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Harnessing Wild Relatives for Crop Improvement: Genetic Resources, Breeding Strategies, and Applications in Enhancing Yield, Quality, and Resilience

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ABSTRACT

Crop wild relatives (CWRs) represent a critical reservoir of genetic variation that is essential for modern crop improvement. These wild and weedy counterparts of domesticated species contribute traits like resistance to biotic and abiotic stresses, enhanced nutritional quality, and greater environmental adaptability. The utilization of CWRs in plant breeding is framed by the gene pool concept, which categorizes genetic proximity into primary, secondary, and tertiary gene pools based on crossability. Despite their potential, the integration of CWRs into elite cultivars is constrained by biological barriers, linkage drag, sterility in hybrids, and complex phenotyping requirements. However, recent advances in genomics, gene editing (e.g., CRISPR/CAS9), molecular marker-assisted selection, and interspecific hybridization techniques have improved the identification and introgression of valuable traits from CWRs into cultivated crops. These innovations, coupled with data-informed germplasm management and supportive policy frameworks, offer new avenues to overcome previous limitations. The strategic use of CWRs enhances crop resilience, productivity, and sustainability in the face of climate change, evolving pest and disease pressures, and resource constraints. This review synthesizes current strategies, tools, and challenges in effectively utilizing CWRs and underscores their pivotal role in securing global food and nutritional security.

Keywords: CAS9 gene editing, CRISPR, Crop wild relatives, Gene pool concept, Interspecific hybridization, Molecular marker-assisted selection

Introduction

Crop wild relatives (CWRs) are the wild and weedy counterparts of domesticated crops, typically found and sustained in their natural habitats within their centers of origin. They include the ancestors or original forms of all cultivated species and serve as valuable reservoirs of genetic diversity for key traits beneficial in plant breeding.[1] For nearly a century, advancements in plant breeding and agronomic practices have significantly contributed to steady increases in global food production. Feeding a population expected to grow by 34% over the next three decades will require boosting food output by 44 million tons annually, equating to a 37% rise above the current annual production level of 32 million metric tons.[2] The use of CWRs genes in crop improvement dates back over 60 years, marking a long-standing recognition of their value in enhancing agricultural traits.[3] CWRS and traditional landrace varieties hold a wide range of valuable traits crucial for enhancing crop resilience in challenging environmental conditions and ensuring the stability of global food production.[4]

CWRs have provided breeders with several 'game-changing' traits or genes that have boosted crop resilience and global agricultural production. Advances in breeding and genomics have accelerated the identification of valuable CWRs for crop improvement.[5] CWRs possess natural resistance genes that can be used to enhance pest resistance in cultivated crops. Their genetic diversity offers breeders valuable traits to develop varieties resilient to evolving pest pressures. Utilizing CWR helps reduce reliance on chemical pesticides, promoting sustainable pest management.[6] In parallel, growing sequence information on wild genomes with precise gene-editing tools provides a fast-track route to transform CWRs into ideal future crops.[3] Still, integrating genes from CWRs into cultivated crop varieties poses significant challenges. Breeders often hesitate to include CWRs in commercial breeding due to crossability barriers, linkage drag, suboptimal agronomic traits, and complex phenotyping requirements. However, the key issues faced by the breeders working to introduce new trait variation from wild or traditional germplasm into elite modern cultivars include biological barriers to compatibility and crossability, sterility in the F1 generation and backcross (BC1) progeny, infertility of offspring, and limited recombination between the genomes of elite and wild species.[7]

However, recent advancements in plant molecular biology data-informed germplasm collection, management strategies, and adequate policy support have opened up new possibilities for addressing many of these issues to improve access to CWRs and their sustainable use in meeting food and nutrition security targets.[3,5] Genes can now be precisely edited in their native locations, allowing for the reintroduction of ancestral alleles associated with beneficial traits into modern elite cultivars, without disturbing the overall genetic makeup of the plant.[5]

These innovations, alongside improved breeding methods, offer promising avenues to overcome the limitations of CWR used in crop improvement. Integrating CWRs into breeding programs can enhance crop performance and resilience, especially in the face of climate change and other environmental stresses. This review explores the role of CWRs in modern crop improvement, the concept of gene pool, the molecular tools and strategies facilitating their use, the challenges involved, and the prospects for using these valuable genetic resources to secure global food production and nutrition in an increasingly unpredictable world.

