R-2613
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REVIEW ARTICLE Agricultural Reviews

Crop Wild Relatives (CWRs) a Genetic Pool for Crop Improvement: A Review

Amandeep Kaur[1], Manjeet Kaur Sangha[1]

10.18805/ag.R-2613

ABSTRACT

Deleterious effects of climatic changes and diverse environmental conditions, possess a major threat to agriculture in terms of growth and yield. So, to meet these challenges, there is a need to develop new crop varieties containing traits resistant against abiotic and biotic stresses and enhanced input use efficiency. Compared with domesticated cultivars, crop wild relatives maintains much higher level of genetic diversity. The high nutrient and bioactive content of many wild edible plants make them valued contributors for balanced diet and play significant role in human nutrition. In this review article, we discussed the importance of crop wild relative in crop improvement programs by giving examples of wild relatives that have been used to enhance abiotic and biotic stress tolerance and yield in various crop species. The advancement in DNA sequence technology enables plant breeders to produce high quality food. Further, combination of re-sequencing and de novo sequencing are efficiently used to explore genomic variation in crop wild relatives and moreover the genome analysis study results in detection of beneficial alleles in wild relatives which has been lost in cultivated species. Thus, conservation of genetic pool of crop wild relatives is essential to maintain sustainability of agriculture and food production.

Key words: Biotic and abiotic stress, Crop wild relatives, Nutritional improvement.

Abbreviations: CWRs: Crop Wild Relatives; QTL: quantitative trait locus; ILs: Introgression libraries; TYLCY: Tomato yellow leaf curl virus; YVMD: Yellow vein mosaic disease; CGMMV: Cucumber green mottle mosaic virus.

Now, a day's challenges faced by a global food security are complex and compounding. The changing climatic conditions such as increasing temperature along biotic and abiotic stresses like salinity and drought condition and new emerging strains of pest and diseases possess a major threat to the agriculture in terms of growth and yield. Moreover, the process of domestication has also results in reduction of diversity in modern crops at both the local and genomic level (Kaur *et al*. 2018). For example more than half of the genetic variation has been lost in cultivated rice (Xu *et al*. 2012) and significant reduction in maize (Wright *et al*. 2005) and cultivated soybean (Zhou *et al*. 2015) has observed in comparison to its progenitors counterparts. So, to meet these challenges, there is a need to develop new crop varieties containing traits resistant against abiotic and biotic stresses such as drought and heat tolerance, increased pest and disease resistance and enhanced input use efficiency.

Crop wild relatives (CWRs) are the primary reserve of genetic variation and these have been widely underutilized in crop improvement. In the 20th century, crop wild relatives were used in sugar cane crop improvement and further their effectiveness was known in breeding programs of major crops like rice and wheat in the 1940s and 1950s (Plucknett *et al*. 2014). The genetic base of modern cultivars is narrow and this poses major hindrance for crop improvement efforts. Germplasm characterization studies have also shown that cultivated plants are less tolerant to abiotic and biotic stresses and nutritional quality when compared to wild relatives (Holland *et al*. 2009). The wild variants are stress tolerant as they have developed stress response mechanisms which may be attributed to higher content of antioxidants and polyphenols. For example the spelt varieties of wheat were depicted to be endowed with high antioxidant activity. As a result the spelt varieties required no pesticide use and lower nitrogen fertilization (Gawlik-Dziki *et al*. 2012). Some of the wild accessions also depicted higher input use efficiency and higher productivity.

Wild food can also contribute to nutrient diversity and richness. Wild edible plants are important components of global food basket and constitute a significant part of human diet. The high nutrient and bioactive content of many wild edible plants make them valued contributors for balanced diet and play significant role in human nutrition, especially as sources of phyto-nutraceuticals. Their consumption, together with staple food crops can provide a balanced and

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[1]Department of Biochemistry, Punjab Agricultural University, Ludhiana-141 004, India.

