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Molecular and Eco-Physiological Responses of Wheat (Triticum aestivum L.) to Drought Stress: Implications for Climate-Resilient Crop Improvement

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Abstract

Drought stress is the most severe and widespread abiotic constraint limiting global wheat (Triticum aestivum L.) production, already causing ~10% yield losses worldwide and projected to intensify under climate change, with every additional 1°C of warming potentially reducing staple calorie production by 4.4%. This review provides a comprehensive synthesis of the molecular and eco-physiological responses of bread wheat to water deficit across multiple scales and developmental stages. It covers morphological adaptations (deeper root system architecture, leaf rolling, reduced leaf area, stay-green phenotype), physiological mechanisms (stomatal regulation via ABA, osmotic adjustment through proline, soluble sugars and K^+, maintenance of relative water content and membrane stability), and biochemical defenses (antioxidant enzyme systems including SOD, CAT, APX, and non-enzymatic scavengers to mitigate ROS damage).

At the molecular level, the review details ABA signaling pathways (PYL-PP2C-SnRK2 core module), key transcription factor families (DREB/ERF, MYB, NAC, WRKY), protective proteins (LEA/dehydrins), and emerging roles of autophagy. Technological advances in field-based high-throughput phenotyping (RGB, thermal, hyperspectral, LiDAR), genomic selection, marker-assisted selection, speed breeding, and CRISPR-Cas9 genome editing are highlighted as powerful tools for dissecting and stacking drought-resilience traits. International efforts by CIMMYT and ICARDA, together with national releases in South Asia (e.g., DBW 187, HD 3271, HI 1634), demonstrate successful translation into farmer-adapted, climate-resilient varieties. The paper concludes with strategic directions toward a “drought-resilient ideotype” integrating deep roots, efficient water-use, robust antioxidant capacity, and multi-omics-assisted breeding for sustainable wheat production under future climate scenarios.

Keywords: Drought Stress, Triticum Aestivum, Climate-Resilient Wheat, ABA Signaling, Osmotic Adjustment, Antioxidant Defense, Root System Architecture, Stay-Green, High-Throughput Phenotyping, Genomic Selection, CRISPR-Cas9, CIMMYT/ICARDA, LEA Proteins, Water-Use Efficiency

1. Introduction

The global food security framework is currently navigating a period of unprecedented volatility, primarily driven by the increasing frequency and intensity of abiotic stressors (Borah et al., 2024).

Among these, drought remains the most pervasive threat to the production of *Triticum aestivum* L., the hexaploid bread wheat that serves as a dietary cornerstone for approximately one-fifth of the human population (Singh et al., 2025). Recent climate data underscores the gravity of this situation; the mean annual air temperature has risen by 0.9°C in the 21st century, while annual rainfall in regions such as Africa has decreased by over 16 mm (Taheri Hosseinkhani, 2025). Such shifts have already exerted a measurable drag on productivity, with global wheat yields estimated to be 10% lower today than they would have been in the absence of anthropogenic climate change (Dwyer, 2025). Projections for a high-emissions future are even more stark, suggesting that every additional degree of global warming could drag down the world's ability to produce staple calories by 4.4%, a scenario equated to the global population effectively "giving up breakfast" (Garthwaite, 2025).

The vulnerability of wheat to water limitation is a multi-scale phenomenon, encompassing anatomical, physiological, and molecular dimensions (Lu et al., 2025). As climate change continues to fuel erratic weather patterns and the depletion of vital groundwater resources which currently support 37% of wheat production in the world's top 20 producing nations the development of climate-resilient cultivars has become a critical priority for sustainable agriculture (Zhou et al., 2025). This report provides an exhaustive analysis of the mechanisms governing the response of *Triticum aestivum* to drought stress, synthesizing recent advances in eco-physiology, molecular biology, and high-throughput phenomics to outline a roadmap for future crop improvement (Liang et al., 2025). As show in figure 1 multi-scale responses of wheat (Triticum aestivum L.) to drought stress including morphological, physiological, biochemical and molecular mechanisms that collectively contribute to drought tolerance and yield stability.

