Plant Genetic Resources: Characterization and Utilization

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From conservation to utilization of wild wheat relatives and allied taxa for climate-resilient wheat improvement in dryland agroecosystems

Abdul Rehman[1], Michael Frei[2], Hakan Ozkan[3,4], Benjamin Kilian[5], Kadambot Siddique[6] and Muhammad Farooq[7]

[1]Department of Agronomy, Faculty of Agriculture and Environment, The Islamia University of Bahawalpur, Bahawalpur, Pakistan; [2]Department of Agronomy and Crop Physiology, Institute of Agronomy and Plant Breeding I, Justus-Liebig-University, Giessen, Germany; [3]Department of Field Crops, Faculty of Agriculture, University of Çukurova, Adana, Türkiye; [4]State Key Laboratory of Wheat Improvement, College of Agronomy, Shandong Agricultural University, Tai'an, Shandong, China; [5]Global Crop Diversity Trust, Bonn, Germany; [6]The UWA Institute of Agriculture, The University of Western Australia, Perth, WA, Australia and [7]Department of Plant Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, Al-Khoud, Oman

Critical Review

Cite this article: Rehman A, Frei M, Ozkan H, Kilian B, Siddique K and Farooq M (2026) From conservation to utilization of wild wheat relatives and allied taxa for climate-resilient wheat improvement in dryland agroecosystems. *Plant Genetic Resources: Characterization and Utilization* 1–17. https://doi.org/10.1017/S1479262126100689

Received: 1 October 2025
Revised: 20 March 2026
Accepted: 8 April 2026

Keywords:
food security; genebanks; pangenomics; pre-breeding; trait diversity

Corresponding author: Muhammad Farooq; Email: farooqcp@squ.edu.om

Abstract

Dryland agriculture faces escalating constraints from water deficit, heat stress and soil salinity, necessitating the harnessing of adaptive diversity beyond modern wheat cultivars. Wild wheat relatives (WWRs) within the Triticeae harbour key dryland-adaptive traits, including deep, plastic root systems, osmotic adjustment, Na^+/K^+ homeostasis and heat-responsive photosynthesis, all of which are critical for maintaining yield stability under water-limited conditions. This review synthesizes recent advances in pangenomics, genome-wide association studies, speed introgression (genome-scale introgression under speed breeding) and genome editing, which enable more precise mining and deployment of WWR alleles while reducing linkage drag and improving selection efficiency. Importantly, we integrate biological constraints with conservation and policy considerations, highlighting how fragmented *ex situ* representation, limited phenotyping capacity in dryland regions, and complex access-and-benefit-sharing frameworks under the Convention on Biological Diversity, the Nagoya Protocol, and the International Treaty on Plant Genetic Resources for Food and Agriculture constrain the practical utilization of WWR diversity. By identifying underexplored WWR and allied taxa (e.g., *Aegilops searsii* and *Elymus* spp.), priority trait categories, and target dryland agroecosystems, this review provides a unified conservation-to-breeding framework that advances beyond previous syntheses and repositions WWR from genetic reservoirs to deployable resources for climate-resilient wheat improvement.

Introduction

Dryland regions, characterized by erratic rainfall, degraded soils and extreme temperatures, are among the most climate-sensitive agroecosystems (Ahmed *et al.* 2022). These fragile environments account for a substantial share of global wheat cultivation, yet productivity is persistently constrained by recurrent drought, heatwaves, and soil salinization (Badaeva *et al.* 2022; Farooq *et al.* 2024a, 2024b). Given that wheat (*Triticum aestivum* L.) contributes about 20% of global caloric intake, enhancing its resilience to dryland stresses is an urgent priority for food security (Bohra *et al.* 2022). Modern wheat cultivars possess a relatively narrow genetic base for abiotic stress adaptation due to domestication bottlenecks and intensive selection, resulting in the loss of allelic and structural variants associated with drought tolerance, heat resilience, salinity exclusion, and nutrient-use efficiency (Özkan *et al.* 2011; Maccaferri *et al.* 2019; Sharma *et al.* 2021; Badaeva *et al.* 2022). Consequently, further yield improvement in dryland systems is increasingly constrained by limited genetic diversity for stress-responsive traits.

The wild wheat relatives (WWRs), wild species across the *Triticeae* tribe, including *Triticum, Aegilops* and allied genera such as *Thinopyrum Secale* and *Elymus*, offer a powerful solution to this bottleneck (Kilian *et al.* 2011; Brozynska *et al.* 2016; Sharma *et al.* 2021). Among these, three taxa emerge as top-tier donors for dryland breeding: *Triticum dicoccoides* (wild emmer), *Aegilops tauschii* (D-genome donor) and *Ae. crassa*. These species combine ecological adaptation, genomic characterization and demonstrated introgression feasibility. These species evolved under strong and heterogeneous selection pressures in the Fertile Crescent and adjacent dry regions, leading to the accumulation of adaptive traits relevant to water-limited and

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stress-prone environments (Peleg *et al.* 2009; Kilian *et al.* 2011; Munns *et al.* 2012; Brozynska *et al.* 2016; Gaurav *et al.* 2021). *Ae. tauschii* harbours allelic variation for deep rooting, transpiration efficiency and sodium exclusion, including the well-characterized *HKT1;5-D* allele conferring salinity tolerance – a rare abiotic stress locus with demonstrated deployment relevance (Munns *et al.* 2012; Gaurav *et al.* 2021). *T. dicoccoides* exhibits substantial intraspecific variation for drought and heat adaptation, including root system plasticity, osmotic adjustment and membrane stability, with several mapped QTL and introgression-derived lines under evaluation (Peleg *et al.* 2009; Avni *et al.* 2017; Balla *et al.* 2025). Although less widely deployed, *Ae. crassa* demonstrates coordinated ion homeostasis and stress-responsive gene expression, marking it as a high-potential but still exploratory donor for salinity resilience (Pour-Aboughadareh *et al.* 2025). Additional taxa, including *Ae. speltoides* or *T. araraticum*, contribute micronutrient enrichment and grain quality traits, though their breeding deployment remains limited and more exploratory (Badaeva *et al.* 2022; Zeibig *et al.* 2022).

Historically, WWR utilization has been uneven. Major progress has been made in single-gene biotic resistance, whereas progress in complex abiotic stress tolerance has been slower due to polygenic inheritance, linkage drag and genotype × environment interactions (Singh *et al.* 2011; Tian *et al.* 2025). This contrast highlights an important distinction: traits governed by major loci (e.g., disease resistance, *HKT1;5*-D) are closer to deployment, whereas complex drought, heat, and nutrient-use efficiency traits remain in advanced discovery or pre-breeding stages. Recent genomic advances have strengthened the bridge between discovery and deployment. High-quality reference genomes and wheat pangenomes now capture extensive presence–absence variation (PAV) and structural polymorphisms previously inaccessible (IWGSC 2018; Walkowiak *et al.* 2020; Tiwari *et al.* 2024; Farooq *et al.* 2025). Population genomics in *Ae. tauschii* and *T. dicoccoides* has identified loci associated with root traits, ion homeostasis and stress-responsive pathways directly relevant to dryland agriculture (Avni *et al.* 2017; Gaurav *et al.* 2021). Importantly, these discoveries are increasingly supported by practical deployment platforms, including synthetic hexaploid wheat (SHW), structured introgression libraries and advanced backcross populations. These platforms enhance recombination, reduce linkage drag and improve compatibility with speed breeding and genomic selection (GS) pipelines (Trethowan and Mujeeb-Kazi 2008; Mastrangelo *et al.* 2023).

This review builds recent syntheses of WWR utilization (e.g., Farooq *et al.* 2025) but provides a targeted focus on dryland agriculture, integrating ecological adaptation, pre-breeding strategies and emerging genomic tools. In addition, it considers how international policy frameworks, including the Convention on Biological Diversity (CBD), the Nagoya Protocol and the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA), shape access to and utilization of WWR genetic diversity (Engels and Ebert 2024). By positioning WWR not merely as reservoirs of genetic diversity but as strategic assets for climate-resilient wheat systems, this review highlights pathways to enhance wheat productivity, yield stability and nutritional quality in water-limited environments.

Origins and ecological adaptations of WWRs

WWRs (*Triticum* and *Aegilops* spp.) primarily originated in the Fertile Crescent and adjacent regions, encompassing parts of modern-day Türkiye, Palestine, Israel, Jordan, Lebanon, Syria, Iraq and Iran, recognized as a major centre of origin and crop diversity (Vavilov 1926; Kilian *et al.* 2011; Avni *et al.* 2017; Eastwood *et al.* 2022). The harsh and fluctuating environments of the Fertile Crescent, characterized by recurrent drought, extreme temperatures and nutrient-poor soils, exerted strong selective pressures that shaped the adaptive evolution of wild populations (Fig. 1; Peleg *et al.* 2011; Brozynska *et al.* 2016). Domestication and subsequent breeding narrowed the genetic base of cultivated wheat, eliminating allelic and structural variants still present in wild taxa such as *T. dicoccoides* and *Ae. tauschii* (Özkan *et al.* 2011 Avni *et al.* 2017; Gaurav *et al.* 2021). Diversity losses were particularly pronounced in low-recombination genomic regions enriched with adaptive haplotypes (Maccaferri *et al.* 2019; Badaeva *et al.* 2022). These patterns underscore the significance of conserving wild populations as both evolutionary archives and reservoirs of alleles relevant for modern agriculture.

