has its own effect on the nature of drought-tolerance in plants. Drought tolerance is a complex trait and genes controlling this trait are present in specific regions in the genome, these regions are called Quantitative Trait Loci. These genomic regions provide insights into where these genes are present and how they control drought tolerance traits in wheat so identifying and mapping these genomic regions is very important for the selection of superior genotypes. A QTL on chromosome 4AL was identified that was responsible for controlling grain-yield and this QTL was also linked with grain filling rate and spike density, contributing to the yield of the plant (Kirigwi et al., 2007). In durum wheat, microsatellite markers were found linked with those genomic regions that control yield components. These QTLs were directly linked to control the traits such as 1000 grain weight and grain-weight per spike under drought stress conditions during late growth stages of durum wheat (Golabadi et al., 2010).

In bread wheat under drought stress conditions, notable markers were identified linked to some agronomic and physiological traits of plants. Genome-Wide Association Studies (GWAS) technique is used to identify these markers that are associated with yield components such as grain-yield and thousand-grain-weight. Some markers found controlling canopy temperature and normalized difference vegetation index (NDVI), whereas numerous QTLs linked to water- stress responsive traits such architecture of root, grain yield and photosynthetic efficiency also found (Bhanbhro et al., 2024; Shokat et al., 2020). For effective Marker Assisted Selection, High-throughput genotyping technologies provide a good approach to locate these genomic regions. By combining QTL mapping and GWAS, we can identify genetic markers that are linked with tolerance traits and recovery traits, such as leaf-wilting score and greenness after re-watering. This combined strategy helps to monitor plants' response to drought stress at the seedling stage and to identify candidate genes responsible for drought stress resistance (Sallam et al., 2022).

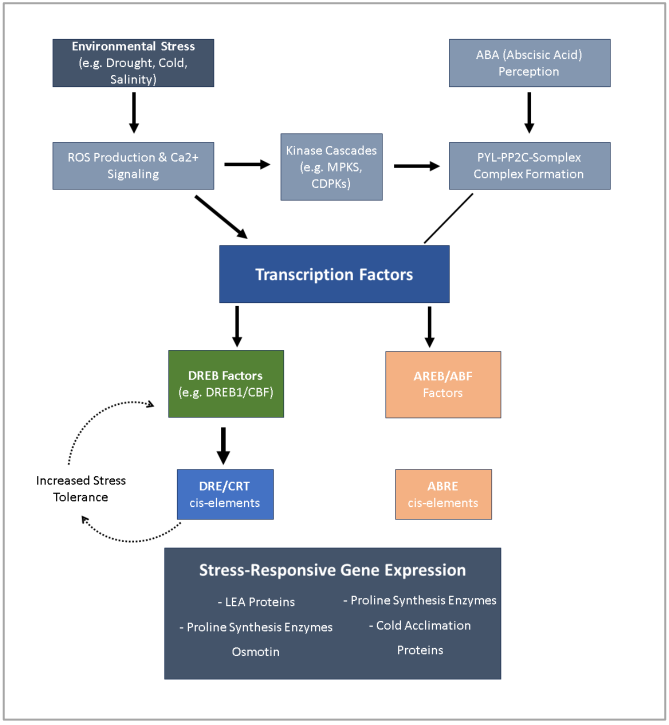
A genotyping array of 90K SNPs was used in Genome-wide association studies, which resulted in the identification of 53 notable SNP markers. These markers were linked with those traits that control the drought stress response of the plant. Furthermore, these markers are associated with stress susceptibility indices and stress-tolerance indices and on chromosomes 2A and 3B, 44 genes were found that could be used by breeders to develop genotypes with desired traits (Nouraei et al., 2024). In wheat, 290 lines were analyzed with Genome-Wide Association Studies, in which 15,000 SNPs were used. These lines show 205 associations between markers and phenotypic traits of plants that were linked with providing resistance to drought stress conditions (Abou-Elwafa & Shehzad, 2020). Although many such QTLs have been successfully located but there is still a constraint in using them for a Marker-assisted breeding program for complex traits (Bapela et al., 2022). Moreover, Meta-QTL analysis was conducted to identify 13 effective MQTLs. These QTLs were present on chromosome 1D, 5A, 3B, 7A, 6D and 7D. Meta-QTL analysis allows to locate exactly those markers that are linked with drought resistance in wheat (Kumar et al., 2020). Meta-QTL analysis is a more comprehensive approach to map genetic markers for tolerance. It was carried out in durum wheat and 85 meta-QTLs were found. These markers are specifically related to tolerance to abiotic stress in durum wheat (Soriano et al., 2021)