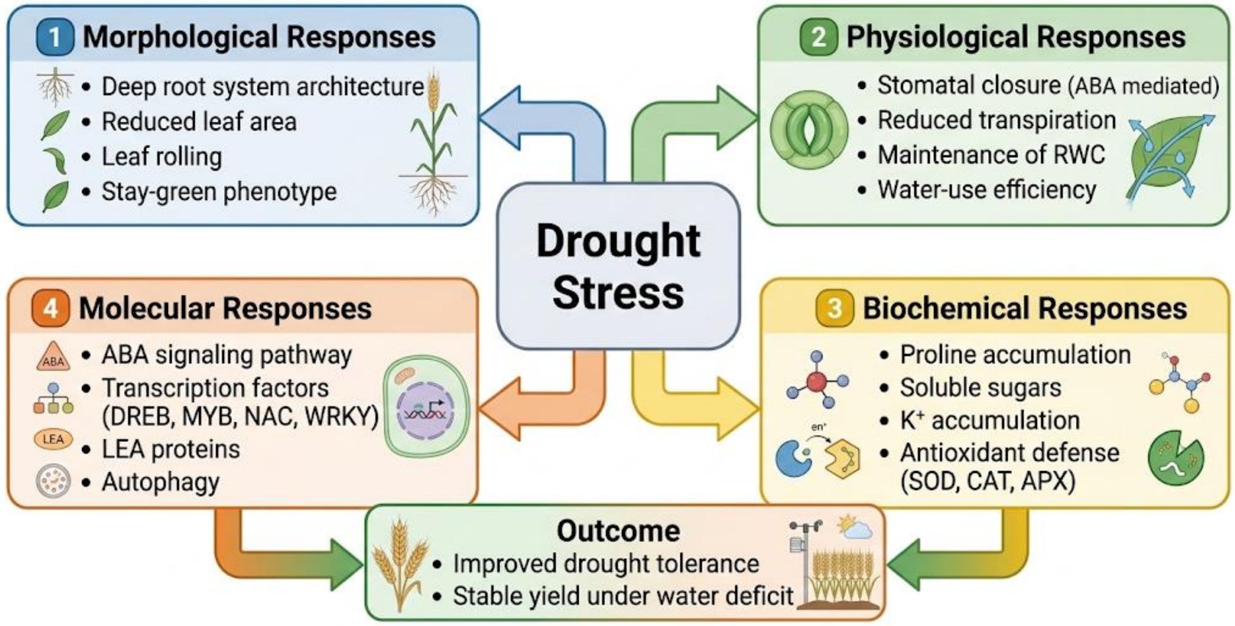


Figure 1: Multi-Scale Response of Wheat to Drought Stress

2. The Global Socioeconomic and Environmental Context of Wheat Production

The importance of wheat in global food security is reflected in the massive investments made into its genetic and physiological characterization. However, the rate of yield increase has slowed significantly since the 1980s, except in major producers like China, India, and Pakistan (Monneveux et al., 2012). This stagnation is particularly concerning given that global demand is expected to rise alongside population growth. Drought, or moisture stress, remains the primary driver of long-term productivity losses, particularly in the drylands of Sub-Saharan Africa and the Middle East, where yields frequently fall below 1 t ha-1 (Khan et al., 2025).

Climate change impacts are not limited to average yields; they also increase interannual variability, which drives price volatility in global markets and threatens the insurability of crops. In modern breadbaskets, yield losses are projected to be as high as 41% by 2100 under high-emission scenarios (Martin et al., 2025). Furthermore, the "CO2 fertilization effect," once thought to be a potential buffer, is increasingly being offset by the negative impacts of heat and drought (Moody's, 2024). High vapour pressure deficit the difference between the air's moisture content and its saturation point is now recognized as a key driver of plant water stress, often exerting a more significant impact than temperature alone by accelerating transpiration and reducing CO2 assimilation (Grossiord et al., 2020).