Drought adaptation

Drought represents one of the most pervasive selective pressures across the native landscapes of WWRs (Peleg *et al.* 2009; Nevo and Chen 2010). *T. dicoccoides*, the progenitor of tetraploid wheat, has evolved robust drought-adaptive traits, including deep, highly branched root systems, efficient osmotic adjustment and superior water-use efficiency (Peleg *et al.* 2009; Avni *et al.* 2017). Experimental evaluations confirm that WWR accessions exhibit greater biomass stability and root plasticity under drought stress than modern cultivars (Pour-Aboughadareh *et al.* 2021). In a pot study, screening of diverse *Aegilops–Triticum* accessions under water stress (90, 50, 25% FC) indicates that accessions with alien genomic constitutions (e.g., *Ae. umbellulata, Ae. crassa, Ae. markgrafii, Ae. cylindrica, T. boeoticum*) displayed strong induction of antioxidant enzymes and maintained higher pigment concentrations, suggesting biochemical buffering as a key adaptive mechanism (Ahmadi *et al.* 2018). Recent integrative analyses combining physiological, biochemical, and transcriptomic data further demonstrate that drought responses in wheat are strongly genotype dependent, with tolerant cultivars exhibiting enhanced antioxidant activity and activation of ABA-mediated stress signalling pathways (Cevher-Keskin *et al.* 2025). Complementing this, a two-year field study across irrigated and rainfed conditions revealed significant genotypic variation in drought-response traits across 110 *Triticum* accessions; water limitation reduced grain yield by 21% and stomatal conductance by 45%, with wild relatives maintaining superior performance via physiological regulation. Notably, *T. dicoccoides, T. urartu, T. boeoticum* and *T. araraticum* expressed isohydric strategies (water-conservative regulation), whereas *T. monococcum* subsp. *sinskajae* and *T. durum* cv. Sambadur showed anisohydric behaviour (maintaining gas exchange under stress), revealing multiple contrasting drought-adaptation strategies within the *Triticum* gene pool (Pantha *et al.* 2025). Together, pot and field evidence demonstrate that drought tolerance in WWR arises from integrated architectural, biochemical and stomatal regulation mechanisms, confirming their value as functional donors for synthetic wheat development and targeted trait introgression for low-water environments.

Heat and thermal stress adaptation

Triticum dicoccoides is a viable genetic reservoir for heat-stress resilience due to its direct lineage to domesticated durum wheat (*T. durum*) and contribution to the A and B subgenomes of

https://doi.org/10.1017/S1479262126100689 Published online by Cambridge University Press

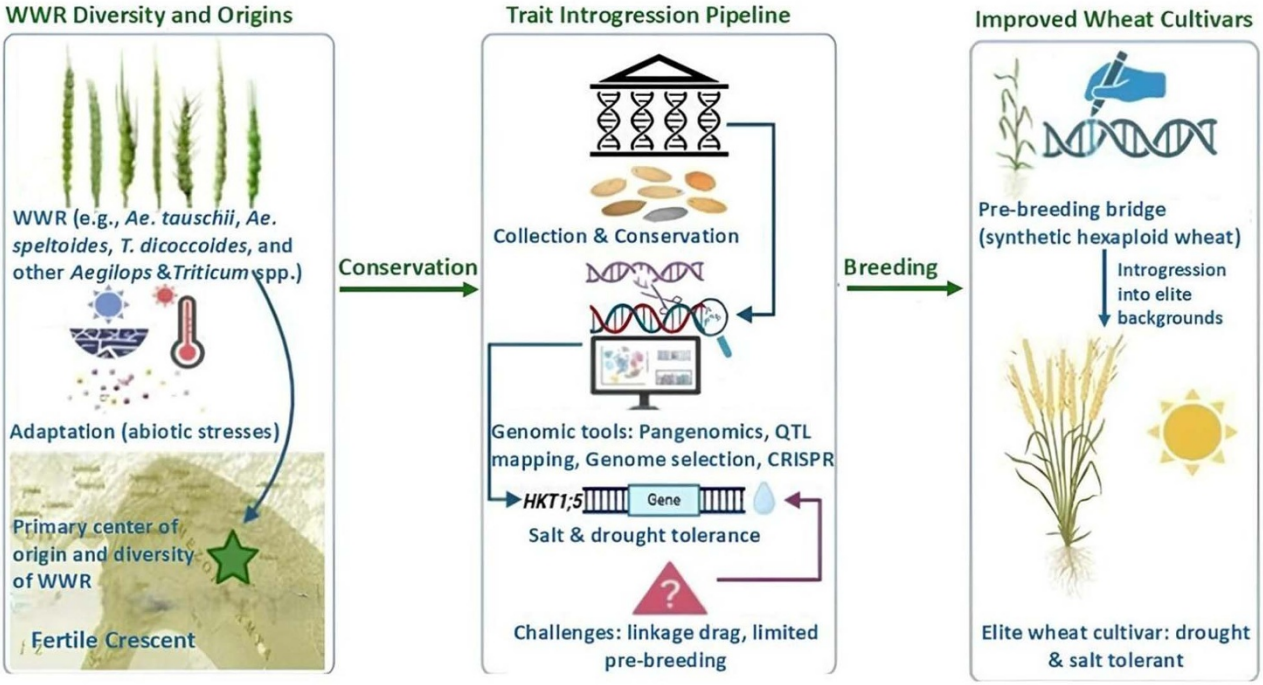


Figure 1. Genetic diversity and trait introgression from wild wheat relatives.
Note: The wild wheat relatives (WWR) originating from the Fertile Crescent exhibit significant genetic diversity and have evolved in response to harsh climatic conditions. Their adaptations to drought, salinity, and high temperature are vital for improving wheat resilience in dryland agroecosystems. By harnessing these adaptive traits, modern wheat varieties can be improved through conservation efforts in genebanks and the use of advanced genomic techniques such as pan genomics, QTL mapping and CRISPR-based genome editing. However, challenges such as linkage drag and limited pre-breeding efforts must be addressed. Ultimately, these efforts contribute to the development of climate-resilient wheat cultivars tailored for dryland agriculture, ensuring food security in increasingly unpredictable and harsh environments.

bread wheat (*T. aestivum*), enabling the transfer of agronomic, physiological, and yield-related traits relevant to thermal tolerance (Peng *et al.* 2013). The feasibility of using this diversity has been demonstrated across both northern and southern evolutionary lineages of *T. dicoccoides*, corresponding to populations from the northern Fertile Crescent (e.g., Türkiye and the northern Levant) and southern regions (e.g., Palestine and adjacent areas), providing multiple allelic routes for improvement. Multi-environment, field-based evaluations across Japan and Sudan indicate that introgression from *T. dicoccoides* captures intraspecific variation for heat resilience in durum wheat × *T. dicoccoides* backcross families. Several families maintained high harvest index, elevated chlorophyll content, and reduced canopy temperature under severe heat stress, while others exhibited increased biomass and seed number, despite overall stress pressure (Balla *et al.* 2025). These superior-performing lines contained introgressed chromosomal segments on chromosomes 1A, 2B, 5B, 6B and 7B, providing candidate regions for heat tolerance absent from elite durum backgrounds (Balla *et al.* 2022). Moreover, WWR and wild-derived genotypes often outperformed elite cultivars for photosynthetic performance, with studies reporting a 2.3-fold range in CO_2 and light-saturated photosynthesis (Amax) and higher capacities for carboxylation, electron transport, and Rubisco activity, alongside faster dynamic responses to light via stomatal and non-photochemical quenching mechanisms (McAusland *et al.* 2020). Notably, the negative impact of heat stress on global wheat production is intensified by the genetic uniformity of modern cultivars, a consequence of breeding within narrow germplasm pools, particularly in developed countries (Fu *et al.* 2015), emphasizing the urgency of reintegrating wild diversity. Harnessing *T. dicoccoides* enables the recovery of genetic variation lost during domestication and provides actionable alleles for high-temperature resilience, positioning WWR as essential assets for future-proofing wheat improvement.

