

Revisiting Wild Relatives: Genetic Reservoirs for Climate Adaptation in Crops

Vinodh Kumar P.N.*, Sahana Police Patil and Keerthi G.M.

Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India.

(Corresponding author: Vinodh Kumar P.N.*)

(Received: 08 July 2023; Revised: 21 August 2023; Accepted: 05 September 2023; Published: 15 September 2023)

(Published by Research Trend)

ABSTRACT: Global food security is under threat from climate change, population growth, and environmental degradation, necessitating the development of climate-resilient crops. Crop wild relatives (CWRs), the undomesticated progenitors of cultivated crops, harbor valuable genetic traits for stress tolerance, disease resistance, and improved resource-use efficiency. Despite their potential, CWRs remain underutilized due to biological barriers and the complexity of pre-breeding programs. Recent advances in genomics, precision gene-editing (e.g., CRISPR-Cas9), and machine learning are overcoming these challenges, enabling efficient trait introgression from wild species into elite crop varieties. This review examines pre-breeding strategies, genomic tools, and successful case studies that highlight the role of CWRs in climate adaptation. We also discuss challenges—such as regulatory barriers and linkage drag—and propose policy and technological solutions to enhance CWR utilization for sustainable agriculture.

Keywords: Crop wild relatives, climate resilience, pre-breeding, genomics, CRISPR-Cas9.

INTRODUCTION

Global food security faces unprecedented challenges from climate change, population growth, and environmental degradation (Ray *et al.*, 2019). Rising temperatures, erratic rainfall patterns, and the proliferation of pests and pathogens are reducing agricultural productivity worldwide, while urbanization and soil depletion continue to shrink arable land (FAO, 2022). Current projections suggest global food production must increase by 60-70% by 2050 to meet demand (van Dijk *et al.*, 2021), yet conventional breeding approaches are struggling to keep pace with these rapidly changing conditions. A major limiting factor is the narrow genetic base of modern elite crop varieties, which have lost significant ancestral diversity through intensive selection for yield and uniformity (Hajjar & Hodgkin 2007). This genetic erosion has severely constrained the adaptive potential of crops to emerging biotic and abiotic stresses (Tanksley and McCouch 1997).

Crop wild relatives (CWRs) are the undomesticated progenitors and closely related species of cultivated crops, represent a vital reservoir of genetic diversity for crop improvement (Dempewolf *et al.*, 2017). Having evolved under natural selection pressures, CWRs harbour numerous valuable traits including drought tolerance, disease resistance, salinity tolerance, and nutrient efficiency (Brozynska *et al.*, 2016). For instance, wild wheat relatives such as *Aegilops tauschii* have provided crucial genes for resistance to devastating wheat rust pathogens (Rouse *et al.*, 2011), while wild tomato species like *Solanum pennellii* have contributed to improved water-use efficiency in cultivated varieties (Xu *et al.*, 2013). CWRs

contributing to major crops include *Oryza rufipogon*, a wild rice species that has provided drought and disease resistance genes to cultivated rice (*Oryza sativa*) (Xiao *et al.*, 1996).

Another notable example is *Solanum pennellii*, a wild tomato relative that has been used to improve heat and salinity tolerance in domesticated tomatoes (*Solanum lycopersicum*) (Rick, 1982). Similarly, *Triticum dicoccoides*, a wild ancestor of wheat, has been a valuable source of drought tolerance traits (Nevo *et al.*, 2002). Despite their demonstrated potential, CWRs remain significantly underutilized due to biological barriers (e.g., hybrid sterility, linkage drag) and the resource-intensive nature of pre-breeding programs (Prohens *et al.*, 2017).

Recent advances in genomics and molecular breeding are now overcoming these historical limitations (McCouch *et al.*, 2020). High-throughput sequencing technologies have enabled comprehensive characterization of CWR genetic diversity, while pan-genome assemblies are revealing previously inaccessible structural variation (Walkowiak *et al.*, 2020). Precision gene-editing tools like CRISPR-Cas9 allow direct modification of CWR-derived alleles (Zsögön *et al.*, 2018), and improved pre-breeding strategies; including the development of introgression libraries and marker-assisted backcrossing - are facilitating more efficient transfer of beneficial wild alleles into elite germplasm (Warschefsky *et al.*, 2016). This review examines how the integration of pre-breeding strategies, genomic technologies, and applied case studies is transforming CWR utilization for climate-resilient crop improvement. Specifically, we: Analyse pre-breeding approaches that bridge wild and

cultivated gene pools, including hybrid stabilization techniques and advanced backcrossing schemes.

