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Wheat Adaptation to Water-Limited Environments: Breeding Strategies for Rainfed and Semi-Arid Regions

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Index Terms

Wheat, drought tolerance, rainfed agriculture, semi-arid, breeding, water-use efficiency.

Abstract

Wheat is one of the most important food crops worldwide, but its production is increasingly threatened by water scarcity, unpredictable rainfall, and rising temperatures. Rainfed and semi-arid regions, which depend entirely on seasonal rains, face the highest risk of yield loss. Developing wheat varieties that can adapt to these water-limited environments is essential for global food security. This review summarizes the main challenges of growing wheat in dry regions, explains the key plant traits that help wheat survive and produce under stress, and compares traditional and modern breeding approaches. Finally, we highlight the importance of combining scientific advances with farmer knowledge, open data sharing, and climate-smart breeding pipelines. By integrating these strategies, breeders can deliver stable, high-yielding wheat varieties tailored to rainfed and semi-arid farming systems.

تكيف القمح مع البيئات التي تعاني من نقص المياه: استراتيجيات التربية للمناطق المعتمدة على الأمطار والمناطق شبه القاحلة

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الكلمات المفتاحية

القمح، تحمل الجفاف، الزراعة المطرية، شبه القاحلة، التربية، كفاءة استخدام المياه.

الملخص

يُعدّ القمح من أهم المحاصيل الغذائية على مستوى العالم، إلا أن إنتاجه يواجه تهديدًا متزايدًا بسبب ندرة المياه، وعدم انتظام هطول الأمطار، وارتفاع درجات الحرارة. وتواجه المناطق المعتمدة على الأمطار والمناطق شبه القاحلة، التي تعتمد كليًا على الأمطار الموسمية، أعلى مخاطر انخفاض المحصول. لذا، يُعدّ تطوير أصناف قمح قادرة على التكيف مع هذه البيئات التي تعاني من نقص المياه أمرًا بالغ الأهمية لتحقيق الأمن الغذائي العالمي. تُقدّم هذه المراجعة ملخصًا لأهم التحديات التي تواجه زراعة القمح في المناطق الجافة، وتشرح السمات النباتية الرئيسية التي تُساعد القمح على البقاء والإنتاج في ظل الظروف الصعبة، وتقارن بين أساليب التربية التقليدية والحديثة. وأخيرًا، نُسلّط الضوء على أهمية الجمع بين التقدم العلمي ومعرفة المزارعين، وتبادل البيانات المفتوحة، وخطط التربية الذكية مناخيًا. ومن خلال دمج هذه الاستراتيجيات، يُمكن للمربين إنتاج أصناف قمح مستقرة وعالية الإنتاجية مُصممة خصيصًا لأنظمة الزراعة المعتمدة على الأمطار والمناطق شبه القاحلة.

1. INTRODUCTION

Wheat (*Triticum aestivum* L.) underpins global food security, supplying approximately one-fifth of daily human caloric intake and serving as a dietary cornerstone across temperate, subtropical, and transitional agroecologies. Despite its agricultural prominence, wheat production remains highly sensitive to hydrological stability. More than sixty percent of global wheat hectares are cultivated under rainfed conditions, with a substantial fraction located in semi-arid zones where seasonal precipitation is both limited and temporally unpredictable (Sharma and Sharma, 2025). In these environments, crop performance is routinely constrained by soil moisture deficits, elevated vapor pressure deficits, and increasingly frequent terminal heat episodes. As climate trajectories shift toward greater hydrological volatility, the reliability of rainfed wheat systems has emerged as a critical determinant of regional food supplies, market stability, and rural livelihood resilience (Lesk et al., 2022).

The capacity of wheat to persist and produce under water-limited conditions does not arise from a single physiological switch, but from a coordinated network of morphological, biochemical, and molecular responses. Root architecture governs the depth and efficiency of soil water extraction, while canopy dynamics modulate transpirational cooling and photosynthetic maintenance during reproductive development (Manschadi et al., 2006). At the cellular level, osmotic adjustment, reactive oxygen species scavenging, and stress-responsive

transcription factors collectively preserve tissue viability during dehydration. Translating these adaptive mechanisms into consistent field performance, however, remains complicated by pronounced genotype-by-environment interactions, epistatic gene networks, and the inherently polygenic architecture of drought resilience. Selection strategies that prioritize isolated traits or narrow environmental testing frequently overlook the dynamic plasticity required for stable yield expression in semi-arid production systems.