The Concept of Gene Pool in Crop Improvement

The “gene pool” encompasses all the genes and alleles found in individuals capable of interbreeding or potentially hybridizing with one another. It represents the collective genetic reservoir of a population or group of related species.[8] The term “gene pool” refers to the entire collection of genes and their various combinations within a particular species population at a given time. Most often, it is used to describe the full set of genetic material shared among individuals of the same species, highlighting the total genetic diversity available within that group.[9] Hence, a gene pool is the full range and quantity of genes and alleles present in a sexually reproducing population that can be passed on to the next generation. It embodies the genetic potential of the population, influencing its adaptability and evolutionary trajectory.[10]

In 1971, Harlan and de Wet introduced a foundational concept in crop improvement, the classification of gene pools. This idea has since become central to the strategic use of plant genetic resources (PGRs). In population genetics, a gene pool refers to the full array of distinct alleles found within a species or a given population. The breadth of this pool directly influences genetic variability; the greater the number of alleles, the richer the genetic diversity. Such diversity is critical, enabling more rigorous and effective selection processes within resilient populations. Harlan and de Wet categorized gene pools into three primary groups, based on how easily different related species or taxa can interbreed.

The Gene Pool Concept Applied to Crop Wild Relatives

The gene pool encompasses the entire genetic diversity within a species’ breeding population, including closely related species capable of interbreeding. Departing from traditional taxonomic classifications, Harlan and de Wet introduced a gene pool-based system to categorize each crop and its related species, emphasizing their genetic relationships and potential for hybridization.[11]

Primary Gene Pool (GP1)

The GP1 consists of closely related taxa, including cultivated, wild, and weedy forms of a crop. Crosses within this group are easily made, producing vigorous, fully fertile hybrids due to normal meiotic pairing. It is the most commonly used gene pool in crop breeding programs.[3] The GP1 includes individuals of the same species that can freely interbreed. Crosses within this group produce fertile hybrids with proper chromosome pairing and gene segregation, which enables efficient gene transfer.[12] Hence, GP1 comprises plants of the same or closely related species that can interbreed and produce viable offspring. Gene exchange occurs easily through conventional crosses, leading to normal seed formation, segregation, and recombination.[13] See Figure 1.

Secondary Gene Pool (GP2)

The GP2 includes taxa that can hybridize with the GP1 members but with some difficulty, producing partially fertile hybrids. Barriers such as differences in ploidy, chromosome structure, or genetic incompatibilities cause this reduced compatibility. Compared to the