Salinity and ion toxicity tolerance

Salinity is a major constraint to wheat productivity in dryland and irrigated systems, where ion toxicity and osmotic imbalance disrupt growth, photosynthesis and yield. The adaptive traits of WWRs are particularly relevant to resilience to abiotic stress (Table 1). WWRs, particularly those harbouring the D genome or alien genomic constitutions, provide mechanistically distinct pathways of salinity tolerance. Salinity tolerance in *Ae. tauschii* is conferred by alleles of the high-affinity potassium transporter *HKT1;5*, which maintain Na^+/K^+ balance and improve ionic homeostasis in wheat introgression lines under saline-soil conditions (Table 1; Munns *et al.* 2012). In a pot study, *Ae. crassa* (MMDD genome) exhibited a broader, system-level salinity response (150–200 mM NaCl), maintaining higher biomass, chlorophyll content, and PSII efficiency (Fv/Fm, Fv/Fo) than other tested materials. This response was accompanied by elevated expression of salt overly sensitive (*SOS1/2/3*), Na^+/H^+ exchanger (*NHX*) and high-affinity potassium transporter (*HKT*) genes, indicating a coordinated, genotype-specific response involving ion exclusion, vacuolar sequestration, and membrane transport signalling rather than a species-wide trait (Pour-Aboughadareh *et al.* 2025). This response exceeded that of *Ae. cylindrica* and *Ae. tauschii*, identifying specific *Ae. crassa* genotypes as promising donors for salinity tolerance introgression. *T. dicoccoides* similarly exhibits adaptive variation relevant to saline environments. In a

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Table 1. Genetic contributions of wild wheat relatives to stress adaptation and resistance

Species/Donor	Trait/Function	Identified genes/QTLs	Breeding relevance	Source
Aegilops. searsii	Abiotic stress tolerance	1Ss, 2Ss chromosomal segments	Underexploited source for stress adaptation	Gong *et al.* 2016
Aegilops speltoides	Disease resistance (rusts, powdery mildew)	*Lr51, Yr40*	Broad-spectrum biotic resistance	Yaniv *et al.* 2015
Aegilops. tauschii	Salt tolerance (Na^+ exclusion)	HKT1;5-D allele	Enhances Na^+/K^+ homeostasis, improves salinity tolerance	Munns *et al.* 2012
Elymus spp.	Drought tolerance (leaf traits, biomass)	Multiple QTLs	Still underutilized in wheat breeding	Khan *et al.* 2022
Secale cereale	Multi-stress resistance (biotic + drought)	1RS translocation	Widely deployed in bread wheat cultivars	Liu *et al.* 2023
Thinopyrum elongatum	Drought resilience (root system)	7DL translocation	Improved water uptake and yield stability	Placido *et al.* 2013
Triticum dicoccoides	Drought adaptation (root length, WUE, yield stability)	QTL on 7A, 2B	Contributes to deeper roots, higher water-use efficiency	Peleg *et al.* 2009
Triticum urartu	Early vigour, grain quality under stress	Mapped QTL on 5A	Improves establishment and nutrient efficiency	Valkoun *et al.* 2001

comparative assessment of 30 *T. dicoccoides* and 14 durum wheat genotypes, the salt tolerance index (0.21–0.97) exceeded that of durum (0.46–0.78) and was strongly associated with shoot K^+/Na^+ ratios and Na^+ exclusion, but not shoot K^+ concentration (Feng *et al.* 2018), confirming ion exclusion and homeostatic regulation as principal mechanisms. Root system traits, particularly length, surface area, and volume, were strongly correlated with tolerance, underscoring below-ground ion avoidance as a complementary adaptation.

Nutrient acquisition and efficiency

Improving nitrogen (N) and phosphorus (P) use efficiency is essential for wheat grown in low-input dryland systems, where nutrient limitations interact with heat and drought stress. WWRs, particularly D-genome donors, provide alleles that enhance nutrient capture and metabolic efficiency under stress. In a multi-environment field study in Sudan, *Ae. tauschii*-derived multiple-synthetic-derivative wheat lines showed wide variation in performance under heat × N stress; despite reductions in grain yield (−14%) and grain N uptake (−28%) under zero N, several lines maintained yield stability. Genome-wide association analysis (GWAS) identified 34 marker-trait associations (mostly in the D subgenome), including a locus on chromosome 5A influencing grain growth and a major locus on 3D explaining 88% of variation in grain N uptake, linked to stress signalling and nitrogen metabolism genes (Emam *et al.* 2025). These results demonstrate the deployable breeding value of *Ae. tauschii* introgressions for nitrogen use efficiency (NUE).

Pot experiments under reduced N–P–K fertilization further show that certain wild taxa sustain productivity by increasing NUE. Diploids were generally inefficient (except *Ae. tauschii*), while tetraploids (*T. carthlicum, T. dicoccoides, T. timopheevii*) and hexaploid *T. sphaerococcum* combined high uptake efficiency with nutrient-stress tolerance, marking them as priority donors (Gorny and Garczyński 2008). Similar patterns appear in alien chromosome addition lines from *Leymus, Agropyron, Hordeum, Secale* and others, where N deficiency reduced biomass and N uptake, while P deficiency constrained plant height and nutrient content (Liu *et al.* 2018), confirming that NUE/PUE (Phosphorus use efficiency) expression is genotype- and nutrient-dependent. Since NUE is multigenic, involving uptake, transport, assimilation, and remobilization (Islam *et al.* 2021; Haider *et al.* 2023), WWRs provide valuable entry points for improving these pathways. Micronutrient acquisition further expands the value of WWR. *T. dicoccoides* is recognized as a strategic germplasm resource for increasing grain iron (Fe) and zinc (Zn) concentrations in cultivated wheat, with diploid and tetraploid wild taxa consistently outperforming modern *T. aestivum* and *T. durum* cultivars for grain micronutrient content (Liu *et al.* 2021; Zeibig *et al.* 2022, 2024a). GWAS-based dissection in emmer-derived lines has identified genomic regions associated with higher Fe and Zn accumulation, reinforcing the biofortification potential of these taxa. Some wild relatives also demonstrate preferential Zn partitioning within tissues and grains (Fan *et al.* 2023), adding mechanistic targets for trait stacking and mineral-use-efficiency improvement.

Nutritional and grain quality traits

Beyond stress resilience, WWRs are valuable reservoirs of nutritional and grain-quality traits. Multiple studies highlight their superior micronutrient composition, particularly Fe, Zn and grain protein content (GPC). Diploid and tetraploid wild wheats consistently outperformed modern *T. aestivum* and *T. durum* for grain Fe and Zn under field conditions (Zeibig *et al.* 2024). Notably, diploid einkorn wheats (*T. monococcum* and *T. urartu*) and the tetraploid *T. dicoccoides* exhibited substantial genetic diversity for these minerals (Fu *et al.* 2024; Zeibig *et al.* 2024), complementing findings that diploid taxa and *T. timopheevii*-lineage species (e.g., *T. araraticum*) possess higher micronutrient content and distinct gluten protein profiles relative to modern cultivars (Zeibig *et al.* 2022). These traits position WWRs as key contributors to global biofortification initiatives aimed at combating micronutrient malnutrition (Tadesse *et al.* 2023). Micronutrient enrichment is further supported by enhanced uptake and preferential grain partitioning, with several wild relatives showing superior Zn allocation to grain tissues compared to common wheat (Fan *et al.* 2023). GPC, which is a key trait for flour functionality and nutritional value, also benefits from WWR introgression. For example, chromosome 1Ns from *Leymus mollis* has been transferred into elite wheat, elevating GPC via improved storage protein subunit

https://doi.org/10.1017/S1479262126100689 Published online by Cambridge University Press

composition (Li *et al.* 2025). Dietary fibres, such as β-glucan and arabinoxylan, which reduce glycemic index and support cardiovascular health, remain limited in the gene pool of modern wheat but show greater variation and enhancement potential in wild relatives (Kapoor *et al.* 2025). Genetic mapping efforts reinforce this potential: GWAS in *T. timopheevii*-derived lines have identified loci associated with gluten content and technologically relevant flour properties (Leonova *et al.* 2023). Moreover, volatile compound profiles from *T. timopheevii* may offer opportunities for improving wheat flour aroma and flavour, adding a sensory dimension to quality improvement (Agarwal *et al.* 2024).

Linking abiotic and biotic stress relevance in drylands

Climate-driven drought and heat can intensify pathogen risks by altering crop phenology, canopy microclimate (temperature and humidity gradients), and host susceptibility windows, thereby influencing epidemic development and host–pathogen interactions. WWRs have coevolved with diverse disease-causing pathogens, providing a wide range of resistance genes. For instance, *T. dicoccoides, Ae. speltoides* and *Ae. geniculate* contribute stem rust (*Sr2*), leaf rust (*Lr51*) and stripe rust (*Yr40*) resistance genes, respectively (Singh *et al.* 2011; Yaniv *et al.* 2015; Steadham *et al.* 2021). Recently, Mastrangelo *et al.* (2025) mapped resistance loci in *T. dicoccoides* populations and identified novel genomic regions associated with resistance to emerging stem rust pathotypes, expanding the genetic toolbox for breeders.

Several WWR-derived resistance loci can confer broad-spectrum protection; however, durability varies across environments, genetic backgrounds, and pathogen populations, highlighting the importance of pyramiding and multi-environment validation (Farooq *et al.* 2025). While abiotic stress tolerance is often polygenic, biotic resistance spans a continuum of genetic architectures: major-effect genes enable relatively straightforward introgression, whereas adult plant and quantitative rust resistance are polygenic and require more complex breeding strategies (McGee *et al.* 2025). Recognizing this spectrum improves alignment between trait discovery and deployment in dryland breeding programmes.

Barriers and bottlenecks to trait deployment

Despite the encouraging progress in identifying stress-resilient traits, the deployment of adaptive alleles from WWRs into modern breeding remains constrained by several biological and technical bottlenecks.