Functional Genomics and Gene Regulation

Functional genomics investigates the precise biological roles of genes and their products. Drought resistance involves global reprogramming orchestrated by Transcription Factors (TFs) and hormone signaling (Bhanbhro et al., 2024). The DREB Family, with over 200 TaDREB genes in wheat, is a central regulator, where isoforms of *TaDREB3* are subject to alternative splicing, generating different functional transcripts as a rapid response mechanism to stress(Egawa et al., 2006; Niu et al., 2020). Functional validation confirms that gain-of-function TaDREB3-AI alleles enhance multi-stress tolerance by promoting antioxidant activity and osmolyte accumulation (Niu et al., 2020).

Figure 3

Central Role of DREB Factors and ABA in the Plant Stress Signaling Cascade



Similarly, NAC and MYB TFs like *TaNAC69-1* and *TaRNAC1* regulate essential root architecture phenotypes, enhancing root length and biomass to promote drought avoidance (Chen et al., 2016, 2017; Yao et al., 2025). This regulatory network is tightly controlled by Abscisic Acid (ABA), the central hormone that governs stomatal aperture and coordinates osmotic defenses via genes such as *TaCIPK23* and *TaFBA1* (An et al., 2019; Bhanbhro et al., 2024; Cui et al., 2018). The general utility of advanced molecular breeding tools, such as GWAS and high-density SSR/SNP marker development for complex traits like disease and stress resistance across different crops (e.g., in peanut breeding programs), further validates this powerful strategy (Asadi et al., 2025). The future ultimate goal is to connect these detailed functional analyses with large-scale genomic variation through pan-omics, which integrates all available data (genomics, proteomics, metabolomics) to build comprehensive knowledge networks for target identification (Yao et al., 2025).

Table 3

Comparison of Molecular Strategies for Drought Tolerance Identification

Strategy	Methodology	Key output/Precision	Role in Breeding	Reference
Marker-Assisted Selection (MAS)	SSR, RAPD, ISSR, KASP (SNP)	Differentiation of genetic diversity; cost-effective selection	Early-stage screening; marker validation	(Khaled et al., 2015)
QTL Mapping / GWAS	Linkage maps; Association panels (SNP arrays)	Identification of Marker-Trait Associations (MTAs); Fine-mapping	Identifying genomic regions of interest	(Sallam et al., 2022)
Meta-QTL (MQTL)	In silico data synthesis across studies	Highly stable and precise genomic locations (MQTLs)	Refined marker development	(Kumar et al., 2020)
Functional Genomics	Gene expression, ABA signaling, DREB analysis	Causal genes (TaDREB3-AI); Molecular mechanism validation	Gene editing targets; Mechanistic understanding	(Niu et al., 2020)

Genetic Engineering and Epigenetics

In previous eras, simple marker-assisted selection was used to identify tolerant and superior genotypes, but now molecular biology has advanced to provide more powerful tools for breeding programs, such as genetic engineering. Genetic engineering is a powerful technique to alter the genome of a plant by modifying specific genes for desired traits such as drought tolerance. As drought tolerance is a complex trait controlled by many genes, each contributing a small effect, genetic engineering allows researchers to combine these different genes into a single genotype through gene pyramiding to provide stronger resistance as a combined effect (Adel & Carels, 2023). For instance, genes identified through functional genomics, like the *TaDREB3-AI* transcription factor, which positively regulates multi-stress tolerance (Niu et al., 2020), become prime candidates for direct manipulation or for introduction into new germplasm using precision tools like CRISPR-Cas9 (Yao et al., 2025). Epigenetics is another promising approach to develop resilient crop varieties by altering the expression pattern of genes without changing the underlying DNA sequence. This is achieved by influencing the epigenome, such as DNA methylation or histone modifications. Another strategy for introducing a desirable phenotype without traditional sexual reproduction is apomixis. Researchers can induce a favorable epigenetic profile in genotypes by combining synthetic apomixes and MSH-1 mutation to develop resistant crop varieties, offering a way to fix a desirable trait configuration (Adel & Carels, 2023). This focus represents a significant shift towards the deliberate and accelerated design of superior wheat cultivars.