Table 1: Impact of Environmental Factors on Global Wheat Productivity

Environmental Factor	**Magnitude of Observed or Projected Change**	**Impact on Wheat Productivity**	**Reference**
Global Warming	+0.9°C to +4.0°C	Yield reduction of 4.4% per degree	(Mwadzingeni et al., 2016; Garthwaite, 2025; OECD, 2025)
Rainfall (Africa)	-16.09 mm per annum	Increased frequency of long-term drought	(Mwadzingeni et al., 2016)
Drought Frequency	Doubled since 1900	Strained power supply, river trade, and food security	(OECD, 2025)
Ground Water	Continuous depletion	37% of production in major countries at risk	(Khan et al., 2025; Zhou et al., 2025)
Yield Potential	Stabilized/Stagnated in many regions	Necessity for 1% annual genetic gain to meet demand	(Singh et al., 2021; Mondal et al., 2021)

3. Morphological Adaptations and Developmental Vulnerabilities

Triticum aestivum exhibits a diverse array of morphological responses to water scarcity, which vary depending on the genotype, the severity of the stress, and the specific developmental stage during which moisture limitation occurs (Alshaharni et al., 2025). These responses generally fall into three categories: drought escape, drought avoidance, and drought tolerance (Ilyas et al., 2021).

3.1 Germination and Early Seedling Establishment

The earliest stages of the wheat life cycle are highly susceptible to moisture deficits. Drought stress at the seedling stage disrupts the process of cell division and elongation, which are essential for healthy germination (Oguz et al., 2022). Water is necessary to stimulate the enzymes that initiate growth and facilitate the breakdown of stored nutrients for the developing embryo. Early-season drought can inhibit parameters such as root length, germination percentage, and the seedling vigor index (Nyaupane et al., 2024).

One critical trait for successful establishment in arid environments is coleoptile length. The coleoptile is a protective sheath that covers the emerging shoot; genotypes with longer coleoptiles can emerge from greater soil depths, allowing farmers to sow seeds deeper where moisture levels are more stable (Rijal et al., 2021). However, shorter coleoptiles under stressed conditions often lead to poor plant establishment. Research also suggests that seed characteristics, such as color and size, play a role; smaller seeds often facilitate faster water absorption due to their thinner outer layers and larger relative surface area (Upretee et al., 2024).

3.2 Vegetative Growth and Tillering Dynamics

As the wheat plant enters the vegetative phase, drought leads to a reduction in plant height and peduncle length, primarily due to the loss of turgor pressure and the resulting dehydration of the protoplasm. Reported an average reduction in plant height of 5.78%, while other studies have observed reductions as high as 34.45% under severe stress (Naeem et al., 2015).

Tillering is particularly sensitive to water availability. Drought at this stage increases tiller mortality, leading to fewer productive spikes per plant (Duvnjak et al., 2023). While selecting for high tiller numbers can be advantageous for early-season vigor, it may become a disadvantage under terminal drought conditions, as excessive tillering can lead to high water consumption early in the season, depleting the soil moisture required for the critical grain-filling phase (Sadhukhan et al., 2024). Semi-dwarf genotypes, which prioritize the allocation of resources to grain rather than structural biomass, typically exhibit a higher Harvest Index (HI) and are more resilient to the yield penalties associated with lodging (Monneveux et al., 2012).

3.3 Root System Architecture as a Selection Criterion

The root system is the plant's primary interface for water acquisition, and its architecture is a major determinant of drought avoidance. Under water-limited conditions, wheat genotypes often exhibit a strategic increase in the root-to-shoot ratio (Asadullah et al., 2024). This adaptation involves the deep spread of roots into the soil to access moisture in the lower profiles. Key traits identified for deep-rooted cultivars include a steeper root growth angle and increased root hair density (Carpentieri-Pipolo, 2025).

However, the expansion of the root system is metabolically expensive. Selecting for reduced root branching density in the topsoil can minimize root metabolism while enhancing deep soil water uptake (Maqbool et al., 2022). Furthermore, excessive roots in dry topsoil can inadvertently increase the levels of abscisic acid (ABA), which may trigger premature stomatal closure and reduce overall photosynthesis (Khadka et al., 2020). ICARDA has prioritized root phenotyping through techniques like "shovelomics" and "root coring" to identify germplasm with optimal root architecture for specific mandate regions (ICARDA, 2020).