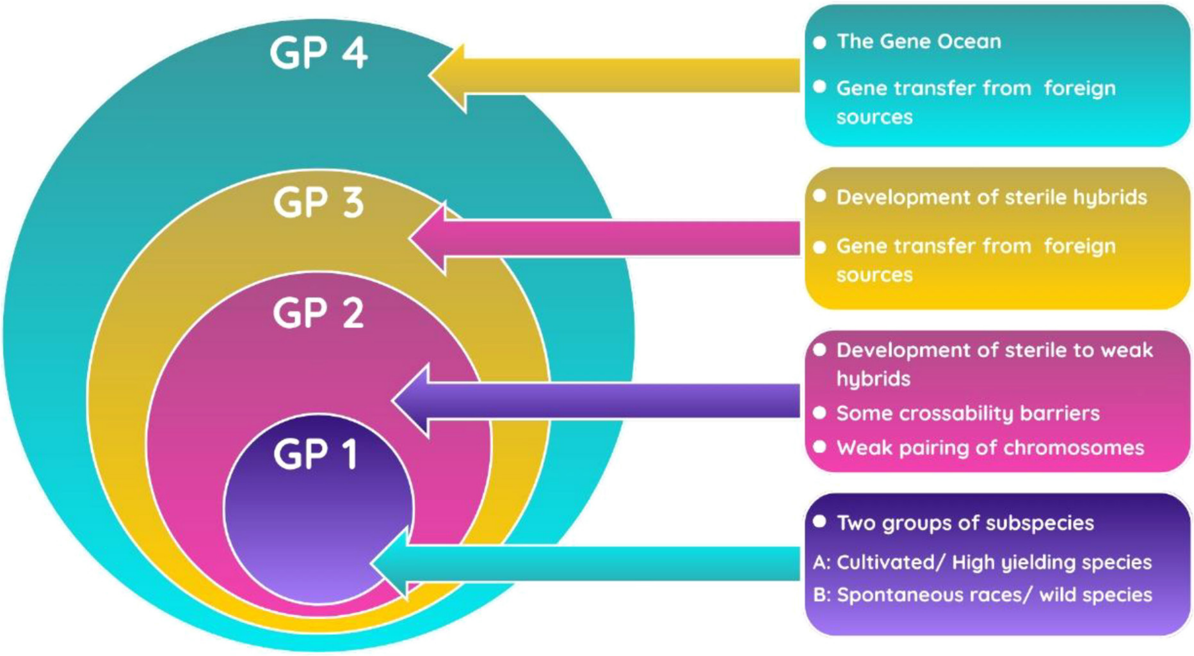

Fig 1 | Schematic representation of the gene pool concept (GP1–GP4), illustrating the gradation of genetic relatedness and crossability with cultivated species. It shows increasing reproductive barriers and the corresponding challenges in gene transfer from primary to more distant gene pools

GP1, these species are less commonly used in breeding.[3] As the total genetic variation found in a population of more distantly related species, this gene pool allows for gene transfer to the crop. However, it is challenging to accomplish using conventional breeding methods.[14]

Tertiary Gene Pool (GP3)

The GP3 includes germplasm from distant wild relatives or even different genera of a crop, where gene transfer through sexual recombination is extremely challenging. Successful hybridization typically requires advanced breeding methods or biotechnological tools. Techniques such as embryo rescue or bridging crosses are often essential to facilitate the transfer of genetic material from GP3 to the GP1.[15]

Solving the Problem of the Genetic Barrier in Wild Species for Crop Improvement using Interspecific Hybridization

Interspecific hybridization plays a significant role in plant evolution, particularly in adaptation and the emergence of new species.[16] While wild relatives of crops hold immense potential for enhancing cultivated varieties, they are seldom utilized directly in breeding programs. Their limited use is primarily due to several challenges, including cross-incompatibility, linkage drag, and poor adaptation to cultivated conditions. Even when wild relatives are cross-compatible within the same species, the presence of undesirable genetic linkages complicates the breeding process, demanding extensive time, effort, and resources to overcome. Developing interspecific hybrids and subsequent populations is often a prolonged and complex task.[17]

Furthermore, wide crosses involving both interspecific and intergeneric hybrids frequently result in reduced viability, sterility, or both in the progeny.[17]

To address these challenges, several breeding strategies and biotechnological approaches have been developed. The image below outlines the key solutions to overcome the barriers in interspecific hybridization and effectively utilize wild relatives for crop improvement. See Figure 2.

Wheat

Wheat is an important staple crop, providing up to 19% of human calories and 21% of protein intake worldwide.[18] The domestication of wheat and other cereals over the years led to their inability to withstand the extreme biotic and abiotic factors, as the main characteristics for selection were predominantly focused on fulfilling the requirements for human cultivation and dietary preference.[19] The distribution of wheat in different ecological zones of the world has given rise to significant levels of phenotypic diversity in the species.[20]

Aegilops species, a renowned wheat wild relative, is a potential genetic source for drought stress tolerance.[21] Carbon isotope discrimination served as an effective physiological indicator to evaluate transpiration and water use efficiency of A. speltoides and T. dicococoides (WWR), which showed greater drought tolerance than cultivated wheat, proving that wild relatives can be a great source for crop improvement.[22] Salinity stress has also damaged wheat production worldwide.[23] Therefore, studies show *Ae. tauschii* and *Ae. neglecta* species has responded well in extreme saline conditions.[24] The recent increase in temperature and global warming has created an alarming situation for crop production. The fluctuations in temperature can significantly affect the development of plants, such as the reduction of chlorophyll concentration and photosynthetic ability of leaves.[25] *Ae. tauschii* has also shown a greater thermostability of the photosynthetic mechanism and