The Integrated Approach: Bridging Phenotype and Genotype

The Need for Integrated Selection Strategies

The loss of genetic diversity in elite lines, compounded by extreme G×E interactions, necessitates strategies that leverage the genetic potential of wild relatives while ensuring marker utility across environments (Bapela et al., 2022; Pantha et al., 2025). The integrated approach is the only way to resolve the critical issue of Tolerance being genetically independent of Recovery. To address this, breeding programs must move beyond single-trait selection by employing integrated indices (Sallam et al., 2022). This includes the Drought Tolerance Index (DTI), a composite score combining the genetically distinct Tolerance Index (TI) (measuring endurance) and Recovery Index (RI) (measuring regrowth potential) into a single, comprehensive score (Sallam et al., 2022). Furthermore, prioritizing phenotypic traits based on Genotypic Correlation (r_g) ensures that breeding efforts are focused on highly heritable traits, providing reliable genetic gain (Ahmed et al., 2020). For example, 61 trait pairs demonstrated a stronger r_g compared to their phenotypic correlation (r_p) in one study, highlighting the need to prioritize intrinsic genetic control(Ahmed et al., 2020). The success of this methodology relies on the high correlation between molecular markers and field-relevant PBTs, such as the relationship established between GWAS markers and physiological indicators like CT and NDVI (Shokat et al., 2020). The independent genetic control of TT and RT is summarized in Table 4.

Table 4

Genetic Evidence Supporting the Independence of Drought Tolerance and Recovery Traits

Trait Group	Phenotypic Focus	Genetic Correlation	Key Genetic Finding	Reference
Tolerance TT	Endurance (Days to Wilting, Leaf Wilting Score)	None/Weak ($r \approx 0.0$)	Controlled by genomic regions distinct from RT QTLs.	(Sallam et al., 2022)
Recovery RT	Regrowth (Days to Regrowth, Regrowth Biomass)	None/Weak ($r \approx 0.0$)	Controlled by genomic regions distinct from TT QTLs.	(Sallam et al., 2022)
Integrated Index	Drought Tolerance Index (DTI)	Strong (DTI vs. TI, RI: $r > 0.60$)	Links genetically independent pathways for comprehensive selection.	(Sallam et al., 2022)

Combining Strategies for Enhanced Selection

Development of drought-tolerant varieties could be accelerated if we are able to accurately link a physical trait of plant with its genotype, that how genes control physical response of plant to stress. This challenge is addressed effectively by combining genotyping techniques with high-throughput phenotyping and by combining conventional methods of breeding with molecular approaches (Bapela et al., 2022). Accurate identification of those QTLs that are linked with drought tolerance traits is conceivable by combining Genome-Wide Association Studies along with QTL mapping (Sallam et al., 2022). Combining these two allows for finding new marker-trait associations that might not be found by following the single approach. Furthermore, this combined approach strengthens the findings from other studies. For example, a set of 290 wheat lines along with 15,000 SNP markers was used in a GWAS study which resulted in the identification of 205 marker-trait association. Molecular makers were found directly linked with phenotypic traits responsible for drought tolerance in wheat under drought stress, through this combined approach (Abou-Elwafa & Shehzad, 2020). Meta-QTL analysis is another powerful approach to locate robust markers for desirable traits by collecting data from different studies. Following this approach, molecular markers were found to be linked precisely with canopy temperature and normalized vegetation index (NDVI). These physiological indicators are easily measured through high-throughput phenotyping techniques (Shokat et al., 2020). In durum wheat, 85 MQTLs were located for abiotic stress tolerance through Meta-QTL analysis. Similarly, 13 MQTLs were identified on six chromosomes following the same approach. Selection for drought-tolerant genotypes can be accelerated by connecting the two: the phenotype of the plant and its genotype, to improve the selection by breeders following molecular techniques (Kumar et al., 2020; Soriano et al., 2021).