3.4 Canopy and Leaf Characteristics

Leaf traits are essential for managing the trade-off between carbon gain and water loss. Drought induces several morphological adjustments in the canopy:

- **Leaf Rolling:** A common drought avoidance mechanism where leaves roll to reduce the surface area exposed to solar radiation by 41-48%. This creates a humid microclimate that helps maintain photosynthesis and lowers leaf temperature (Ali et al., 2022).
- **Cuticular Wax and Trichomes:** Increased waxiness and trichome density on the leaf surface reduce non-stomatal water loss and help reflect excess radiation (Naeem et al., 2015).
- **Leaf Area Reduction:** Plants may reduce their total leaf area to minimize the transpirational surface, although this directly impacts the capacity for dry matter accumulation (Querejeta et al., 2022).
- **Stay-Green Strategy:** This refers to the ability of some genotypes to delay leaf senescence, maintaining photosynthetic activity longer into the grain-filling period. This trait is strongly associated with higher yields under terminal drought (Mondal et al., 2021).

4. Eco-Physiological and Metabolic Reprogramming

Drought stress triggers a cascade of physiological and biochemical changes that aim to maintain cellular homeostasis. These responses are highly dynamic and vary between resistant and susceptible genotypes.

4.1 Water Relations and Stomatal Regulation

The preservation of leaf water status is a fundamental requirement for drought tolerance. Parameters such as Relative Water Content (RWC) and Cell Membrane Stability (CMS) are widely used as indicators of stress severity (Bashir et al., 2021). Under drought, RWC can drop from approximately 80% to 70% in sensitive genotypes, leading to a significant loss of turgor (Haghpanah et al., 2024).

Stomatal closure is the plant's immediate response to declining water potential, mediated by the hormone ABA. While this reduces transpiration, it simultaneously limits the entry of CO2, leading to a decline in net photosynthesis and Rubisco activity (Li et al., 2020). The resulting trade-off between water conservation and photosynthetic efficiency is a central challenge in breeding for high-yielding, drought-resilient wheat (Liu et al., 2022).

4.2 Photosynthetic Impairment and Metabolic Shift

Drought stress leads to the downregulation of genes related to the photosynthetic apparatus, particularly components of Photosystem I and II. Transcriptomic analysis has shown that plants undergo a profound metabolic shift, prioritizing stress defense over growth-related processes (Hao et al., 2025). This involves:

- **Inhibition of the Calvin Cycle:** Reduced activity of key enzymes leads to decreased starch accumulation in the grains (Fatma et al., 2023).
- **Source-to-Sink Mobilization:** Drought can impair the remobilization of reserve carbohydrates from the stem to the grain, particularly if the peduncle length is significantly reduced (Yang et al., 2025).
- **Metabolic Dormancy:** In some extremely tolerant genotypes, the induction of a semi-dormant metabolic state helps preserve cellular integrity until moisture becomes available (Rafique, 2025).

4.3 Osmotic Adjustment and Compatible Solutes

To maintain water uptake from drying soil, wheat plants accumulate compatible solutes that lower the cellular osmotic potential without interfering with enzymatic functions (Mahmood et al., 2020). These include:

- **Proline:** Perhaps the most studied osmoprotectant, proline not only assists in osmotic adjustment but also acts as a molecular chaperone and a scavenger of free radicals (Munns et al., 2020).
- **Soluble Sugars and Polyols:** Compounds like sucrose, trehalose, and glycerol help stabilize membranes and proteins (Alshaharni et al., 2025).
- **Inorganic Ions:** The accumulation of K+ is particularly important, as its mobility in the soil decreases during drought. Enhancing K+ use efficiency is a key target for improving yield under stress (Khan et al., 2025).
- **Metabolic Pathway Regulation:** The conversion of gamma-amino butyraldehyde (AB-ald) into gamma-aminobutyric acid (GABA) by enzymes like BADH2 is an important metabolic reaction linked to both stress tolerance and grain quality (S_R54; S_R88) (Sinchai et al., 2026).

4.4 Oxidative Stress and the Antioxidant Buffer

The disruption of photosynthesis and electron transport leads to the accumulation of Reactive Oxygen Species (ROS), such as superoxide radicals and hydrogen peroxide. ROS can cause irreversible damage to DNA, lipids, and proteins. Wheat manages this through a robust antioxidant defense system (Mansoor et al., 2022).