Corresponding Author: Amandeep Kaur, Department of Biochemistry, Punjab Agricultural University, Ludhiana-141 004, India. Email: amandeepkaurbrar413@gmail.com

How to cite this article: Kaur, A. and Sangha, M.K. (2023). Crop Wild Relatives (CWRs) a Genetic Pool for Crop Improvement: A Review. Agricultural Reviews. doi: 10.18805/ag.R-2613.

Submitted: 29-11-2022 **Accepted:** 22-02-2023 **Online:** 16-03-2023

healthy diet to malnourished people. Substantial economic and nutritional gains have been achieved by consuming edible wild okra (Gutiérrez *et al*. 2017). Loskutov *et al*. (2017) reported that biochemical like fatty acids, amino acids and sugars exhibited wider range in wild species in comparison to the cultivated ones. The wild relatives of tomato depicted higher total soluble solids and ascorbic acid content than cultivated tomato (Kumar *et al*. 2019). High yielding varieties with proven tolerance to biotic and abiotic stresses, superior nutritional profiles and ability to adapt to the changing environment are needed for continued agricultural sustainability. So, Crop wild relatives (CWR) can be exploited to enhance genetic diversity in cultivated crops which offer a diverse array of traits with the potential to decrease the amount of yield loss. The wild relatives serve as signiûcant gene pool for improving the existing crop plants for adaptation, tolerance, yield and nutritional quality (Chauhan *et al*. 2021) and find application in nutraceutical, pharmaceutical, food and cosmetic industries (Singh and Abhilash 2018). In this review article, we discussed some representative examples in which wild relatives were used against stress resistance and improving yield and nutritional quality in their cultivated descendants.

CWRs in crop improvement

Improvement in yield and quality trait factors

Over the past decades, great progress has been made to produce nutritionally improved food crops. The genomic diversity within wild species provides useful traits for improving the nutritional value of specific crops (Nawaz *et al*. 2018). Biofortified staple crops such as fruits and vegetables are generated which harbor essential micronutrients that become a very important part of human nutrition. This article explores the improvement in nutritional status of crop and its positive impact on human health. In the following paragraph, several examples of nutritionally enhanced crops will be discussed which have been developed by using biotechnological approaches.

Increase in nutritional quality is either achieved *via* altering the biochemical structure of plants or by modifying the genotypes of staple crops for example; nutritional improvement in case of potato is achieved through interspecific hybridization involving wild and cultivated species. Hameed *et al*. (2018) studied that cultivated potato *i.e*. *solanum tuberosum* contain fewer amount of protein (0.85-4.2%) lacking in essential amino acids but introgression of protein enhanced wild gene *Amaranthus hypochondriacus (AmA1)* in cultivated potato raised the protein content upto 60%. Similarly, Starch amylose content also has been increased in potato tubers by introducing recessive allele *IAm* (Increased amylose) from wild potato *solanum sandemanii* into *solanum tuberosum* which result in generation of potato tuber with enhanced amylose content upto 28-59%. Actually IAm trait was introgressed to *S. tuberosum* cultivars by marker assisted technique to increase the amylose content. The increase in amylose content might be due to high granule associated phosphorylase 1 (Pho1) and decreased starch synthase (SS) activity (Krunic *et al*. 2018). Gur and Zamir (2004) also depicted that introgression of three independent yield-promoting genomic regions from wild species *Solanum pennellii* into *Solanum lycopersicum* lead to generation of hybrids with 50% increase in yield over the leading variety under both wet and dry field conditions that received 10% of the irrigation water. The probability of increasing seed yield by using wild relatives was seen to be unlikely. But Frey (1976) observed that crossbreeding between *Avena sterilis* and *Avena sativa* resulted in increase in seed yield by 25–30%. After this, various examples of crop wild relatives contributing to increase in yield has been reported. Recently in wild tomato, quantitative trait locus (QTL) has been identified which contribute to increase in yield.