Synthesis of Key Findings

This reviewed literature emphasizes the advancement from a single approach to combined approaches to accelerate the development of drought-tolerant cultivars of bread wheat. The main finding from this review aim to reveal that:

Identification of drought-tolerant genotypes through phenotype analysis is still a primary approach followed by breeders. Assessment of key drought-responsive traits such as grain-yield, root-system architecture and physiological indicators, is very important to screen for resistant genotypes of wheat.

Selection for tolerant cultivars using molecular approaches is a refined method of selection at early growth stages of plants following Marker-Assisted Selection and QTL- mapping. These techniques help to identify and validate genes responsible for drought resistance in superior genotypes of wheat.

Instead of following a single approach, a combined strategy is a much better method followed by breeders for efficient selection. Combining GWAS and meta-QTL analysis allows for accurate linking of a plant's phenotype to its genotype.

Modern methods of breeding for the development of tolerant wheat varieties are moving toward the use of functional genomic, pan-genomics and gene editing tools.

High-throughput screening can be used to overcome the challenges faced by breeders such as genotype-by-environment interaction and the occurrence of more than one stress at a time, such as heat and drought stress.

Challenges and Future Perspectives

Major Challenges

The complex nature of the drought tolerance trait is a major challenge for plant breeders. Another hurdle for breeders while developing resistant cultivars is genotype-by-environment (G x E) interactions. One genotype performing well in one location may not perform the same in another location due to the impact of the environment, making it difficult for breeders to select well-adapted cultivars (Bapela et al., 2022). Another challenge for breeders is that they cannot screen large populations for some key drought-responsive traits, such as root architecture, as it is a destructive method of screening. Wheat under the combined stress of drought and heat has resulted in severe yield loss of 55.9% as compared to wheat under drought stress only, which led to a yield loss of 41.11% (Yashavanthakumar et al., 2021). A thorough assessment for enhancing drought and heat tolerance together in wheat is required as many approaches used before were partly successful (Langridge & Reynolds, 2021).

Future Directions

Future research in drought tolerance should focus on a more holistic approach that combines phenotyping with advanced molecular techniques. Initiation of high-throughput phenotyping platforms is very important for rapid measurement of many traits. Integrating high-throughput phenotyping techniques with genomic sequencing and bioinformatics will be a holistic approach to locate novel genes and QTLs. Furthermore, genomic selection has been identified as a reliable method to be used in the future, as it allows for the precise selection of complex traits such as drought tolerance. Genomic selection allows to determine breeding value of individuals by using genome-wide molecular markers (Bapela et al., 2022).

In addition to these, the use of proteomics and RNA sequencing approaches will help to get a better understanding of regulatory networks that regulate the response to drought stress conditions (Bhanbhro et al., 2024). For advancement in breeding drought-resistant cultivars, pan-omics and advanced biotechnology could be exploited to identify those genes and alleles that are no longer found due to domestication. Diverse germplasm of wheat could be analyzed for greater genetic variation present in wheat following Pan-genomics (Yao et al., 2025). Additionally, gene editing tools such as CRISPR-Cas9 provide exact identification of those genes that confer resistance to stresses in wheat cultivars(Adel & Carels, 2023; Trono & Pecchioni, 2022).

Automated high-throughput systems accelerate the process of identification of drought and heat-tolerant wheat genotypes, with stable yield performance and adaptability across different environments. This system further enables to identification of physiological traits linked with heat and drought tolerance in wheat (Correia et al., 2022; Langridge & Reynolds, 2021).

CONCLUSION

Integrated approaches are required to develop drought-tolerant wheat varieties to overcome the challenges encountered by breeders. Breeders can develop tolerant cultivars by combining phenotyping tools along with molecular tools for efficient and precise selection. Combining QTL mapping and GWAS studies allows for the identification of validated marker-trait associations. High-throughput phenotyping tools along with molecular tools, such as Marker-Assisted Selection, provide a reliable way to develop climate-resilient wheat cultivars. Use of pan-genomics and advanced genetic engineering in future breeding programs will be a comprehensive approach to accelerate the development of stable wheat cultivars to ensure food security in changing climate eras.

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