Table 2: Components of the Antioxidant Defense System in Wheat

Antioxidant Component	**Function**	**Reference**
Superoxide Dismutase (SOD)	Dismutates superoxide radicals into O2 and H2O2	(Zhou et al., 2025; Hao et al., 2025)
Catalase (CAT)	Neutralizes H2O2 into water and oxygen	(Zhou et al., 2025; Hao et al., 2025)
Peroxidase (POD)	Scavenges H2O2 and other organic peroxides	(Singh et al., 2025; Hao et al., 2025)
Ascorbate Peroxidase (APX)	Involved in the ascorbate-glutathione cycle	(Singh et al., 2025; Zhou et al., 2025)
Glutathione (GSH)	Non-enzymatic scavenger of ROS	(Zhou et al., 2025)
Carotenoids / alpha-tocopherol	Protects membrane lipids from peroxidation	(Zhou et al., 2025)

Robust drought tolerance in genotypes like "Müfitbey" is characterized by stable CAT activity and elevated SOD activity, which together mitigate oxidative damage and preserve photosynthetic stability (Sachdev et al., 2021).

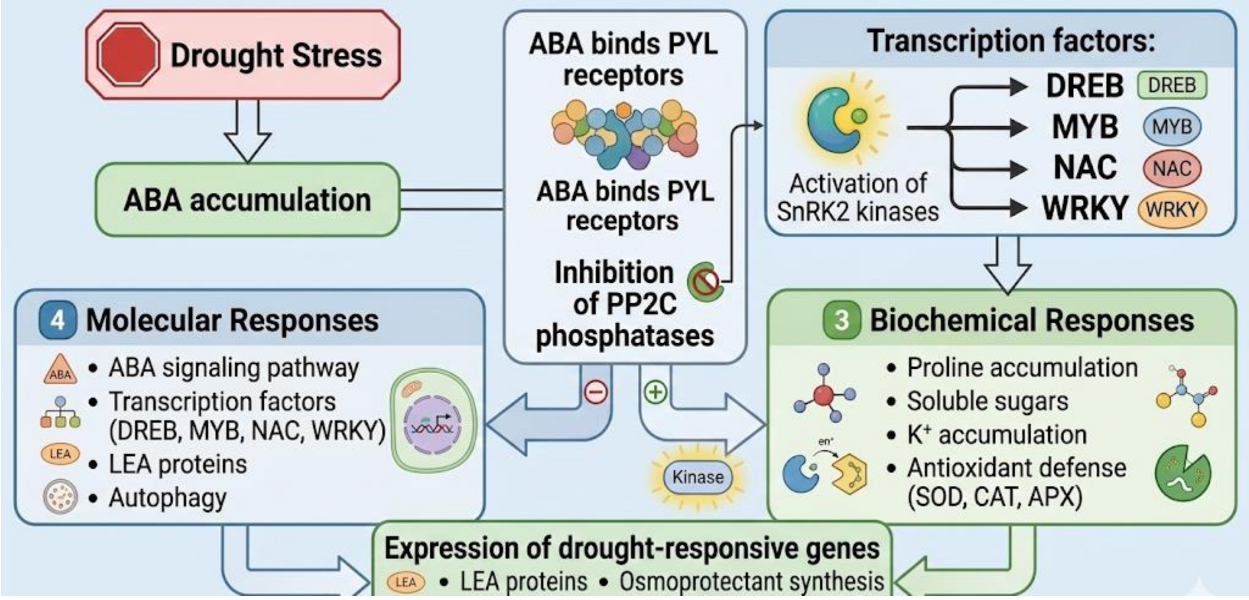
5. Molecular Signaling and Genomic Foundations of Resilience

The complex physiological responses described above are governed by a sophisticated network of gene regulation and signaling pathways. Advances in multi-omics genomics, transcriptomics, and metabolomics have begun to unravel these interactions (Badia-i-Mompel et al., 2023).