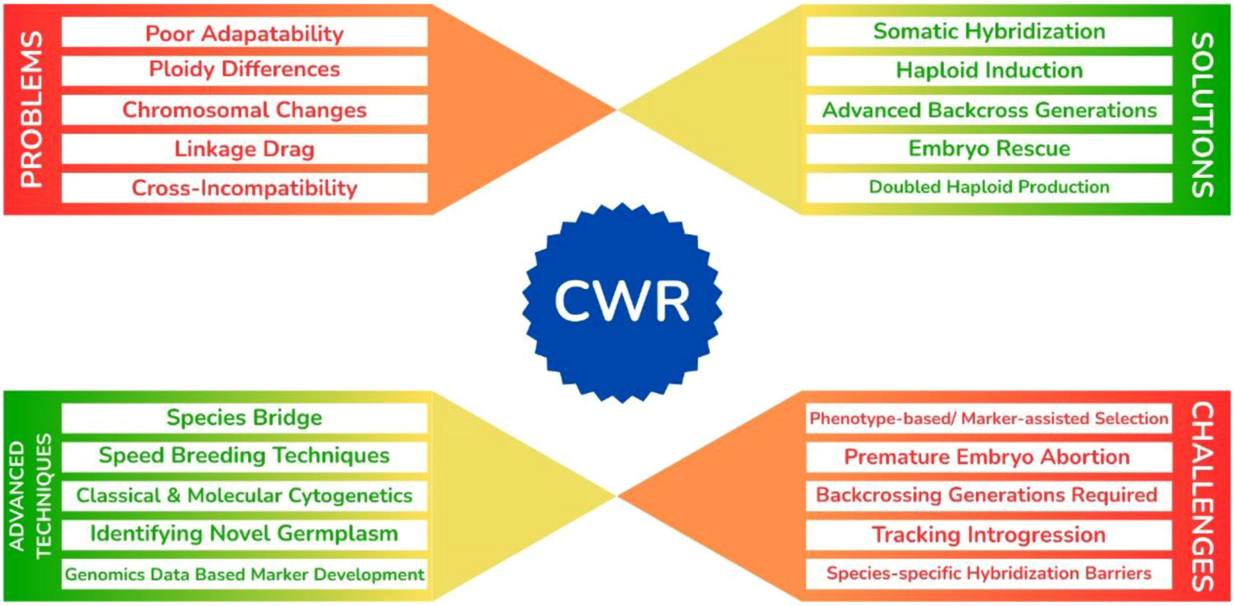

Fig 2 | Showing the key barriers and advanced techniques in utilizing CWRs for plant breeding, highlighting challenges such as poor adaptability and solutions like molecular marker-assisted selection

Ae. geniculate and Ae. speltoides showed greater tolerance to high temperature for grain yield.[26] Biotic stressors, like environmental pressures, have also been persistently threatening global wheat production, with pathogen resurgences from the monoculture of wheat cultivars.[27] *Aegilops tauschii* also helped enhance wheat productivity during the Green Revolution by introgressing stem resistance in cultivars.[28] The polyploid *Triticum and Aegilops* species have been used to transfer resistant genes in modern cultivars through backcrossing and hybridization for cultivar development.[29,30] Interspecific crosses involving the two wild relatives *Triticum timopheevii* and *Aegilops kotschy* led to the development of T- and K- cytoplasms, developing cytoplasmic male sterility in wheat, which offers potentional for harnessing hybrid vigor.[31]

Rice

Oryza nivara, a prominent rice wild relative, serves as a major source of GSV (grassy stunt virus) resistance, which is a wild rice from India obtained after screening 7000 wild accessions for GSV.[28] Interspecific crosses with CWR induce cytoplasmic sterility (CMS), which is a widespread approach for hybrid seed production.[31] *Oryza sativa* f. *spontanea* (weedy wild rice) and *Oryza rufipogon* (wild rice) have been used to develop CMS systems in rice hybrid breeding programs.[31] In another study, the researchers used wild allotetraploid *Oryza alta* for de novo domestication. With the help of CRISPR/CAS9, base editing, and multiplex editing, they improved traits like seed shattering, plant height, grain size, stem thickness, and heading date.[32]

Wild rice relatives are crucial in enhancing insect and disease tolerance in cultivated rice. A major rice pest, Brown planthopper (BPH), causes severe damage and is a vector for several viruses, like rice grassy stunt virus. Host plant resistance is preferred regarding environmental safety and cost effectiveness instead of solely relying on pesticides.[33,34] In wild species like *O. officinalis* and *O. rufipogon*, many BPH genes have been identified, out of which genes like Bph14 and Bph29 have been successfully cloned and introgressed into elite lines.[35,36] Rice Blast caused by *Magnaporthe oryzae* is a global threat. Japonica and indica are sources of over 100 genes identified for resistance, but wild species like *O. minta* and *O. rufipogon* also provided many valuable genes.[37,38] *Xanthomonas oryzae*, the causative agent of bacterial blight in rice, led to the discovery of resistant genes such as Xa21 and Xa23, with wild relatives being the key source for the broad, durable resistance.[39,40] These examples highlight the importance of wild relatives for sustainable rice cultivation.