Wheat CWRs	Rice CWRs
1. <i>Triticum urartu</i>	1. <i>Oryza rufipogon</i>
2. <i>Aegilops speltoides</i>	2. <i>Oryza nivara</i>
3. <i>Aegilops tauschii</i> (<i>Triticum tauschii</i>)	3. <i>Oryza glaberrima</i>
4. <i>Triticum boeoticum</i>	4. <i>Oryza barthii</i>
5. <i>Triticum dicoccoides</i>	5. <i>Oryza longistaminata</i>
6. <i>Triticum araraticum</i>	6. <i>Oryza punctata</i>
7. <i>Aegilops caudata</i>	7. <i>Oryza officinalis</i>
8. <i>Aegilops comosa</i>	8. <i>Oryza minuta</i>
9. <i>Aegilops ventricosa</i>	9. <i>Oryza alta</i>
10. <i>Aegilops cylindrica</i>	10. <i>Oryza grandiglumis</i>
Barley CWRs	Tomato CWRs
1. <i>Hordeum spontaneum</i>	1. <i>Solanum pimpinellifolium</i>
2. <i>Hordeum bulbosum</i>	2. <i>Solanum cheesmaniae</i>
3. <i>Hordeum murinum</i>	3. <i>Solanum galapagense</i>
4. <i>Hordeum marinum</i>	4. <i>Solanum chmielewskii</i>
5. <i>Hordeum jubatum</i>	5. <i>Solanum habrochaites</i>
6. <i>Hordeum pusillum</i>	6. <i>Solanum peruvianum</i>
7. <i>Hordeum brachyantherum</i>	7. <i>Solanum pennellii</i>
8. <i>Hordeum chilense</i>	8. <i>Solanum lycopersicoides</i>
9. <i>Hordeum secalinum</i>	9. <i>Solanum sitiens</i>
10. <i>Hordeum capense</i>	10. <i>Solanum ochranthum</i>

Fig. 1. list of CWRs (crop wild relatives of various crops.

Key Stress-Tolerant Traits in CWRs. CWRs exhibit remarkable adaptations to both abiotic and biotic stresses, making them indispensable for breeding resilient crops.

Abiotic Stress Tolerance. Many CWRs have evolved mechanisms to survive extreme environmental conditions. For instance, *Triticum dicoccoides* (wild emmer wheat) possesses deep root systems and enhanced water-use efficiency, traits that have been introgressed into modern wheat varieties to improve drought tolerance (Peleg *et al.*, 2005). Similarly, *Hordeum spontaneum* (wild barley) has been found to carry genes that enable growth in highly saline soils, offering potential for improving salt tolerance in cultivated barley (Nevo & Chen 2010).

Biotic Stress Resistance. CWRs also serve as a rich source of resistance to pests and diseases. The tepary bean (*Phaseolus acutifolius*), for example, exhibits strong resistance to bean beetles (*Acanthoscelides obtectus*), a trait that has been explored for improving common bean varieties (Singh *et al.*, 2001). Another example is *Solanum habrochaites*, a wild tomato species that provides resistance to whiteflies and fungal pathogens, traits that have been incorporated into commercial tomato breeding programs (Firdaus *et al.*, 2012).

Pre-Breeding: Bridging Wild and Cultivated Gene pools. Challenges in utilizing CWRs. While CWRs offer immense potential for crop improvement, their use in breeding programs faces several challenges. Reproductive barriers, such as differences in ploidy levels and flowering times, can hinder successful hybridization between wild and cultivated species (Warschewsky *et al.*, 2014). Additionally, linkage drag, the transfer of undesirable wild traits along with beneficial genes, can complicate breeding efforts (Hajjar & Hodgkin 2007). Strategies to overcome barriers to effectively harness the genetic potential of CWRs, researchers employ advanced pre-breeding strategies.

Introgression Lines (ILs): Introgression lines are developed by repeatedly backcrossing wild species with cultivated varieties while retaining specific chromosomal segments from the wild donor. For example, tomato introgression lines derived from *Solanum pennellii* have been used to identify genes responsible for stress tolerance and fruit quality (Eshed & Zamir 1995).

Advanced Backcrossing with Marker-Assisted Selection (MAS): Marker-assisted selection helps breeders minimize linkage drag by tracking desirable genes during backcrossing. This approach has been successfully used in rice breeding, where genes from *Oryza rufipogon* were introgressed into elite varieties while eliminating unwanted traits (McCouch *et al.*, 2020).