Historically, wheat improvement in moisture-stressed regions has relied on empirical phenotypic selection, recurrent introgression of landrace germplasm, and multi-location field evaluation. These conventional approaches have delivered numerous drought-adapted cultivars and established foundational insights into stress physiology. Yet, the accelerating pace of climate variability has exposed structural limitations in traditional breeding cycles: extended generational timelines, dependence on favorable weather windows for accurate phenotyping, and difficulty in capturing time-resolved stress responses. Modern breeding pipelines have responded by integrating genome-wide marker data, predictive statistical frameworks, and accelerated generation advancement. Genomic selection, for example, enables early-cycle prediction of complex adaptive traits by modeling whole-genome marker effects, while speed breeding compresses reproductive cycles through controlled photoperiod and temperature regimes (Shlibak and Zencirci, 2021). When coupled with high-throughput phenotyping platforms and environmental covariate mapping, these tools collectively enhance selection accuracy and reduce the interval between cross design and varietal release.

This review synthesizes current knowledge on wheat adaptation to water-limited environments, with specific emphasis on rainfed and semi-arid agricultural systems. This study examines the physiological and genetic foundations of drought and heat resilience, trace the evolution from phenotype-driven to genotype-informed breeding, and evaluate the operational integration of emerging technologies into functional breeding pipelines. Additionally, we address the role of climate-analog testing, participatory variety evaluation, and open-access germplasm networks in accelerating deployment to smallholder and commercial farming systems. By consolidating advances across plant physiology, quantitative genetics, and breeding informatics, this work outlines a structured framework for developing next-generation wheat cultivars capable of maintaining yield stability under increasingly unpredictable moisture regimes.

1.1 Hydrological Constraints and Environmental Complexity in Rainfed Wheat Systems

Water scarcity in semi-arid and rainfed wheat production zones cannot be reduced to a simple deficit in precipitation. Rather, it manifests as a dynamic interplay of climatic variability, soil–plant–water interactions, and phenological vulnerability. In these agroecologies, crop performance is governed less by total seasonal rainfall and more by its temporal distribution, intensity, and alignment with critical developmental windows. The convergence of hydrological unpredictability, edaphic limitations, and reproductive-stage stressors creates a compounded constraint environment that challenges both physiological resilience and agronomic predictability (Nusret et al., 2021).

TABLE I. SYNTHESIS OF HYDROLOGICAL AND ENVIRONMENTAL CONSTRAINTS IN RAINFED WHEAT SYSTEMS

Traits	Environmental & Hydrological Details	Impact on Rainfed Wheat Systems d	Reference
Hydrological Constraints (Water Scarcity & Precipitation)	• Water scarcity is not merely a simple deficit in total rainfall. • Precipitation is highly erratic: characterized by irregular onset, premature cessation, and high-intensity bursts. • High-intensity events frequently exceed the soil's infiltration capacity.	Substantial proportion of water is lost to surface runoff rather than retained in the soil. • Disrupts initial crop establishment. • Reduces the effective growing period.	Apon et al., 2026
Environmental Complexity *(Climate, Soil & Interplay)*	Driven by a dynamic interplay of climatic variability, edaphic (soil) limitations, and soil-plant-water interactions. • Crop performance depends more on the temporal distribution and intensity of rain rather than total seasonal volume.	Creates a compounded, multi-layered constraint environment. • Challenges the physiological resilience of the crop. • Reduces overall agronomic predictability for farmers	Nusret et al., 2021
Rainfed Wheat Systems (Phenology & Crop Demand)	Severe mismatch between water availability and critical crop developmental windows. • Rainfall often arrives outside of optimal sowing or growth phases, or fails to align with reproductive stages	• Induces severe reproductive-stage stress. • Ultimately constrains total biomass accumulation and crop yield	Apon et al., 2026

Precipitation in semi-arid regions is inherently erratic, characterized by irregular onset, premature cessation, and episodic high-intensity events that frequently exceed soil infiltration capacity. When rainfall arrives outside optimal sowing or developmental phases, or when it occurs in concentrated bursts, a substantial proportion is

lost to surface runoff rather than being retained in the soil profile for plant access. This mismatch between water availability and crop demand disrupts establishment, limits canopy development, and reduces the effective growing period, ultimately constraining biomass accumulation (Apon et al., 2026).