Many key targets – including drought, salinity, and heat tolerance – are polygenic, involving numerous small-effect loci that complicate introgression and stable phenotypic expression in elite backgrounds (Sharma *et al.* 2021; Kashyap *et al.* 2022; Tian *et al.* 2025). Complex genetic architectures require the simultaneous transfer and stabilization of multiple alleles across several breeding cycles, making selection less predictable than for single-gene traits. These challenges are further intensified by genotype × environment interactions, particularly in dryland agroecosystems, where trait expression fluctuates across locations and seasons, reducing breeding predictability and slowing selection for broad adaptation (Chairi *et al.* 2020; Nyine *et al.* 2025). Addressing these biological complexities requires large multi-environment trials and GS strategies that capture polygenic signals across variable environments.

Genomic constraints (linkage drag, recombination suppression)

Introgression from WWR is often hindered by linkage drag, especially when beneficial alleles reside in low-recombination or pericentromeric regions. Recombination suppression in these regions makes separating beneficial alleles from adjacent deleterious chromatin extremely difficult, frequently necessitating extensive backcrossing and large breeding populations (Summers and Brown 2013; Murray 2024). Effective utilization of WWR alleles may therefore require advanced strategies, including targeted introgression, large mapping populations or the identification of recombination-friendly genomic intervals to facilitate allele transfer while minimizing unwanted genomic baggage.

Translational constraints: phenotyping and validation gaps

Beyond biological and genomic barriers, translational bottlenecks arise from limited phenotyping capacity and field validation. Many promising physiological traits – such as root architecture, osmotic adjustment or water-use efficiency – are often characterized under controlled conditions or in limited field trials. However, the expression of these traits can vary substantially across diverse dryland production systems, where multiple stresses frequently occur simultaneously. Limited multi-environment validation, therefore, restricts the translation of these discoveries into breeding pipelines, as the agronomic stability of candidate traits remains uncertain (Zeibig *et al.* 2024b; Nyine *et al.* 2025).

Recent genomic advances provide a pathway to overcome these bottlenecks. High-quality pangenomes and genome assemblies reveal extensive PAV and structural rearrangements between wild and cultivated wheats, enabling targeted allele mining (Avni *et al.* 2017; Walkowiak *et al.* 2020; Kilian *et al.* 2021). Pre-breeding platforms – including synthetic hexaploids, introgression libraries and advanced backcross populations – help bridge wild and elite germplasm (Trethowan and Mujeeb-Kazi 2008; Mastrangelo *et al.* 2023; Li *et al.* 2024a, 2024b; Farooq *et al.* 2025). Precision approaches, such as gene editing, speed breeding and *de novo* domestication, can accelerate the deployment of alleles once causal variants are identified and functionally validated (Özkan *et al.* 2002; Kilian *et al.* 2021; Farooq *et al.* 2025; Mastrangelo *et al.* 2025). Collectively, integrating conservation, pre-breeding and genomics-informed validation pipelines is essential to translate WWR-derived diversity into climate-resilient wheat for dryland agriculture.

WWR as a resource for dryland agriculture

WWRs represent highly valuable genetic resources for improving wheat's resilience in dryland agroecosystems. Originating in the Fertile Crescent and nearby areas, these plants have adapted to unpredictable rainfall, temperature extremes, soil salinity and nutrient deficiencies, resulting in adaptive traits that remain underexploited in breeding pipelines, particularly root system architecture (RSA), ion homeostasis, micronutrient-use efficiency and heat-responsive photosynthetic regulation (Fig. 1; Özkan *et al.* 2011; Kilian *et al.* 2011; Farooq *et al.* 2025). While domestication and intensive selection improved agronomic performance, they also narrowed wheat's genetic base; modern cultivars generally lack adaptive alleles retained in wild progenitors and close relatives (Farooq *et al.* 2025). This section advances prior syntheses by distinguishing between demonstrated breeding gains and traits still under evaluation, identifying mechanisms underlying stress adaptation, and clarifying the biological and technical bottlenecks limiting deployment.

https://doi.org/10.1017/S1479262126100689 Published online by Cambridge University Press

Demonstrated successes: synthetic wheat and introgressions

SHW, developed by crossing *Ae. tauschii* with durum wheat (*T. durum or T. dicoccon*), has become a major strategy for expanding D-genome diversity in bread wheat breeding programmes. Major initiatives led by the International Maize and Wheat Improvement Center (CIMMYT) and partner institutions have generated large SHW libraries that primarily serve as pre-breeding resources rather than direct cultivar replacements (Warburton *et al.* 2006; Mujeeb-Kazi *et al.* 2008). These synthetics have introduced alleles conferring improved tolerance to abiotic stresses and foliar diseases, although performance remains uneven and most lines are still embedded in pre-breeding pipelines (Tian *et al.* 2025). The lines derived from synthetic wheat exhibit excellent RSA traits (e.g., root length, volume, and surface area), which directly support water capture in low-rainfall systems and improve performance under conservation agriculture, thereby benefiting dryland production systems (Gaikwad *et al.* 2023). Introgressions from WWRs have further shaped modern wheat adaptation (Fig. 1). Both intentional breeder-mediated introgressions and historical gene flow events have contributed to the genomic and phenotypic diversity of elite cultivars. For example, an *Ae. Tauschii*-derived introgression increased yield by >50% under heat stress and reduced canopy temperature by 2 °C in field trials, without a yield penalty under favourable conditions (Molero *et al.* 2023).

Comparative pangenome analyses reveal extensive PAV and structural polymorphisms in elite wheat germplasm, reflecting past introgression events from wild relatives (He *et al.* 2019; Walkowiak *et al.* 2020). However, the functional significance of many PAVs remains uncertain, requiring further validation to confirm their phenotypic contributions. For example, the cultivar Pamukale carries an ∼14 Mb segment on chromosome 7D introgressed from a wild donor, conferring powdery mildew resistance (PmPam), yet suppressed recombination restricts fine-mapping and limits segment optimization for breeding purposes (Heuberger *et al.* 2024). This study exemplifies both the value and the challenges of WWR introgression.

Mechanisms underpinning adaptation to dryland stresses

Ion homeostasis and salinity

Abiotic stress resilience derived from WWR remains underutilized compared with disease resistance, though recent studies underscore its potential. The *Ae. tauschii*-derived *HKT1;5* allele, a canonical example, reduces sodium accumulation and enhances salinity tolerance (Munns *et al.* 2012). Synthetic vs. bread wheat comparisons under salt stress confirm that SHW lines retain higher chlorophyll levels, photosynthetic activity, and antioxidant enzyme activity, along with favourable Na^+/K^+ ratios (Alghabari and Shah 2024). *T. dicoccoides* displays variation in salt tolerance index correlated with Na^+ exclusion and root architectural traits (Feng *et al.* 2018). These mechanistic pathways offer targets for controlled introgression but require careful selection to avoid co-transfer of undesirable linked loci.

Drought adaptation and root system architecture

Root traits from WWRs, including deeper rooting angles, enhanced branching, and improved root hydraulic conductivity, facilitate access to subsoil moisture and enhance transpiration efficiency (Peleg *et al.* 2009). *Thinopyrum elongatum* 7DL translocations enhance root biomass and drought tolerance, though some backgrounds carry growth penalties under optimal conditions (Placido *et al.* 2013). These outcomes underscore a persistent trade-off between stress resilience and productivity, challenging the assumption that deeper or larger root systems are universally beneficial. In *Aegilops* accessions, drought tolerance is often attributed to coordinated osmotic adjustment, antioxidant defence, and stomatal regulation (Sultan *et al.* 2012; Jadidi *et al.* 2025). Nevertheless, these responses are typically controlled by complex, multi-layered regulatory networks, limiting their predictable transfer into elite germplasm. Consequently, trait stacking remains a major bottleneck in drought breeding, as simultaneous optimization of root architecture, physiological buffering, and yield stability has proven difficult to achieve without unintended trade-offs.

Heat tolerance and photosynthetic stability

Heat resilience in wild relatives is associated with canopy temperature regulation, maintenance of chlorophyll content, and stable light-saturated photosynthesis (Amax). Emmer wheat (*T. dicoccon*)-derived hexaploid progenies with 1–43% emmer genomic contribution outperform recurrent parents under reproductive-stage heat stress, though responses vary across environments (Ullah *et al.* 2021). These findings emphasize the role of polygenic buffering mechanisms, including Rubisco efficiency and dynamic stomatal responses (McAusland *et al.* 2020). The WWRs exhibit a set of adaptive mechanisms, including antioxidant defences, osmotic adjustment, stomatal regulation and improved RSA, which translate into improved survival and yield stability under suboptimal growth conditions (Sultan *et al.* 2012; Akman *et al.* 2017; Jadidi *et al.* 2025). Nevertheless, their use in elite backgrounds is constrained by polygenic complexity, frequent yield trade-offs, and genotype × environment interactions. The plant's adaptive traits under stressful environments are often negatively associated with productivity, creating a breeding dilemma that has limited widespread adoption.