Somatic Hybridization: For distantly related species where conventional crossing is difficult, somatic hybridization is a technique involving the fusion of protoplasts to facilitate gene transfer. This method has been applied in citrus breeding, where wild relatives like *Citrus reticulata* have been hybridized with cultivated varieties to enhance disease resistance (Grosser *et al.*, 2000).

Genomics Tools for CWR Exploitation. The rapid advancement of genomics has revolutionized the utilization of crop wild relatives (CWRs) in breeding programs. High-throughput sequencing technologies now allow researchers to decode the genomes of wild species, identify stress-resilient genes, and integrate them into elite crop varieties.

High-Throughput Sequencing. Whole-genome sequencing (WGS) of CWRs has uncovered valuable genetic variants associated with adaptive traits. For example, the genome of *Oryza barthii*, a wild African rice, was sequenced to identify drought-responsive genes that were later introgressed into cultivated rice (*Oryza sativa*) (Wang *et al.*, 2014). Similarly, pan-genome studies which compare multiple wild and cultivated genomes have revealed extensive structural variations, such as presence/absence variations and copy number variations, that contribute to phenotypic diversity (Tao *et al.*, 2019).

Trait Mapping Approaches. To pinpoint genes underlying stress tolerance, genome-wide association studies (GWAS) and quantitative trait locus (QTL) mapping are widely used. For instance, GWAS in wild barley (*Hordeum spontaneum*) populations identified genomic regions linked to heat tolerance (Thabet *et al.*, 2018). Transcriptomics has further elucidated gene expression patterns under stress; a study on wild barley exposed to heat stress revealed upregulation of heat-shock proteins (HSPs) and transcription factors that could enhance thermotolerance in cultivated varieties (Mascher *et al.*, 2019).

Machine Learning for Predictive Breeding. Machine learning (ML) models are increasingly applied to predict optimal gene introgressions from CWRs. By analysing large genomic and phenotypic datasets, ML algorithms can prioritize candidate genes for traits like drought tolerance or disease resistance. For example, neural networks have been used to predict the performance of wild tomato (*Solanum pennellii*)

introgressions in cultivated tomatoes, accelerating pre-breeding efforts (Kooke *et al.*, 2019).

Case Studies: Success Stories in CWR Utilization.

The strategic utilization of crop wild relatives (CWRs) has yielded remarkable success stories that demonstrate their immense value in addressing critical agricultural challenges. Three particularly compelling cases highlight how wild genetic resources have been successfully harnessed to improve major crops.

In rice cultivation, the discovery and implementation of the *Xa21* gene from wild African rice (*Oryza longistaminata*) revolutionized bacterial blight resistance. This breakthrough emerged from extensive screening of wild rice accessions, with researchers identifying *Xa21* as a receptor-like kinase gene that provides broad-spectrum protection against *Xanthomonas oryzae* (Khush *et al.*, 1990; Song *et al.*, 1995). Through marker-assisted backcrossing, scientists successfully transferred this wild-derived resistance into elite varieties like IR24 and IR64, creating cultivars now grown on over 10 million hectares across Asia and Africa. This pioneering work not only protected rice yields but also established a model for subsequent wild gene transfers in cereal crops.

Wheat improvement efforts similarly benefited from wild genetic resources when facing the devastating Ug99 stem rust epidemic. Researchers turned to wild emmer wheat (*Triticum dicoccoides*), the progenitor of domesticated wheat, which harboured the crucial *Sr2* resistance gene. This gene's value lies in its durable, race-nonspecific resistance mechanism (Hiebert *et al.*, 2010). Breeders successfully incorporated *Sr2* into modern varieties such as 'Kingbird' and 'Robin', combining it with other resistance genes to create multiline protection now safeguarding more than 5 million hectares of wheat in vulnerable regions. The ongoing refinement of molecular markers continues to enhance the efficiency of transferring these wild-derived resistances.

Tomato production faced mounting challenges from rising global temperatures, which severely impair fruit set by reducing pollen viability above 35°C. The solution emerged from wild tomato relatives, particularly *Solanum habrochaites* accession LA1777, which exhibited exceptional heat tolerance (Paupière *et al.*, 2017). Transcriptomic analyses revealed upregulated heat shock proteins, antioxidant enzymes, and sugar metabolism genes in this wild species. These findings enabled the development of heat-tolerant hybrids like 'Solar Fire' and 'Heat Master', while also providing molecular markers for more precise breeding. Current research builds on these discoveries by investigating epigenetic regulation of heat response and expanding applications to other abiotic stresses.