1.2 Physiological and Morphological Traits Underpinning Drought and Heat Adaptation

Climate resilience in wheat does not emerge from isolated phenotypic markers but from the coordinated expression of morphological, physiological, and biochemical traits that operate across developmental stages. Adaptation to concurrent water and thermal stress requires a trait architecture that balances resource acquisition, conservation, and reproductive assurance under fluctuating environmental conditions (Shalibak, & Zencirci, 2019). Successful genotypes integrate below-ground exploration, above-ground canopy dynamics, precise gas exchange regulation, photosynthetic longevity, reproductive thermotolerance, and cellular osmotic homeostasis into a cohesive adaptive response (Shlibak, et al., 2021; Zencirci et al., 2021).

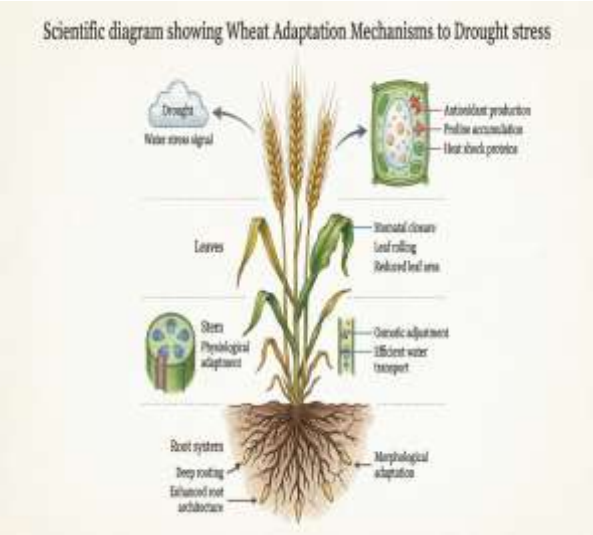


Figure 1. Wheat Adaptation Mechanisms to Drought Stress.

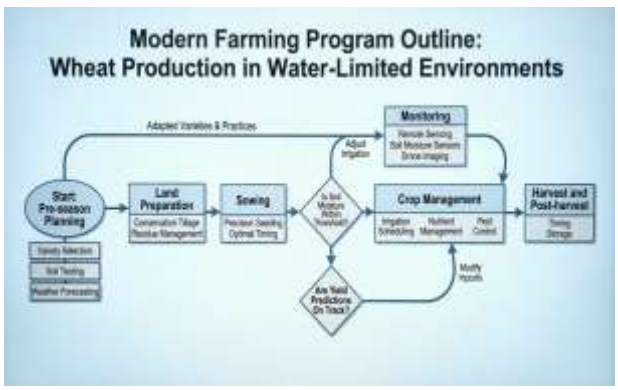


Figure 2. Wheat Production in Water- Limited Environments

1.2.1 Root Architecture and Soil Exploration

Below-ground morphology fundamentally determines a plant's capacity to access and utilize soil moisture. Genotypes exhibiting deeper rooting profiles, enhanced root length density, and favorable root angle distributions can extract water from subsoil horizons during terminal dry periods. These architectural traits are tightly coupled to xylem hydraulic conductivity and the maintenance of leaf water potential, enabling sustained transpiration and carbon assimilation when surface moisture is depleted. Root system plasticity, particularly the capacity to proliferate in moist soil patches and maintain metabolic activity under low matric potential, serves as a primary buffer against rainfall unpredictability (Soliman et al., 2026b; Soliman et al., 2026c).