For abiotic factors like drought and heat stress, wild relatives like *O. glaberrima,* although low yielding, have shown excellent drought tolerance, while wild species like *O. bhartii and O. australiensis* exhibit variability in plant height and tillering, making them promising donors for stress-resilient breeding.[41,42] Aluminum toxicity, which drastically hampers root growth and nutrient uptake, is common in acidic soils. *O. rufipogon*, the one collected from acidic soils in Vietnam (IRGC106424), has been a key donor in breeding aluminum-tolerant cultivars like AS996.[41,43] A halophytic wild rice, *Porteresia coarctata,* showed high tolerance to both salinity and submergence, which is attributed to significant transcriptional reprogramming.[44,45] *O. rufipogon* also accounts for 40% of cold tolerance OTL, variation needed in hybrids with cold sensitivity.[46] These findings highlight the breeding potential of wild rice relatives for climate-resilient agriculture.

Maize

Maize (*Zea mays L.)* is cultivated on nearly 100 million hectares across 125 developing countries. It ranks as one of the three most widely grown crops, and this demand is projected to double by 2050.[47]

However, teosinte (a renowned maize wild relative) and its relatives have shown remarkable tolerance to several biotic stress factors through physical, chemical, and genetic traits. The toughness of Balas teosinte leaves and high trichome density reduce herbivory by pests like the fall armyworm and leafhopper, which is vital for insect resistance.[48,49] Additionally, toxic secondary metabolites and higher benzoxazinoid concentrations are the chemical defenses that play a key role in resistance against insects like the maize spotted stalk borer.[50,51] Teosinte also harbors major quantitative trait loci (QTLs) that help against resistance in diseases like leaf spot and corn smut, while *Z. diploperennis* shows great immunity levels against various viral diseases.[52–54] *Z. diploperennis* maize wild relative demonstrates greater weed tolerance to parasitic weed Striga by preventing parasite attachment and vascular penetration.[55,56] Eastern gamagrass has also contributed to maize for the resistant genes against for not only *S. hemonthica* but as well as rust and leaf blight diseases.[57,58]

For abiotic stress factors, wild relatives of maize such as Eastern gamgrass *Z. nicaraguensis* offer promising stress tolerance traits. Eastern gamagrass has deep penetrating roots with better nutrient use physiology and maintenance of proper photosynthesis during water-scarce conditions, which helps it demonstrate impressive drought-tolerant ability.[59,60] Moreover, another study showed how drought tolerance from Tripascum could be introgressed into maize.[61] In a similar study, Tripascum ability to tolerate aluminum toxicity under acidic conditions was explored for maize improvement.[61] Eastern gamagrass also has traits that adapt through sodium conservation in leaves and a reduced root/shoot ratio that aids in water balance and maintaining turgor for growth essential for fighting against salinity stress.[62,63] *Z. nicaraguensis* surpasses all other Zea species in waterlogging resistance as it has adventitious roots that form a radial oxygen loss (ROL) barrier to sustain root growth under low oxygen soil.[64,65] Eastern gamagrass also forms root aerenchyma that facilitates internal oxygen transport.[66,67] Although introgression into maize remains challenging due to complex genetic inheritance.[68]

Table 1 | Showing the improvement potential of various wild relatives of major crops (Wheat, Rice, Maize, and Cotton). The listed wild species offer valuable traits such as disease resistance, drought and salinity tolerance, pest resistance, and yield-related traits, highlighting their importance in crop breeding and genetic enhancement