5.1 The Central Role of Abscisic Acid (ABA)

ABA is the primary stress hormone in plants, serving as a master regulator of the drought response (Salvi et al., 2021). The core ABA signaling pathway in wheat includes receptors such as TaPYL1-1B, TaPYL4, and TaPYL9, and negative regulators like the PP2C phosphatases (DIW1/TaPP2C158). Under stress, ABA binds to the receptors, which then inhibit the PP2Cs, allowing SnRK2 kinases (TaSnRK2.10) to activate downstream transcription factors (Zhou et al., 2025). Figure 2. Core ABA signaling pathway regulating drought response in wheat through the PYL–PP2C–SnRK2 module leading to activation of stress-responsive transcription factors and protective genes.

Figure 2: ABA Signaling Pathway in Wheat Drought Response



5.2 Transcription Factor Families and Regulatory Networks

Several transcription factor (TF) families have been identified as key contributors to drought tolerance in *Triticum aestivum*:

1. **DREB/ERF (Dehydration-Responsive Element Binding):** These factors regulate genes involved in osmoprotectant synthesis and desiccation tolerance. Overexpression of DREB1A from Arabidopsis in wheat has been shown to improve water-use efficiency (WUE) (Khazaei et al., 2025).
2. **MYB Factors:** The TaMYB7-A1 gene was recently identified through an integrative omics approach as a critical regulator. It directly activates TaPIP2;2-B1 (an aquaporin for water transport), TaRD20-D1 (for stomatal regulation), and TaABCB4-B1 (for root growth) (Bie et al., 2026).
3. **WRKY and NAC Factors:** These are involved in the broader stress response, including the regulation of senescence and the synthesis of secondary metabolites (Singh et al., 2025).

5.3 Protective Proteins: LEAs and Dehydrins

Late Embryogenesis Abundant (LEA) proteins and their subgroup, dehydrins, are crucial for protecting cellular components from the physical stress of desiccation. These small, hydrophilic proteins are intrinsically disordered under hydrated conditions but fold into ordered alpha-helices during dehydration (Graether, 2022). This structural transition allows them to stabilize membranes by interacting with phospholipids and to protect enzymes like catalase from inactivation (Szlachtowska et al., 2023). In durum wheat, eight Group 1 LEA genes (TtEM) have been identified, with TtEM1 and TtEM4 acting as molecular chaperones that enhance tolerance to heat, cold, and drought (Azarkina et al., 2015).

5.4 Autophagy and Cellular Recycling

A novel dimension of the wheat drought response is the role of autophagy, a process where the cell recycles damaged or unwanted proteins and organelles. The dehydrin protein TaCOR410 has been shown to interact with the key autophagy protein TaATG8 via an ATG8-interacting motif (AIM) (Hickey et al., 2022). This interaction promotes autophagy, which helps remove harmful substances generated during stress, thereby improving the plant's overall drought resistance (Sedaghatmehr et al., 2024).

6. Technological Innovations in Wheat Phenotyping

The ability to accurately characterize the phenotypes of large breeding populations is a major bottleneck in modern crop improvement. High-throughput phenotyping (HTP) platforms are transforming this process by providing non-destructive, accurate measurements of complex traits (Yang et al., 2020).

6.1 Field-Based High-Throughput Phenotyping (FHTP)

FHTP utilizes various remote-sensing devices deployed on ground-based platforms (vehicles) or aerial platforms (unmanned aircraft systems or UAS). These platforms enable the repeated measurement of thousands of plots throughout the growing season, capturing the dynamic response of different genotypes to the environment (Adak et al., 2024).

Table 3: Common Sensors and Parameters in High-Throughput Wheat Phenotyping

Sensor Type	Parameters Measured	Advantages	Reference
RGB Cameras	Shoot biomass, leaf area, canopy color, senescence	Affordable; identifies morphological changes	(Adak et al., 2024; Singh et al., 2025)
Thermal Sensors	Canopy temperature (CT)	Proxy for stomatal conductance and water status	(Naeem et al., 2015; Singh et al., 2025)
Hyperspectral	Chlorophyll content, nitrogen, NDVI, photosynthesis	High precision; multi-band data detection	(Adak et al., 2024; Singh et al., 2025)
NIR / SWIR	Leaf and canopy water content	Sensitive to water reflectance changes	(Adak et al., 2024; Singh et al., 2025)
LiDAR	Canopy structure, plant height, lodging	3D structural information	(Adak et al., 2024)
Fluorescence	Chlorophyll fluorescence (Fv/Fm)	Directly measures photosynthetic efficiency	(Adak et al., 2024; Singh et al., 2025)