Biotic stress resistance

Biotic stress resistance demonstrates clearer breeding tractability because major-effect genes govern many resistance traits. Well-documented examples include *Sr2* and *Yr15* from *T. dicoccoides, SrTA10171* and *SrTA10187* from *Ae. tauschii*, and diverse rust resistance loci from *Aegilops* taxa (Singh *et al.* 2011; Olson *et al.* 2013). These successes contrast with the slower progress in abiotic stress improvement and underscore why disease resistance has historically dominated WWR contributions. However, durability and pleiotropic effects, such as the yield-quality trade-offs associated with the 1RS rye (*Secale cereale*) translocation, highlight the need for judicious deployment and trait stacking strategies (Kaur *et al.* 2018).

Collectively, WWR-derived alleles have been most successfully deployed for single-gene biotic resistance and a limited set of abiotic mechanisms such as ion homeostasis and root traits. In contrast, complex drought, heat and nutrient-related traits remain difficult to translate into stable yield gains. These contrasting outcomes highlight the need for mechanism-based introgression, haplotype-level selection and robust multi-environment validation to overcome polygenic control, linkage drag and genotype × environment interactions in dryland wheat breeding.

Challenges, trade-offs and barriers

Despite the success reported in earlier sections, the utilization of WWR faces both biological and breeding-system constraints. From

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a biological perspective, many adaptive traits relevant to dryland agriculture (e.g., drought, salinity, heat and nutrient-use efficiency) are polygenic and strongly influenced by genotype × environment interactions, which reduces predictability of trait expression across heterogeneous dryland gradients (Chairi *et al.* 2020; Nyine *et al.* 2025). Yield penalties associated with WWR-derived alleles are therefore genotype- and environment-dependent rather than universal, often becoming evident under favourable rather than stress-prone conditions (Murray 2024; Tian *et al.* 2025). Cytogenetic constraints further limit deployment, including linkage drag, suppressed recombination in pericentromeric regions and large alien introgressions. Such constraints are exacerbated in tertiary gene pool species, including *Thinopyrum* and *Elymus*, due to structural rearrangements, homoeologous interference, and low crossover frequency (Wijerathna-Yapa *et al.* 2022).

Beyond intrinsic biological barriers, the effective deployment of WWRs is constrained by several breeding-system limitations. Modern wheat cultivars possess a narrow genetic base due to prolonged selection for yield and uniformity, reducing adaptive diversity and increasing vulnerability to emerging stresses (Przewieslik-Allen *et al.* 2021; Wani *et al.* 2022). Although WWRs harbour extensive genetic variation, their integration into elite germplasm is impeded by reproductive isolation barriers, including low crossability, hybrid inviability and sterility, often requiring prolonged backcrossing to mitigate linkage drag and restore agronomic performance (Mondal *et al.* 2016). These challenges are compounded by the difficulty of detecting and tracking introgressed segments within the large (≈17 Gb), highly repetitive hexaploid wheat genome, where even modern single-nucleotide polymorphism (SNP) based genotyping platforms, including Kompetitive Allele Specific PCR (KASP) assays, may struggle to resolve small but beneficial introgressions (Ma *et al.* 2019; Keilwagen *et al.* 2022). In addition, slow breeding cycles, limited high-throughput phenotyping for complex stress-adaptive traits, and uncertainty in identifying donor species for unknown introgressions further delay the translation of WWR-derived variation into elite cultivars (Mondal *et al.* 2016; Keilwagen *et al.* 2022). Collectively, these constraints highlight the need for integrated genomics, phenotyping, and pre-breeding pipelines to more efficiently harness WWR diversity (Wani *et al.* 2022).

Genomics and molecular tools for harnessing WWR diversity

Recent genomic advances are reshaping the utilization of WWR, enabling more strategic and predictive breeding approaches to address genetic erosion, climate change, and food security challenges (Özkan *et al.* 2002; Kilian *et al.* 2021; Sharma *et al.* 2021; Farooq *et al.* 2025; Mastrangelo *et al.* 2025). These tools can be organized hierarchically according to their roles in tracking introgressions, trait discovery, deployment acceleration and precision modification.

Tracking introgressions and diversity

Marker-assisted selection (MAS) remains a cornerstone for tracing desirable alleles from WWR into elite wheat backgrounds, particularly in marker-assisted backcrossing schemes aimed at minimizing linkage drag (Sanjay and Prakash 2024). High-throughput SNP platforms and chromosome-specific KASP markers have enabled precise detection of *Aegilops* and *T. urartu* introgressions, facilitating rapid screening of large breeding populations (Przewieslik-Allen *et al.* 2019; Grewal *et al.* 2021). Beyond marker systems, sequence-based detection approaches such as coverage analysis allow genome-wide identification of introgressions and inference of donor species, even in complex or unknown material (Keilwagen *et al.* 2022). Application of these methods has revealed that introgressions from wild relatives can increase bread wheat genetic diversity by 4–32%, underscoring their substantial but often cryptic contribution (Zhou *et al.* 2020).

Discovery: Pangenomes and GWAS

Pangenomic frameworks and GWAS have substantially expanded the discovery of adaptive variation in WWR (Walkowiak *et al.* 2020; Leonova *et al.* 2023). Sequencing of key wild progenitors, such as *Ae. tauschii* (D-genome donor), *T. dicoccoides* and *Secale cereale*, has revealed PAV, copy number variation and introgressed haplotypes linked to stress adaptation (Table 2; Avni *et al.* 2017; Keilwagen *et al.* 2022). Pangenome analyses show that many adaptive loci lost during domestication remain conserved in WWR populations, providing a reservoir of alleles for crop improvement (Table 1; Walkowiak *et al.* 2020; Fernandez *et al.* 2022; Awan *et al.* 2022). For example, alien introgressions that still segregate in elite cultivars confer resistance to rusts and mildew while also affecting RSA and osmotic regulation.

Despite these advances, several methodological limitations persist. The large and polyploid wheat genome reduces GWAS mapping resolution due to extensive linkage disequilibrium and homoeologous gene copies, complicating the identification of causal variants for complex traits (Maccaferri *et al.* 2019). Rare alleles, often enriched in wild relatives, may be missed due to limited statistical power (Alqudah *et al.* 2019). Environmental variability further challenges stress-related GWAS, as genotype × environment interactions strongly influence drought, salinity, and heat tolerance traits, potentially obscuring genetic signals and reducing reproducibility unless multi-environment phenotyping is conducted (Reynolds *et al.* 2021; Tene *et al.* 2022). Additionally, many WWR species, such as *Ae. searsii* and *Elymus* spp., remain poorly represented in genomic databases, leaving critical gaps in the catalogue of stress-adaptive alleles (Table 1).

Complementing pangenomic resources, GWAS in *T. dicoccoides* and related taxa has identified loci underlying resistance to biotic stresses and tolerance to drought and salinity, highlighting the value of combining population-level diversity with high-resolution phenotyping (Tene *et al.* 2022). Collectively, pangenomics and GWAS provide complementary tools for dissecting the complex genetic architecture of adaptive traits, while also revealing priorities for future resource development (Fernandez *et al.* 2022; Tene *et al.* 2022).

Deployment accelerators: Speed breeding and introgression platforms

The deployment of WWR-derived variation can be accelerated through speed breeding, which manipulates photoperiod and temperature to shorten generation time, enabling up to four to five wheat generations per year under controlled conditions (Li *et al.* 2024a). Importantly, speed breeding primarily accelerates generation turnover and does not increase recombination frequency or resolve recombination suppression in low-recombination genomic regions. When combined with marker-assisted introgression and GS, speed breeding facilitates rapid fixation and evaluation of wild-derived alleles for stress adaptation and yield stability (Gudi *et al.*

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Table 2. Reference genomes, resequenced diversity panels, and pangenomes of domesticated and wild wheat types

Species/taxa	Reference/project	Key contributions	Reference
		Reference genomes	
Triticum aestivum	IWGSC RefSeq v1.0, IWGSC RefSeq v2.1	High-quality, chromosome-level genome assembly	IWGSC (2018), Zhou *et al.* (2021)
Triticum durum	Svevo genome	High-quality reference genome for tetraploid wheat	Maccaferri *et al.* (2019)
Triticum urartu	*T. urartu* genome	A genome model for wheat evolution and domestication	Ling *et al.* (2013)
Ae. tauschii	*Ae. tauschii* genome	D-genome donor genome crucial for modern wheat variety studies	Luo *et al.* (2013)
Resequenced diversity panels			
Triticum aestivum	10 + wheat genomes project	Global diversity of bread wheat varieties	Walkowiak *et al.* (2020)
Triticum dicoccoides	Wild emmer resequencing	Significant genetic variation for wheat improvement	Avni *et al.* (2017)
Ae. tauschii	*Ae. tauschii* diversity panel	Revealed significant genetic diversity in *Ae. tauschii*	Arora *et al.* (2019), Cavalet *et al.* (2024)
Pangenomes			
Triticum aestivum	Wheat pangenome	Genetic diversity across multiple cultivars; core and dispensable genes	Walkowiak *et al.* (2020)
Triticum durum	Durum wheat pangenome	Comprehensive genetic diversity within tetraploid wheat	Gaurav *et al.* (2021)

2022). However, accelerated generation cycling alone does not guarantee genetic gain unless coupled with accurate phenotyping and predictive selection. Complex traits such as drought, salinity, and heat tolerance still require multi-environment testing to capture genotype × environment interactions, which cannot be fully replicated under controlled conditions (Watson *et al.* 2018; Potts *et al.* 2023).