Tomato shows genetic variability for beta carotene content that had been utilized to breed varieties with high carotene content (Chauhan *et al*. 2021). The highest levels of vitamin C, lycopene, solids contents and phenolics were found in wild relative *i.e*. *Lycopersicon pimpinellifolium* (Colak*et al*. 2020). The crossing of *Lycopersicon pimpinellifolium* with *Lycopersicon chmielewskii* resulted in 2.4% increase in solid content of the fruit reported by Esquinas-Elcázar (1981) which was equivalent to worth of estimated 250 million US$ in California. Hefferon *et al*. (2015) also studied that tomatoes have been transformed with the grape encoding gene *i.e.* stilbene synthase in presence of fruit specific promoter. They found that these transgenic tomato plants are able to accumulate trans-resveratrol-glucopyranoside and trans-resveratrol and reached up to the level of 53 µg/g upon ripening. Resveratrol is bioactive compound that can helps to improve the nutritional value of tomatoes. Crop wild relatives of tomato such as *S. chilense*, *S. peruvianum*, *S. habrochaites* and *S. pimpinellifolium* were also found to be resistant to pest and diseases and abiotic stress tolerance (Ebert and Schafleitner 2015). Certain accessions of *S. Habrochaites* and *S. Chilense* were resistant to leaf curl begomoviruses (Hajjar and Hodgkin 2007).

Wild germplasm has limited use in quality characteristics, because of their genetic complexity. However, wild grasses have a higher level of protein as compared to its related domesticated cultivars. Nevo (2007) also reported that durum wheat varieties were improved in protein content through crossing with wild relative, *Triticum turgidum var dicoccoides* which had high protein content. The accession FA15-3 accumulates 40% protein in presence of nitrogen. Further, FA15-3 lines of wheat have been used to transfer the *Gpc-B1* gene (for high protein) into hard red spring wheat which resulted up to 3% more protein than the parallel lines. Alleles from *Oryza rufipogon* increased grain weight in a Korean wild rice cultivar (Xie *et al*. 2006). Kaur *et al*., (2020) also studied that promoter element of wild *Oryza rufipogon* accession (IRGC89224) has lowest expression of *Phospholipase D alpha1* (OsPLDα1) enzyme which is responsible for rice bran oil rancidity. Therefore, *Oryza rufipogon* accession (IRGC89224) have been used as potential donor in back crossing programmes to transfer the desired trait into elite cultivars of rice to improve shelf life of rice bran. High protein content of seed has also been incorporated from wild *Cajanus* species, such as *C. sericeus*, *C. scarabaeoides* and *C. albicans* into cultivated pigeonpea (Singh and Abhilash 2018). Similarly, Barabeau and Hilu (1993) reported that crop wild progenitor of fingermillet *E.corocana subsp*. *Africana* has higher value of protein which ranges from 7.5 to 11.7%. The Fe and Ca content of wild relatives were also significantly greater than its cultivated cultivars. Moreover, these wild species also found to have high lysine and other essential amino acids content. Thus, results showed that the nutritional value of fingermillet may be significantly improved by selective crossbreeding of its wild and cultivated cultivars. However, the nutritional value of grain is higher than cereals and making them essential component of balance diet.

Among grains, soybean [*Glycine max* (L.) *Merril*] is the world's most important seed legume and also considered as an oilseed crop. Although its seeds are rich source of protein (Qin *et al*. 2014), but it has lower amount of sulphur containing amino acid such as methionine, which confines their nutritional quality. However the latest studies suggested that the seed specific expression of enzyme of methionine biosynthesis pathway i.e. *Arabidopsis thaliana cystathionine ã-synthase* (*AtCGS*) give rise to higher methionine content in the seeds of three soybean cultivars, Bert and Misuzudaizu and Zigongdongdou (Cohen *et al*. 2016).