6.2 Data Integration and Machine Learning in Phenomics

The volume of data generated by HTP platforms requires advanced analytical tools. Machine learning (ML) and deep learning models, such as convolutional neural networks (CNN), are used to process images and predict traits like yield, water stress, and flowering dates with high accuracy (Sheikh et al., 2024). For example, CNN-based models have achieved over 88% accuracy in identifying water stress in cereal crops. These tools bridge the "genotype-to-phenotype gap" by allowing breeders to relate complex field performance to specific genetic markers (Gill et al., 2022).

7. Precision Breeding and Biotechnological Strategies

The polygenic nature of drought tolerance necessitates the integration of multiple breeding approaches. Conventional strategies are now being augmented by molecular tools that accelerate the development of climate-resilient varieties (Rosero et al., 2020).

7.1 Marker-Assisted Selection (MAS) and Genomic Selection (GS)

MAS uses molecular markers linked to specific quantitative trait loci (QTLs) for drought-related traits. In wheat, multi-omics studies have identified regulatory variants (eQTLs) and metabolic hotspots associated with drought response (Hao et al., 2025). Genomic Selection (GS) goes a step further by using genome-wide marker data to predict the breeding value of a line, allowing for selection in early generations or off-season nurseries. This significantly shortens the breeding cycle, which is essential for adapting to the rapid pace of climate change (Khedr et al., 2025).

7.2 The Synergistic Future of CRISPR-Cas9

CRISPR-Cas9-mediated genome editing provides a precise tool for modifying specific genes without the introduction of foreign DNA (IOMC World, 2024). This technology has been successfully applied to target genes involved in:

- **Stomatal Density and Movement:** Modifying genes like TaSal1 to enhance water conservation (Xue et al., 2021).
- **Hormonal Regulation:** Knocking out negative regulators of the ABA pathway to improve stress sensitivity (Jacinto et al., 2020).
- **Transcriptional Activation:** Using CRISPR activation systems to overexpress beneficial transcription factors like AREB1 or DREB2 (Javaid et al., 2022).
- **Disease Immunity:** CRISPR has also been used to knock down susceptibility genes like MKP1, boosting resistance to rust while simultaneously increasing yield (Janik et al., 2020).

7.3 Speed Breeding and Haplotype-Based Approaches

Speed breeding utilizes artificially extended photoperiods and controlled temperatures to grow up to four generations of wheat per year, compared to only two under normal field conditions (Maqbool et al., 2022). This, combined with "haplotype breeding" which focuses on identifying and stacking beneficial allelic combinations allows for the rapid integration of drought resilience into elite germplasm (Querejeta et al., 2022).

8. Global Efforts and Case Studies in Resilient Wheat Development

International research centers and national programs have made significant strides in deploying drought-resilient wheat varieties to farmers (Bashir et al., 2021).

8.1 CIMMYT and ICARDA Programs

The International Maize and Wheat Improvement Center (CIMMYT) and the International Center for Agricultural Research in the Dry Areas (ICARDA) are at the forefront of this effort. CIMMYT's Global Wheat Program delivers over 1% annual genetic gain for grain yield and provides germplasm grown on 40 million hectares in the developing world (Liu et al., 2022). ICARDA's "PhysioTron" and precision phenotyping platforms in Morocco allow for the dissection of abiotic stress mechanisms under controlled water regimes (ICARDA, 2020).

The Stress Adapted Trait Yield Nursery (SATYN) has been a primary vehicle for delivering physiological pre-breeding germplasm to national agricultural research systems in South Asia (Mondal et al., 2021).

- **1st SATYN:** Identified drought-tolerant lines such as GID 6056139 and GID 6056165
- **9th SATYN:** Identified lines GID 8101631 and GID 8101711 for drought stress tolerance
- **Impact:** Varieties released from these nurseries include "Borlaug-16" and "Pakistan-13," which have significantly improved yields in water-limited regions (Ali et al., 2022).