Crop	Wild Relative	Trait(s) with Improvement Potential
Wheat	*Aegilops tauschii*	Source of resistance genes (e.g., for rusts), D-genome donor in bread wheat
	Thinopyrum elongatum	Resistance to Fusarium head blight (FHB), salinity tolerance
	Aegilops speltoides	Resistance to leaf rust, stem rust, and powdery mildew
	Thinopyrum intermedium	Resistance to multiple rusts and leaf spot diseases
	Aegilops geniculata	Resistance to Hessian fly and other insects
	Aegilops ventricosa	Resistance to cereal cyst nematode, rusts, and mildew
	Triticum monococcum, T. dicoccoides	Drought tolerance, grain protein content, and mineral nutrition
Rice	*Oryza nivara*	Resistance to the grassy stunt virus (GSV)
	O. sativa f. spontanea, O. rufipogon	CMS systems for hybrid breeding
	O. alta	Improved traits via genome editing (e.g., seed shattering, plant height)
	O. officinalis, O. rufipogon	Resistance to brown planthopper (e.g., Bph14, Bph29)
	O. minuta, O. rufipogon	Resistance to rice blast disease
	O. rufipogon	Source of bacterial blight resistance (e.g., Xa21, Xa23)
	O. glaberrima	Drought tolerance
	O. barthii, O. australiensis	Plant height, tillering, heat, and drought stress
	O. rufipogon (IRGC106424)	Aluminum tolerance
	Porteresia coarctata	Salt and submergence tolerance
	O. rufipogon	Cold tolerance (40% of cold tolerance QTLs)
Maize	*Zea mays ssp. parviglumis, Z. mays ssp. mexicana* (Teosinte)	Leaf toughness, trichomes for insect resistance; QTLs for leaf spot, corn smut
	Z. diploperennis	Resistance to viral diseases, Striga weed tolerance
	Tripsacum dactyloides	Drought and aluminum toxicity tolerance
	Z. nicaraguensis	Salinity and waterlogging tolerance (ROL barrier, aerenchyma)
	Eastern gamagrass (Tripsacum spp.)	Drought tolerance, photosynthesis efficiency, resistance to Striga, rust, and leaf blight
Cotton	*G. barbadense, G. hirsutum* (MU 8b)	Jassid resistance (H1 gene) via dense trichomes
	Pilose	Fleahopper resistance via flower bud morphology
	G. tomentosum	Nectariless trait, pest, drought, heat, and salt tolerance
	G. barbadense × G. hirsutum	Glandless seed + glanded plant for pest resistance and seed utility
	G. longicalyx, G. barbadense	Nematode resistance (via hybrids like HLA, HTL)
	G. arboreum	Resistance to bacterial blight and CLCuV
	G. thurberi	Resistance to Verticillium wilt
	G. sturtianum	Resistance to Fusarium wilt
	G. darwinii	Drought tolerance, resistance to Fusarium/Verticillium wilts, finer fiber
	G. tomentosum × G. hirsutum	Salt tolerance (8 QTLs identified)

Cotton

Like other crops, pest and disease tolerance can be enhanced in cotton by traits introgressed from wild species and landraces. Leafiness is considered a valuable trait for insect resistance. The H1 gene from *G. barbadense* and *G. hirsutum* types, such as MU 8b, imparts jassid resistance through dense trichomes.[69] Flower bud morphology is greatly responsible for flea hopper resistance derived from Pilose.[70] Nectarless trait, found in *G. tomentosum*, reduces insect attraction.[71] Glandless seed and glanded plant lines combine pest resistance with improved seed utility.[72] For nematodes, resistant sources such as *G. longicalyx* and *G. barbadense* were successfully introgressed into Upland cotton via hybrids like HLA and HTL.[73,74] *G. arboretum* proved to be a great source for bacterial blight and CLCuV disease resistance.[75,76] *G. thurberi* and *G. sturtianum* resisted Verticillium and Fusarium wilts, respectively.[77,78]

Wild cotton species offer a valuable reservoir of genes conferring tolerance to various abiotic stresses, making them crucial for cotton improvement. *G. tomentisum* exhibits a great deal of drought, heat tolerance, and salt and pest tolerance, making it a great reservoir for resistant genes.[79] Similarly, *G. darwinii* possesses tolerance to drought and resistance to both Fusarium and Verticillium wilts, along with producing finer fiber, which is beneficial for enhancing commercial cotton cultivars.[79] To utilize these traits, *G. tomentosum* was intercrossed with *G. hirsutum*, resulting in the identification of eight QTLs associated with salt tolerance.[80] See Table 1.

Conclusion

Crop wild relatives (CWRs) are indispensable assets in modern agriculture, offering an expansive genetic reservoir to combat emerging challenges in food production. Their inherent resistance to pests, diseases, and environmental stresses makes them vital for enhancing crop resilience, yield, and nutritional quality. Despite significant biological and technical barriers, such as cross-incompatibility, sterility, and linkage drag, ongoing advances in molecular genetics, genomics, and precise gene editing have opened new pathways for their effective utilization. Applying the gene pool concept, along with innovative breeding techniques like interspecific hybridization and cytoplasmic male sterility systems, has further facilitated the transfer of valuable traits from wild species to elite cultivars.

As global agriculture faces mounting pressures from climate change, resource limitations, and population growth, the strategic use of CWRs offers a sustainable solution to ensure food and nutritional security. Future breeding programs must prioritize the conservation, characterization, and utilization, supported by robust policy frameworks, germplasm repositories, and international collaboration. By integrating cutting-edge biotechnology with traditional breeding knowledge, the full potential of CWRs can be harnessed to develop climate-resilient, high-performing crops for the challenges of tomorrow.

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