Abiotic and biotic resistance

Crop Wild relatives (CWRs) found in an extensive environment conditions act as a good source of genotypes that are adapted to new environments in agricultural production region. Adaption to new environment means adaption to biotic or abiotic stresses that can be discovered by whole genome analysis. The analysis of genomic variation in progenitors in different environmental conditions may bring better understanding to point that how plants are adapted to various climatic disparities under natural selection (Henry and Nevo 2014). So, this idea may be defined as a way to utilize the CWRs to increase stress tolerance and thereby improve productivity in crops such as the major cereal grains, wheat, rice, maize, grain legumes and fruits.

Abiotic stress tolerance

Salinity and Drought are the two most important environmental factors that limit production of any crop (Feyisa *et al*. 2022). Effect of both stresses have been extremely observed in crops like tomatoes, soybeans, cereals and as well as in their wild relatives (Qi *et al*. 2014). Here, we discuss the utilization of CWRs for salt and drought tolerance in wheat, soybeans and barley respectively.

Wheat is the third most produced cereal after maize and rice and it is significantly affected by salinity (Mujeeb-Kazi and De Leon 2002). Continuously, efforts have been made to produce a salt tolerant wheat variety by transferring an allele TmHKT1;5-A from its wild relative *Triticum monococcum* by using crossbreeding method. Munns *et al*. (2012) suggested that TmHKT1;5-A gene reduces the sodium concentration in the plant leaves that prevents loss of yield under salinity stress and moreover results also showed that new salt tolerant variety, produce 25% greater yield as compared to its Tamaroi parent. Ebert and Schafleitner (2015) also reported that two Na+/K+ transporter gene from wild *S. Cheesmaniae* act as a salt stress tolerant genes.

Soybean [*Glycine max* (L.) *Merril*] can also affected by salinity stress and results upto 40% decrease in yield (Chang *et al*. 1994). A salt tolerant gene *GmCHX1* was recently recognised in the wild relative of soybean called Glycine soja (Qi *et al*. 2014). Moreover, the finding of *GmCHX1* and another salt tolerant gene, *GmSALT3* (Guan *et al*. 2014), proposed that salt tolerant alleles might have been lost in soybean during domestication. Both the salt tolerant genes (*GmCHX1* and *GmSALT3*) help in regulating ion homeostasis and production of commercial soybean varieties with improved salt tolerance. The CWR of sunflower, *Helianthus paradoxus* is used for tolerance to salinity in sunflower and *Helianthus argophyllus* for tolerance to drought stress (Miller and Seiler 2003).

Drought is another important constraint that affects growth and development of crop production. Although several drought tolerant genes have been identified in wild relatives of crops such as barley (Suprunova *et al*. 2007), rice (Quan *et al*. 2010) and tomatoes (Fischer *et al*. 2013) but the applications of these gene for improving drought tolerance have not proven as successful as expected. The development of backcross introgression libraries (ILs) by using single gene of wild parent provides a useful substitute method for the transfer of drought tolerant genes. Honsdorf *et al*. (2014) a reported that wild barley *Hordeum spontaneum* introgressed lines were used to induce drought tolerance. The introgression lines were also prepared by crossing between the German spring barley cultivar Scarlett (*Hv*) and the Israeli wild barley to improve yield, pathogen resistance and malting quality traits.

Biotic stress tolerance

Plant yield are also reduced due attack from various biotic stresses such as pathogens like bacteria, viruses, fungi, insect pests and nematodes. Even after use of limited insecticides and pesticides, these pathogens continuously causing harm to the crops because they evolve very quickly and become tolerant. To overcome this problem, plant breeders have been exploiting exotic genetic resources such as crop wild relatives by using various strategies of biotechnology to develop broad spectrum biotic stress resistant varieties (Hajjar and Hodgkin 2007).