Complementary introgression platforms, such as structured populations derived from *Ae. tauschii*, enable systematic transfer of D-genome diversity into bread wheat, supporting targeted exploration of adaptive alleles for stress resilience and agronomic performance (Li *et al.* 2024a). Integrating these platforms with pangenomic resources, MAS, and GS provides a translational bridge from allele discovery in wild relatives to practical breeding deployment. Together, pipelines combining genomic discovery, structured introgression, speed breeding and predictive selection offer a feasible path to accelerate the utilization of WWR diversity in climate-resilient wheat improvement.

Precision modification: Opportunities and limitations

CRISPR/Cas genome editing offers precise allele modification, including gene knockouts, base editing, and targeted deletions relevant to domestication and stress-response traits (Kelliher *et al.* 2019; Borah *et al.* 2024). In wheat, the hexaploid genome complicates editing because most genes exist in three homoeologous copies across the A, B, and D subgenomes (Peng *et al.* 2013). Achieving a complete phenotypic effect often requires simultaneous editing of all homoeologs, increasing the technical complexity of multiplex genome editing. Practical limitations also include low transformation efficiency, regulatory hurdles, and challenges in achieving consistent edits across homoeologous in the large, repetitive genome (Zhou *et al.* 2023; Awan *et al.* 2022). Multiplex editing can partially overcome these challenges, but often requires extensive screening to identify fully edited lines.

Limitations also arise from sgRNA design tools trained on non-plant datasets, variable delivery systems, and cell-type-specific DNA repair pathways (Tan *et al.* 2024), all of which reduce predictability and increase off-target risk. Consequently, genome editing is currently better suited for validating and fine-tuning already identified loci rather than for discovering new adaptive variation (Kelliher *et al.* 2019; Borah *et al.* 2024). In wheat improvement pipelines, CRISPR is most effective for confirming candidate gene function, modifying regulatory elements, or optimizing favourable alleles identified through genomics or pre-breeding (Awan *et al.* 2024; Borah *et al.* 2024; Tan *et al.* 2024). Advances in delivery technologies, tissue culture optimization, and DNA-free editing (e.g., ribonucleoprotein-mediated systems) offer promising avenues to improve efficiency while mitigating regulatory constraints.

Pre-breeding pipelines: Bridging wild and elite germplasm

Pre-breeding provides the critical interface between WWR and elite breeding programmes by converting exotic diversity into usable genetic materials. Global initiatives at CIMMYT, International Center for Agricultural Research in the Dry Areas (ICARDA), and partner institutions have established structured pipelines that emphasize population development, controlled introgression, and early-stage evaluation of wild-derived alleles. A cornerstone of these efforts is SHW, which enables efficient transfer of D-genome diversity while partially overcoming crossability barriers (Warburton *et al.* 2006; Mujeeb-Kazi *et al.* 2008; Aberkane *et al.* 2020).

In addition to SHW, introgression libraries, advanced backcross populations and nested association mapping panels are increasingly used to expose wild alleles in agronomically relevant backgrounds. These resources allow breeders to evaluate stress-adaptive

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variation under managed and target environments, accelerating the identification of promising donor segments. Nevertheless, translating wild-derived variation into cultivars remains a long-term process. From the initial development of SHW or wide-cross derivatives to the release of improved cultivars, breeding pipelines typically require 10–15 years, reflecting multiple generations of selection, backcrossing, and multi-environment field validation. Furthermore, only a small proportion of early-generation introgression lines ultimately progress to advanced breeding programmes due to linkage drag, poor agronomic performance, or instability of stress-adaptive traits (Mondal *et al.* 2016; Gudi *et al.* 2022).

Accurate phenotyping represents an additional bottleneck in effectively utilizing wild germplasm. While genomic tools facilitate the detection of introgressed regions, validating adaptive traits requires robust phenotyping under realistic stress conditions. Recent advances in high-throughput phenotyping – including UAV-based remote sensing, canopy temperature and spectral reflectance measurements, root phenotyping platforms, and managed drought or salinity screening systems – are increasingly enabling large-scale evaluation of physiological traits relevant to dryland adaptation, such as water-use efficiency, canopy temperature depression, and root architecture (Gill *et al.* 2022). Emerging molecular and genomic tools are beginning to strengthen pre-breeding efficiency. Functionally informed markers and validated regulatory modules, such as salinity-related Na^+ exclusion pathways, enable more targeted introgression and reduce reliance on large, undirected wild segments (Wang *et al.* 2024). Genome editing approaches offer additional opportunities to refine pre-breeding outputs, particularly for removing undesirable genomic regions during wide-cross derivatives, although their routine use in wheat remains technically and institutionally constrained (Schulthess *et al.* 2022; Borah *et al.* 2024). Collectively, integrating genomic prediction, targeted introgression and high-throughput phenotyping platforms is expected to accelerate the conversion of wild wheat diversity into deployable breeding materials.

Functional impacts and gaps in utilization

Functional validation of WWR-derived alleles demonstrates substantial potential for improving wheat resilience under abiotic and biotic stress. Well-characterized examples include the *HKT1;5-D* allele from *Ae. tauschii,* validated in elite wheat backgrounds and multi-environment field trials for enhanced salinity tolerance (Munns *et al.* 2012). Similarly, several root-related QTLs from *T. dicoccoides* have been identified in mapping populations and pre-breeding materials, associated with improved root architecture and water-use efficiency under drought. In addition, introgression of a 7DL chromosome segment from *Agropyron elongatum* (*Thinopyrum elongatum*) enhances drought adaptation by increasing root biomass and improving water uptake under stress (Placido *et al.* 2013). Chromosomal translocations from *Secale cereale*, particularly the widely deployed 1RS arm, have been extensively incorporated into commercial cultivars worldwide, providing durable disease resistance and improved stress robustness (Liu *et al.* 2023).

Despite these successes, the practical use of WWR in breeding programmes remains concentrated in a small subset of species and traits. Historically, most successful introgressions have targeted major biotic stress resistance genes, such as rust and pest resistance from species including *Ae. tauschii, S. cereale* and *Thinopyrum* spp., whereas complex adaptive traits like drought tolerance, heat resilience and RSA remain comparatively underutilized in modern cultivars (Dempewolf *et al.* 2017; Reynolds *et al.* 2021).

Several taxa with documented adaptive traits remain underrepresented in breeding pipelines. For example, *Ae. searsii* harbours powdery mildew resistance and quality-related alleles but remains largely confined to pre-breeding research due to limited genomic resources and marker development (Gong *et al.* 2016). Likewise, species within the genus *Elymus* exhibit exceptional drought tolerance and perennial growth habits, yet their distant phylogenetic relationship to wheat imposes severe crossing and ploidy barriers (Khan *et al.* 2022). These challenges illustrate that biological barriers and limited genomic resources still constrain the broader deployment of many wild relatives.

A critical bottleneck in translating wild diversity into breeding gains is not the discovery of genetic variation, but the phenotypic validation of adaptive traits. While genotyping and genome sequencing of wild germplasm collections have expanded rapidly over the past decade, large-scale phenotypic characterization under realistic field conditions has progressed more slowly. Traits such as drought tolerance, root architecture, and water-use efficiency require multi-environment testing and precise physiological measurements, making them considerably more difficult to evaluate than simple Mendelian resistance traits (Sansaloni *et al.* 2020; Reynolds *et al.* 2021; Farooq *et al.* 2025). Consequently, limited phenotyping capacity across diverse environments remains a principal barrier to fully exploiting wild wheat diversity in modern breeding programmes. Addressing this imbalance will require coordinated efforts to expand genomic resources for underutilized species, integrate high-throughput phenotyping platforms with genomic analyses, and prioritize traits with clear agronomic relevance for dryland and stress-prone environments.

Integrated pathways for climate-resilient wheat

Technological pipelines for harnessing WWR diversity

Maximizing WWR's contribution to climate-resilient wheat requires clearly defined technological pipelines that link allele discovery, validation and deployment rather than treating these processes independently (Fig. 2). Genomic resources, including reference genomes, pangenomes and GWAS, enable the discovery of adaptive loci associated with drought tolerance, ion homeostasis, RSA and heat-responsive photosynthetic regulation (Avni *et al.* 2017; IWGSC 2018; Walkowiak *et al.* 2020). The MAS and GS translate these discoveries into breeding populations, while speed breeding accelerates the fixation of favourable alleles and shortens breeding cycles (Mwadzingeni *et al.* 2017; Watson *et al.* 2018). GS is particularly valuable for WWR-derived traits because many adaptive responses to drought, heat and salinity are polygenic and strongly influenced by genotype × environment interactions. By leveraging genome-wide marker information to predict breeding values, GS enables the selection of complex stress-adaptive traits before extensive field evaluation, thereby improving selection efficiency during pre-breeding and introgression programmes (Budhlakoti *et al.* 2022). However, prediction accuracy can decline under strong environmental variation, underscoring the need to train populations across representative stress environments.