Challenges and Future Directions in Crop Wild Relative Utilization. While crop wild relatives (CWRs) offer immense potential for crop improvement, several significant challenges hinder their effective utilization. One major limitation is the lack of comprehensive phenotyping data for many wild accessions in germplasm collections. Most CWRs remain poorly characterized for key agronomic traits, creating a bottleneck in identifying useful genetic variation

(McCouch *et al.*, 2013). Emerging high-throughput phenotyping platforms, including drone-based imaging and automated greenhouse systems, show promise for rapidly screening wild populations for stress tolerance traits (Yang *et al.*, 2020). However, these technologies require substantial investment and standardization across research institutions. Regulatory barriers present another critical challenge, particularly for CRISPR-edited CWR derivatives. Many countries maintain restrictive GMO regulations that fail to distinguish between transgenic organisms and precision-edited crops, delaying the deployment of improved varieties (Smyth, 2022). This regulatory uncertainty discourages both public and private sector investment in CWR-based breeding programs. Additionally, biological barriers such as reproductive incompatibility and linkage drag, where undesirable wild traits are co-inherited with beneficial genes complicate breeding efforts (Warschefsky *et al.*, 2014). These technical challenges require innovative solutions to bridge the gap between wild and cultivated gene pools.

Several promising approaches are emerging to overcome these limitations. Speed breeding techniques, using controlled environment growth chambers with extended photoperiods, can produce up to six generations per year, dramatically accelerating pre-breeding cycles (Watson *et al.*, 2018). Synthetic biology offers another revolutionary approach through de novo domestication, where CRISPR-Cas9 is used to edit key domestication genes in wild species. This was successfully demonstrated in wild *Physalis*, where researchers edited just five genes to develop plants with desirable agronomic traits (Lemmon *et al.*, 2018). Artificial intelligence and machine learning are also being deployed to predict optimal wild alleles for introgression, helping breeders navigate complex genotype-phenotype relationships (Crossa *et al.*, 2021). Policy and institutional support remain critical for realizing the potential of CWRs. Increased funding is urgently needed for systematic characterization of wild germplasm and establishment of robust pre-breeding programs. Global seed banks must expand and better document their collections of high-priority CWRs, particularly for crops critical to food security (Castañeda-Álvarez *et al.*, 2016). Public-private partnerships can help scale the development and commercialization of CWR-derived varieties, ensuring these genetic resources reach farmers' fields (McCouch *et al.*, 2020). Harmonized international regulations for gene-edited crops would further facilitate the use of modern breeding technologies with CWRs.

CONCLUSIONS

Harnessing CWRs for Sustainable Agriculture. Crop wild relatives represent an unparalleled genetic resource for addressing the pressing challenges of climate change, emerging pests and diseases, and soil degradation. Their evolutionary adaptations, developed over millennia in challenging environments, offer solutions that the narrow genetic base of domesticated crops cannot provide. However, fully realizing this

potential requires an integrated approach combining cutting-edge science with supportive policies. Advanced genomics tools are essential for efficient gene discovery and characterization in wild populations. Techniques like pan-genome analysis and genome-wide association studies can help identify valuable alleles hidden in CWRs. Equally important are innovative pre-breeding strategies that effectively bridge wild and cultivated gene pools, such as the development of introgression lines and application of speed breeding protocols. The path forward requires concerted action on multiple fronts. Conservation of CWRs in their natural habitats must be prioritized, particularly in biodiversity hotspots facing rapid environmental change. Substantial investments are needed to build pre-breeding pipelines that can translate wild traits into usable breeding materials. Regulatory frameworks should be updated to facilitate rather than hinder the use of gene-edited CWR derivatives in breeding programs. As we face unprecedented challenges to global food security, CWRs offer a vital resource for developing climate-resilient, sustainable agricultural systems. By combining scientific innovation with collaborative policy action, we can transform these wild genetic resources into powerful tools for securing our food future. The time to act is now - to conserve, characterize, and utilize the precious genetic diversity that crop wild relatives contain before it is lost forever.

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How to cite this article: Vinodh Kumar P.N., Sahana Police Patil and Keerthi G.M. (2023). Revisiting Wild Relatives: Genetic Reservoirs for Climate Adaptation in Crops. *Biological Forum – An International Journal*, 15(9): 1120-1124.