For example bacterial leaf blight, has been one of the most widespread rice disease caused by *Xanthomonas oryzae pv*. *oryzae* (Xoo). However, introduction of new bacterial blight-resistant genes *Xa21* from wild rice variety *Oryza longistaminata A*. *Chev*. *et Roehrich* into *Oryza sativa* has proved as a significant example of using wild relatives in cultivated rice for conferring leaf blight-resistance in rice

(Zhou *et al*. 2011). Ballini *et al*. (2007) also reported that bacterial leaf blight resistance has been obtained from introgression of resistant gene *Pi33* from wild rice, *Oryza rufipogon* into rice blast resistance variety IR64. Similarly, in United State, corn blight disease in maize was resolved by the introduction of blight resistance genes from the wild Mexican maize *Tripsacum dactyloides* L. Into commercial corn lines (Zhang *et al*. 2016). Among diploid wheat *Triticum monococcum*, progenitor of common hexaploid wheat has been used to mark the traits related to resistance genes against leaf rust and powdery mildew. Using marker assisted selection, one adult plant resistance gene (APR) for leaf rust and stripe rust has been transferred from *T. monococcum* to bread wheat WL711 and one gene for leaf rust has been transferred to PBW343 background (Singh *et al*. 2007). In case of cultivated oats, the wild progenitor *Avena barbata* used as a gene reservoir for powdery mildew pathogen resistance (Swarbreck *et al*. 2011).

Oilseeds are also major food crops, known for their protein and oil rich properties but major drawback in oilseed production are abiotic and biotic stresses. Wild black mustard i.e. *Brassica nigra* represents wild gene pool to improve cultivated Brassicas against various pathogens e.g. interspecific allopolyploids between *B. rapa* , *B. Fruticulosa* and *B. nigra* aid the use of CWRs in Brassicas as bridge species (Chen *et al*. 2011*). L. grandiflorum* a CWR of linseed has potential for linseed bud fly and Alternaria blight (Allaby *et al*. 2005). Among CWRs of pulses, *Vignamungo var. sylvestris*, *V.tribolata* and *V. radiatavar. sublobata* have provided resistance to yellow mosaic virus. *V. vexillata* has resistance to cowpea pod sucking bug and bruchids and it is crossable with *V. Radaita* and *V. Unguiculata* (Kaur *et al*. 2018).

Among different vegetable crops, potato is genetically more uniform which make it more vulnerable to abiotic and biotic stresses. Late blight is one of most important disease of potato which is caused by the *Phytophthora infestans (Mont.) de Bary*. Late blight resistance genes were transferred from wild species namely *S. stoloniferum* and *S. Demissum* into cultivated potato in different parts of the world (Bethke *et al*. 2017). Many novel genes for late blight resistance, virus resistance and other useful traits are available in diploid wild potato species like *Solanum tuberosum, S. pinnatisectum*, *S. acaule, S. brachistotrichum, S. cardiphyllum, S. jamesii, S. stoloniferum, S. Polyadenium etc.* Similarly, in tomato, the improvement in biotic resistance has benefitted significantly when various traits from wild relatives were transferred into cultivated species (*Solanum lycopersicum*). These traits include resistance to bacteria, fungi, viruses, insect pests and nematodes. The wild relatives of tomato that have been used for introgression are *Solanum habrochaites*, *S. chilense*, *S. peruvianum* and *S. pimpinellifolium*. These varieties act as richest source of genetic diversity. For example, five Ty genes that exhibit wide range of tolerance to tomato yellow leaf curl virus (TYLCY) were successfully introgressed into cultivated varieties (Menda *et al*. 2014). Nowicki *et al*. (2012) reported that genetic resistance to tomato late blight has been identified in *S. habrochaites*, *S. pennellii* and *S. Pimpinellifolium* and three main late blight resistance genes namely *Ph-1, Ph-2, Ph-3* have been reported in four *S. pimpinellifolium* accessions and among these three genes, *Ph-3* is considered most effective source of late blight resistance.