1.2.2 Early Vigor and Canopy Development

Above-ground, rapid early biomass accumulation and timely canopy closure fulfill dual adaptive functions. Dense ground cover intercepts photosynthetically active radiation efficiently while simultaneously suppressing soil evaporation, thereby conserving limited soil moisture for later reproductive phases. Early vigor also establishes a larger photosynthetic foundation that improves radiation use efficiency and provides metabolic reserves to buffer against transient stress episodes during stem elongation and booting (Liu et al., 2025).

1.2.3 Stomatal Regulation and Canopy Temperature Dynamics

At the physiological level, precise stomatal control mediates the trade-off between carbon assimilation and water loss. Genotypes that maintain optimized stomatal conductance under declining soil moisture exhibit lower canopy temperatures, a measurable proxy for transpirational cooling and hydraulic efficiency. Canopy temperature depression, particularly during anthesis and grain filling, consistently correlates with yield stability in semi-arid environments. Effective stomatal responsiveness to vapor pressure deficit and abscisic acid signaling prevents uncontrolled dehydration while preserving sufficient gas exchange for photosynthetic maintenance (Lim ChaeWoo et al.., 2015).

1.2.4 Stay-Green Phenotype and Delayed Senescence

The retention of functional leaf area through delayed canopy senescence extends the duration of post-anthesis photosynthesis and enhances assimilate partitioning to developing grains. This "stay-green" trait is governed by coordinated downregulation of senescence-associated transcriptional programs, sustained chloroplast integrity, and efficient nutrient remobilization from vegetative tissues. By reducing premature leaf degradation under stress-induced oxidative pressure, genotypes with this phenotype maintain grain-filling duration and improve harvest index even when soil moisture is limiting (Zang et al., 2022).

1.2.5 Intrinsic Water-Use Efficiency

Water-use efficiency (WUE) reflects the ratio of carbon fixed per unit of water transpired and serves as a critical indicator of drought adaptation. Wheat lines with

superior intrinsic WUE typically exhibit optimized stomatal behavior, enhanced mesophyll conductance, and favorable carbon isotope discrimination ($\Delta^{13}C$) patterns. However, high WUE must be balanced with adequate transpiration rates; excessive stomatal restriction can limit carbon assimilation and reduce yield potential under moderate stress conditions. Optimal genotypes therefore maintain a dynamic equilibrium that maximizes biomass production per unit of available water without compromising reproductive output (Hafeez et al., 2024).

1.2.6 Reproductive-Stage Thermotolerance

Reproductive development represents the most temperature-sensitive phase in the wheat life cycle. Microsporogenesis, pollen viability, and fertilization are highly vulnerable to episodic heat waves, which can accelerate anther dehiscence, impair pollen tube growth, and disrupt ovule development (Dwivedi et al., 2017). Adaptive genotypes maintain membrane thermostability, upregulate heat shock proteins and molecular chaperones, and sustain antioxidant enzyme activity during flowering (Shlibak and ben Dalla, 2019). Preservation of metabolic homeostasis under thermal stress directly determines grain set and final kernel number (Wilhelm et al., 1999).

1.2.7 Osmotic Adjustment and Cellular Protection

At the cellular scale, osmotic adjustment enables turgor maintenance through the accumulation of compatible solutes such as proline, glycine betaine, trehalose, and soluble sugars. These osmoprotectants stabilize protein produces more biomass or grain per unit of water, heat tolerance during flowering, and protects pollen viability and grain set under high temperatures (Singh et al., 2017).

1.3 Traditional Breeding Approaches: Foundations, Practices, and Operational Limits

Conventional wheat breeding has served as the primary engine of genetic improvement for over a century, establishing the agronomic and physiological baselines upon which modern programs operate. At its core, traditional breeding relies on phenotypic selection—identifying and propagating individuals that demonstrate superior performance, stability, or stress tolerance under target growing conditions (Kumar et al., 2025). This approach operates through recurrent crossing, pedigree advancement, and empirical field evaluation, gradually accumulating favorable alleles while purging deleterious genetic load. In rainfed and semi-arid contexts, selection has historically emphasized broad adaptation, disease resistance, and yield stability across variable moisture regimes, often leveraging locally adapted landraces and historical cultivars as foundational genetic donors.