8.2 National Case Study: India's Climate-Resilient Varieties

India’s ICAR-IIWBR has deployed over 90 climate-resilient varieties to address the challenges of the Indo-Gangetic plains. These varieties are characterized by low Heat Sensitivity Indices and Drought Sensitivity Indices (<1) (Harisha et al., 2024).

Table 4: Key Climate-Resilient Wheat Varieties Released in India

Variety Name	Year of Release	Target Condition	Key Resilient Characteristics	Reference
DBW 187	2019	Irrigated, timely sown	High potential yield (6.47 t ha-1); heat/drought resilient	(ICAR-IIWBR, 2024; Mondal et al., 2021)
HD 3271	2020	Irrigated, very late sown	Adaptability to thermal fluctuations	(Mondal et al., 2021)
HI 1634	2021	Irrigated, late sown	High stability and yield potential (7.06 t ha-1)	(Mondal et al., 2021)
HS 562	2016	Rainfed & Irrigated	Multi-stress tolerance for northern hills	(Mondal et al., 2021)
KRL 210	2012	Saline-alkaline soils	Tolerates combined salt and osmotic stress	(Mondal et al., 2021)

9. Future Perspectives and Strategic Directions

The evolution of wheat improvement is moving toward a highly integrated, multi-disciplinary approach that combines systems biology, digital agriculture, and innovative soil management (Wani et al., 2020).

9.1 Emerging Resilience Strategies

1. **Microbial Biostimulants:** The application of Plant Growth-Promoting Rhizobacteria (PGPR) can enhance nutrient and water absorption by altering root development and the rhizosphere environment (Khan et al., 2025).
2. **Nanotechnology:** Nanoparticle treatments are being explored to augment water absorption capacity and strengthen molecular resilience (Khadka et al., 2020).
3. **Soil Amendments:** Biochar application improves soil moisture retention and the accessibility of nutrients like K+, particularly in arid soils (Yang et al., 2025).
4. **Epigenetic Priming:** Understanding how plants retain "stress memory" where exposure to terminal drought can lead to better performance in subsequent generations through changes in seed composition could lead to new methods for priming seeds for resilience (Tabassum et al., 2017).

9.2 The Vision for the Resilient Cereal Ideotype

The ultimate goal for future breeding is the development of a "drought-resilient ideotype" tailored to specific regional climates. This ideotype would combine deep rooting, a stay-green canopy, efficient stomatal regulation, and robust antioxidant profiles (Fatma et al., 2023). Success will depend on the continued integration of high-throughput phenotyping with genomic and phenomic prediction models to accelerate genetic gains (Adak et al., 2024).

10. Conclusion

Wheat responds to drought through a finely orchestrated, multi-layered defense system that spans morphological plasticity, eco-physiological adjustments, and sophisticated molecular reprogramming. Genotypes that combine deeper and more efficient root systems, rapid stomatal control mediated by ABA, effective osmotic adjustment with proline and compatible solutes, robust antioxidant machinery to neutralize ROS, activation of key transcription factors (DREB, MYB, NAC), accumulation of LEA/dehydrin proteins, and enhanced autophagy consistently exhibit superior tolerance and sustained productivity under water-limited conditions.

Recent integration of high-throughput phenotyping platforms, multi-omics data, genomic selection, speed breeding, and precise genome editing (CRISPR-Cas9) has dramatically accelerated the identification and deployment of these resilience traits, shortening breeding cycles and enabling targeted stacking of beneficial alleles. Landmark achievements by CIMMYT, ICARDA, and national programs particularly in South Asia have already delivered high-yielding, drought-tolerant varieties that are cultivated on millions of hectares, proving that 1% annual genetic gain under stress is achievable.

To meet the escalating demands of a changing climate, future wheat improvement must embrace an integrated "systems" approach: development of regionally tailored drought-resilient ideotypes, incorporation of beneficial microbiomes and soil amendments, exploitation of epigenetic stress memory, and seamless linkage between phenomic prediction and genomic selection. By continuing to translate mechanistic understanding into practical breeding outcomes, the global wheat research community can safeguard food security, stabilize yields in arid and semi-arid regions**,** and build truly climate-resilient cropping systems for the decades ahead.

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