In okra, yellow vein mosaic disease (YVMD) is the most serious disease among biotic stresses (Kumar and Reddy 2015) whereas leaf hopper, shoot and fruit borer are the major insect pests. Resistance genes for YVMD, leaf hopper, shoot and fruit borer are observed in okra wild species *A. manihot*, *A. Moschatus* and *A. tuberculatus* respectively (Singh *et al*. 2006). Gangopadhyay *et al*. (2017) also reported *A. manihot*, *A. caillei* and *A. Moschatus* possess resistant against YVMD, while *A. moschatus*, *A. caillei, A. tuberculatus*, *A. manihot* to leaf hopper and shoot and fruit borer. In addition to this, a single dominant resistant gene against powdery mildew (*Peronospora destructor*) was introgressed from wild onion species namely *A. roylei* into cultivated onion (Kim *et al*. 2016).

Among cucurbits, wild *Cucumisfigarei* exhibited absolute resistance to cucumber green mottle mosaic virus (CGMMV), Fusarium wilt and higher level of resistance to downy mildew (Kaur *et al*. 2018). The wild species *C. anguria* and *C. ficifolius* showed no symptoms and reported resistance to CGMMV virus (Ruiz *et al*. 2021). However, wild species *Cucumis hardiwickii* has been reported with strong resistance to powdery and downy mildew diseases (Pitchaimuthu *et al*. 2012).

Limitation to use CWRs within breeding programmes

There are numerous obstacles that prevent use of CWRs as a source of potential alleles that can be incorporated into elite cultivated germplasm.

1. The compatibility, relatedness and crossability of crop wild relatives to their cultivated counterparts inhibit the direct introgression of CWR trait into cultivated genotype. For example, in cotton highly disease resistant sources were identified (such as *G. Somalense* J.B. Hutch; *Gossypium longicalyx* J.B. Hutch and B.J.S. Lee.) but due to their genetic incompatibility and ploidy, breeders were unable to use these resources (Tirnaz *et al*. 2022).
2. Trait identification and selection may be significantly influenced by environment as there are radically different selection regimes in a wild region compared to a domesticated region and a trait that is useful in a domesticated state may not be useful in the wild and vice versa. For example Parker *et al*. (2020) proposed tha the decreased-pod dehiscence (PD) among domesticated common bean is due to the different fitness landscape imposed by domestication, where stronger selection pressure was used against PD in the arid conditions of North Mexico compared to tropical lowlands, where environmental humidity masks susceptibility to PD and reduces selection pressure against it (Parker *et al*. 2020).
3. Even if beneficial wild derived traits are introgressed into elite material, linkage drag can often have a negative

effect on yield or yield-related traits. For example, introduction of disease resistance genes improve some resistance but are detrimental to other agronomic traits (Trinaz *et al*. 2022).

4. Furthermore, when CWR genetic material is introduced into cultivated germplasm, sterility issues can arise, most commonly at the F1 or BC1 generation (Wang *et al*. 2020; Bohra *et al*. 2022).

There are also several challenges to using CWR in breeding that have been alleviated by the availability of more genomic resources and advances in laboratory techniques such as genome editing methods (CRISPR/Cas9), marker-assisted selection techniques, or RenSeq technologies (Bohra *et al*. 2022). But lack of knowledge about gene-trait relationships in wild species, uncertainty about how allelic combinations will be expressed in different cultivated crop backgrounds and challenges with transferring genes of interest into crops is major drawback.

CONCLUSION

Crop Wild relatives (CWRs) as a source of abiotic and biotic resistance are imperative for the genetic improvement of crops in multiple ways. To cope with problems arising from environmental changes and pathogens and population growth, it is essential to use wild genetic diversity to inflate agriculture production. Developed biotechnological applications such as genomics-assisted breeding, are used for the transfer of favorable traits from wild relatives into cultivated ones, despite incompatibility barriers. Nevertheless, now the advancement in DNA sequence technology particularly the combination of resequencing and de novo sequencing is efficiently used to explore genetic variation in crop wild relatives. The conservation of the genetic pool of wild relatives of the crop will be important for providing the key agronomic traits to breeding programs. Moreover, the utilization of the biodiversity present in the wild gene reservoir will allow cultigens to adapt rapidly to varying climatic conditions and enhance agricultural production to ensure global food and nutrition security.

Conflict of interest

The author declare that there to be no conflict of interest.

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