The strategic deployment of genetic diversity remains central to conventional breeding pipelines. Landraces, though typically lower yielding under optimal conditions, harbor extensive allelic variation for root architecture, osmotic regulation, and phenological plasticity developed through centuries of natural and farmer-mediated selection. Breeders systematically introgress these adaptive alleles into elite backgrounds through controlled crosses followed by multi-generational backcrossing or pedigree selection. Recurrent selection schemes further enhance population-level adaptation by iteratively selecting superior recombinants across stress-exposed generations (Addai et al., 2025).

While effective, these methods require precise control of mating designs, rigorous progeny testing, and careful management of linkage drag, which can inadvertently co-select undesirable agronomic traits alongside target adaptive loci.

Evaluating breeding lines across contrasting environments constitutes the cornerstone of traditional selection for rainfed systems. Multi-environment trials (METs) expose candidate genotypes to the full spectrum of hydrological, thermal, and edaphic variability characteristic of target production zones. Statistical frameworks such as AMMI (Additive Main Effects and Multiplicative Interaction) and GGE biplot analysis are routinely applied to partition phenotypic variance into genetic, environmental, and genotype × environment (G×E) components. Lines demonstrating consistent performance across stress gradients are classified as broadly adapted, while those excelling under specific moisture regimes are designated for targeted deployment. However, the accuracy of G×E prediction remains constrained by seasonal weather volatility, limited trial networks, and the difficulty of replicating compound stress conditions with sufficient statistical power (Bista et al.,2026).

Recognizing the limitations of centralized selection, many programs have integrated participatory plant breeding (PPB) into conventional pipelines. PPB engages farmers directly in the evaluation and selection process, aligning breeding objectives with local agronomic practices, market preferences, and risk tolerance thresholds. Field-based selection by end-users often identifies traits overlooked in station trials, such as early biomass for fodder, threshing efficiency, or resilience to erratic planting windows. This decentralized approach enhances varietal adoption rates and ensures that released cultivars perform reliably under real-world management constraints. Nevertheless, PPB requires sustained institutional support, standardized phenotyping protocols, and careful integration with formal breeding cycles to maintain consistent genetic gain (Lasdun et al., 2024).

Despite its historical success, conventional breeding faces structural constraints in the context of accelerating climate variability. Phenotypic selection for complex, polygenic traits such as drought resilience exhibits moderate to low heritability, requiring large population sizes and extended evaluation periods to achieve meaningful genetic progress. The typical release cycle for a new wheat cultivar spans eight to twelve years, a timeline that frequently lags behind shifting climate baselines. Additionally, reliance on natural rainfall patterns for stress imposition introduces temporal inconsistency, complicating the accurate ranking of genotypic merit. These limitations have catalyzed the integration of molecular tools, predictive modeling, and accelerated generation systems, which now complement

rather than replace traditional methodologies in modern breeding architectures.

2. CONCLUSION

Developing climate-resilient wheat for rainfed and semi-arid systems requires transitioning from isolated trait selection to integrated breeding frameworks that address compound stresses and polygenic adaptation. While conventional breeding established essential genetic foundations, its extended generational cycles and limited capacity to resolve complex genotype-by-environment interactions are increasingly misaligned with accelerating climate variability. Modern pipelines overcome these constraints by coupling genomic selection, accelerated generation systems, and high-throughput phenotyping, which collectively enhance predictive accuracy and compress varietal release timelines. Translating these advances into field-level resilience, however, depends on functional seed multiplication networks, participatory evaluation, and sustained regional breeding infrastructure. Future progress will hinge on accurately modeling drought-heat synergy, characterizing root-soil-microbiome interactions under moisture stress, ensuring equitable germplasm access, and optimizing multidimensional trait portfolios. Ultimately, shifting from reactive selection to proactive, climate-informed breeding design is critical to stabilizing wheat productivity and safeguarding the socioeconomic resilience of communities dependent on rainfed cereal agriculture.

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