Emerging tools such as speed introgression and genome editing provide opportunities to fine-tune wild alleles, for example, by reducing the size of salinity-tolerance introgressions, such as HKT1;5, to minimize yield penalties under non-stress conditions (Munns *et al.* 2012; Li *et al.* 2024a).

https://doi.org/10.1017/S1479262126100689 Published online by Cambridge University Press

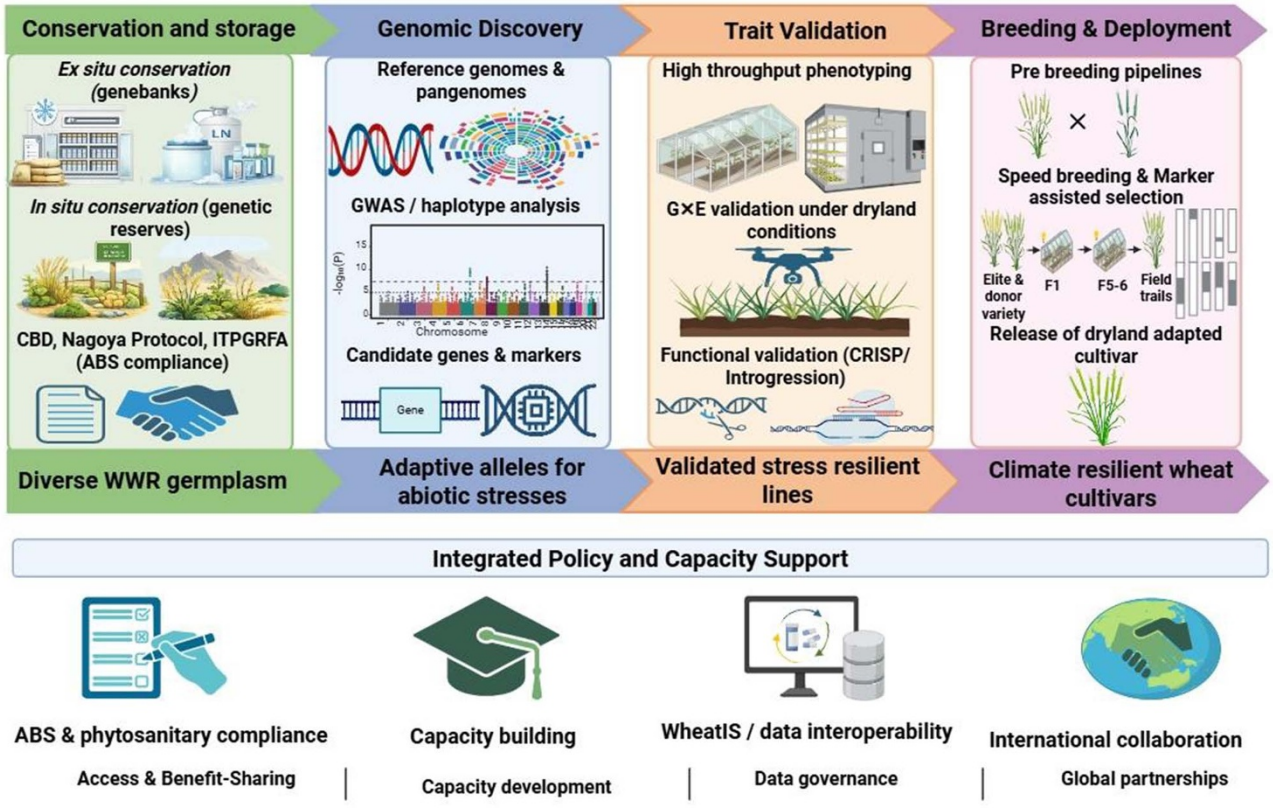


Figure 2. Stepwise conservation-to-deployment pipeline for harnessing wild wheat relatives in dryland wheat improvement.
Note: Stepwise pipeline for utilizing wild wheat relatives (WWR) in dryland wheat improvement, linking conservation, genomic discovery, trait validation and breeding deployment. The framework integrates enabling policy, access and benefit-sharing (ABS), capacity building, and data interoperability to support equitable and efficient utilization of WWR-derived adaptive alleles.

Complementary case studies illustrate the deployment spectrum: CRISPR/Cas9-mediated knockout of the yield-related negative regulator *TaD27* in an elite wheat cultivar increased tiller number and grain yield without morphological penalties, demonstrating how targeted editing can optimize major-effect genes directly in breeding-ready backgrounds while avoiding linkage drag (Awan *et al.* 2024). In contrast, high-throughput whole-genome speed-introgression platforms have enabled rapid transfer of the *Ae. tauschii* genome into elite wheat within approximately two years, providing scalable access to complex, polygenic stress-adaptive variation that remains difficult to capture through conventional introgression (Li *et al.* 2024a). Together, these approaches indicate that genome editing is most effective for precise trait optimization, whereas accelerated introgression pipelines remain essential for mobilizing polygenic resilience traits from WWR. Nevertheless, their practical deployment is constrained by regulatory uncertainty surrounding genome editing, limited high-throughput phenotyping capacity, and high operational costs, particularly in dryland breeding programmes of low- and middle-income countries, highlighting the need for coordinated investment and capacity building to translate technological advances into field-level impact (Louafi and Welch 2021; Zhu *et al.* 2026).

Conservation modalities: from static preservation to dynamic use

Ex situ and *in situ* conservation approaches are complementary rather than interchangeable, and both are required to sustain WWR's adaptive potential under climate change (Fig. 2; Maxted *et al.* 2016; Dempewolf *et al.* 2017). *Ex situ* genebank collections provide immediate and well-documented access to germplasm for genomic analysis, pre-breeding, and trait discovery. However, evidence shows that such collections often capture only a portion of the diversity present in natural populations, frequently exhibiting reduced heterozygosity and allelic richness when sampling is limited (Fu 2017; Wei and Jiang 2021). Sampling strategies that include 30–50 individuals distributed across a species' geographic range substantially improve the genetic representativeness of *ex situ* collections (Wei and Jiang 2021). Similarly, Özkan *et al.* (2005) argue that for *Hordeum spontaneum*, priority should shift toward sampling a greater number of populations rather than increasing the number of individuals within a single population, in order to better capture and safeguard genetic diversity in the wild barley gene pool. We consider this population-focused approach to be equally applicable to WWR. *In situ* conservation complements these limitations by maintaining WWR populations within their native habitats, where they continue to evolve under environmental pressures such as drought, salinity and pathogen stress (Maxted *et al.* 2016; Bellon *et al.* 2017). Global gap analyses indicate that nearly 30% of crop wild relatives are underrepresented in genebanks, and more than 70% require additional collecting, underscoring significant gaps in current conservation coverage (Castañeda-Álvarez *et al.* 2016). Targeted international initiatives have begun addressing these gaps; for example, coordinated collecting missions between 2013 and 2018 secured over 4,500 new crop wild relative accessions representing 355 taxa across 25 countries, many of which are

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now incorporated into pre-breeding programmes (Eastwood *et al.* 2022). Nevertheless, regional analyses still reveal significant underrepresentation. In the Fertile Crescent, assessments of 441 priority crop wild relatives found that 30% are absent from genebanks and 57% are represented by fewer than 10 accessions, highlighting the vulnerability of adaptive diversity and the need for targeted conservation strategies (Vincent *et al.* 2013; Zair *et al.* 2021). Importantly, ongoing evolution in natural populations – particularly under the pressures of climate change – generates new adaptive alleles that may be critical for future crop improvement. The loss of wild populations through habitat degradation therefore risks eliminating valuable genetic variation before it can be characterized or incorporated into breeding programmes.

An integrated conservation framework that links static preservation with dynamic evolutionary processes is therefore essential. Genebanks should increasingly function as genomics-informed resources supported by broad geographic sampling and improved characterization, while *in situ* genetic reserves should be strategically established in diversity hotspots relevant to dryland agriculture (Vincent *et al.* 2022; Wambugu *et al.* 2022). Aligning conservation priorities with breeding needs can ensure that WWRs are preserved not only as biodiversity assets but also as practical reservoirs of climate-adaptive variation for future wheat improvement.

Integrated conservation-to-deployment pathways

Translating WWR diversity into climate-resilient cultivars requires coordinated conservation-to-deployment pipelines that integrate genomic discovery, phenotyping, and breeding. A practical framework includes: (i) targeted gap-filling of underrepresented WWR gene pools through coordinated *ex situ* and *in situ* conservation; (ii) genomic and haplotype-based discovery of adaptive alleles using pangenomes and GWAS; (iii) multi-environment phenotyping to evaluate yield–stress tolerance trade-offs and (iv) deployment through pre-breeding platforms such as synthetic wheats, introgression libraries and genomic prediction (Fig. 2; Mujeeb-Kazi *et al.* 2008; Warburton *et al.* 2006; Kilian *et al.* 2021; Farooq *et al.* 2025).

The efficiency of this pipeline depends not only on scientific advances but also on the governance frameworks that regulate access to WWR germplasm. Delays or uncertainty in access procedures can prolong the establishment of pre-breeding populations, thereby slowing the introgression and fixation of adaptive alleles and delaying the assessment of yield stability across target environments.

Future innovations, including haplotype-informed pangenome selection and *de novo* domestication, hold high potential but differ markedly in feasibility and time horizon, largely due to differences in regulatory frameworks, infrastructure requirements, and phenotyping capacity (Kilian *et al.* 2021; Zhu *et al.* 2026). In particular, access conditions may vary depending on the taxonomic status of the material: while many cultivated *Triticum* resources and some closely associated *Aegilops* materials are exchanged through the ITPGRFA multilateral system, numerous wild relatives fall outside Annex 1 and are therefore subject to bilateral access and benefit-sharing (ABS) procedures under the CBD and Nagoya Protocol (Sherman and Henry 2021; Ebert *et al.* 2023; Engels and Ebert 2024). These distinctions influence how rapidly WWR diversity can move from conservation collections into pre-breeding and applied breeding pipelines. Ensuring equitable participation in this pipeline is therefore critical. Without improved access to conserved germplasm, genomic tools, and phenotyping platforms in dryland countries, the benefits of WWR-derived resilience are unlikely to reach the regions most vulnerable to climate stress (Louafi and Welch 2021). Aligning genebanks, international breeding programmes, and enabling policy frameworks into a unified pipeline can reposition WWR from passive genetic reservoirs into active drivers of climate-resilient wheat improvement, while maintaining realistic expectations about yield stability and adoption timelines (Özkan *et al.* 2002; Kilian *et al.* 2021; Mastrangelo *et al.* 2025).

Policy and international cooperation

Scientific advances in genomics, phenotyping, and pre-breeding have substantially increased WWR's potential to support climate-resilient wheat improvement. However, translation into breeding impact ultimately depends on policy environments and international cooperation (Fig. 2). Access to WWR, the movement of germplasm and data, and the equitable sharing of benefits are governed by complex legal and governance frameworks that can either enable or constrain innovation. Integrating these governance considerations with breeding pipelines is therefore essential to ensure that WWR-derived diversity is conserved, accessed and deployed efficiently, particularly in dryland regions where climate adaptation needs are most urgent.

Harmonizing access, benefit-sharing, and digital sequence information

Effective conservation and utilization of WWR for climate-resilient wheat improvement depend on coherent implementation of international ABS frameworks, particularly the CBD, the Nagoya Protocol and ITPGRFA. As discussed in the conservation-to-deployment pathway above, differences between the ITPGRFA multilateral system and bilateral ABS procedures can influence the speed at which WWR germplasm enters pre-breeding and applied breeding programmes. Greater harmonization across these frameworks is required to reduce legal uncertainty for pre-breeding and genomics-assisted research.

The rapid expansion of genomic sequencing has intensified debates around Digital Sequence Information (DSI), as breeders increasingly access adaptive alleles through sequence data rather than physical germplasm. Current ABS mechanisms inadequately address DSI, creating risks of bypassing benefit-sharing obligations and eroding trust with provider countries (Sherman and Henry 2021; Lawson *et al.* 2024). Internationally agreed guidance that links DSI use to transparent benefit-sharing mechanisms is therefore essential to sustain genomic research on WWR while ensuring equity.

Enabling equitable utilization: Capacity, infrastructure and data

Policy effectiveness is ultimately determined by national and regional capacity to conserve, characterize and deploy WWR. Many diversity-rich, dryland regions lack well-resourced genebanks, molecular characterization facilities and high-throughput phenotyping platforms, limiting their ability to participate meaningfully in WWR-based breeding pipelines (Ebert *et al.* 2023). Recent multi-country assessments applying standardized monitoring and evaluation frameworks across 20 Global South countries demonstrate that systematic genebank

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performance reviews can identify operational gaps, guide targeted capacity development and improve the efficiency and effectiveness of *ex situ* conservation systems. Thus, strengthening genebank infrastructure and investing in genomic and phenotypic characterization are critical prerequisites for effective WWR utilization.

Beyond physical infrastructure, interoperable data systems are essential to translate conserved diversity into usable breeding knowledge. The value of *ex situ* collections depends on the systematic integration of passport, phenotypic, environmental and omics data within federated digital infrastructures that enable discovery, reuse and traceability (Shaw *et al.*). The Wheat Information System (WheatIS) exemplifies this approach by linking genomic and phenotypic datasets to accession-level metadata across distributed repositories, allowing climate-adaptive traits identified in WWR to be traced through pre-breeding materials and into applied breeding pipelines (Langridge *et al.* 2022; Tian *et al.* 2025). Consistent with the Global Information System vision, WheatIS operates as part of a federated network rather than a centralized database, relying on shared standards, application programming interfaces, and persistent identifiers such as Digital Object Identifiers to address long-standing challenges of data fragmentation and germplasm traceability (Shaw *et al.*). However, the effectiveness of such platforms depends on equitable global participation. Many diversity-rich, climate-vulnerable regions remain underrepresented in global datasets, reinforcing data asymmetries that limit trait discovery and bias downstream utilization. Expanding WheatIS-like infrastructures through sustained engagement with provider countries, alongside support for data curation, standardized phenotyping, and identifier assignment, is therefore critical to ensure that WWR-derived knowledge contributes meaningfully to climate-resilient wheat improvement where it is most urgently needed.

Cooperative models, regional hubs and long-term sustainability

International cooperation provides practical pathways to translate policy frameworks into operational impact (Fig. 2). The Consultative Group for International Agricultural Research (CGIAR) genebanks demonstrate how large-scale conservation, standardized germplasm exchange, and coordinated benefit-sharing can support global crop improvement (Engels and Ebert 2024). Complementing these operational models, coordination platforms such as the Wheat Initiative (https://www.wheatinitiative.org/) play a critical enabling role by aligning research priorities, data standards and pre-breeding efforts across public institutions, genebanks and breeding programmes worldwide. Regional initiatives such as the European Genebank Integrated System further highlight the value of coordinated conservation tailored to specific ecological contexts.

Building on these models, the establishment of regional conservation–breeding hubs in WWR diversity hotspots offers a promising pathway forward. However, many of these diversity hotspots, including parts of the Fertile Crescent and West Asia, are affected by geopolitical instability, which can threaten both *in situ* conservation and long-term access to genetic resources, underscoring the importance of distributed conservation strategies. Embedding WWR explicitly within national climate adaptation strategies can further align conservation priorities with breeding demand (Reynolds *et al.* 2021; Bohra *et al.* 2024). Long-term funding commitments for genebanks and genetic reserves, coupled with transparent tracking of germplasm utilization, are essential to sustain trust and ensure fair benefit-sharing. Initiatives such as the Crop Trust's BOLD Project (Biodiversity for Opportunities, Livelihoods and Development) – a decade-long, Norway-funded programme designed to strengthen conservation, documentation, and use of crop diversity in collaboration with national genebanks and breeding partners – illustrate how stable resourcing and coordinated capacity support can enhance both conservation and use of diversity by breeders and farmers alike (https://bold.croptrust.org/). Critically, co-development of pre-breeding pipelines with provider countries rather than one-directional germplasm extraction will be key to transforming WWR from conserved assets into active drivers of climate-resilient wheat improvement.

Conclusion

The WWRs constitute an indispensable genetic foundation for enhancing wheat resilience to drought and salinity in dryland agroecosystems. This review advances previous syntheses by integrating adaptive trait biology, modern genomic deployment tools, and policy and access constraints into a unified framework that links WWR discovery to practical breeding outcomes. The review highlights that while pangenomics, GS, speed introgression and genome editing have markedly improved the precision and pace of WWR utilization, their impact remains uneven due to persistent challenges, including polygenic stress tolerance, genotype × environment interactions, linkage drag, regulatory uncertainty around genome editing, and limited pre-breeding and phenotyping capacity in many dryland regions.

A realistic pathway forward requires prioritization rather than breadth. Key near-term opportunities lie in well-characterized gene pools such as *Ae. tauschii* and *T. dicoccoides*, targeted deployment in representative dryland agroecologies, and focused mitigation of bottlenecks in allele validation and introgression. Strengthening conservation–breeding linkages through genomics-enabled *ex situ* and *in situ* strategies, alongside equitable access frameworks under the CBD, Nagoya Protocol, and ITPGRFA, will be essential to sustain the flow of adaptive diversity. Ultimately, WWR should not be viewed as auxiliary resources but as core components of future dryland wheat improvement, without which durable adaptation to increasing climatic variability is unlikely to be achieved. Progress in WWR utilization can be monitored through practical indicators, including the number of WWR-derived introgressions released in commercial cultivars, the expansion of introgression libraries in breeding programmes, and the frequency of WWR alleles deployed in multi-environment trials.

Declaration of AI Assistance in Language Editing The authors used ChatGPT to improve language clarity and to correct minor grammatical and stylistic errors. All suggestions were carefully reviewed, and the authors retain full responsibility for the content of this publication.

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