



MODERN PLANT BREEDING

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**Dr. Gita R. Chaudhari
Dr. Krishna Prakash
Ms. Sheetal R. Patel**



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22 B/5 Ground Floor, Desh Bandhu Gupta Road,
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Ph.: + 91 (11) 4155-8799
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Gene Introgression: Strategy for Utilization of Crop Genetic Resources

Rakesh Pathak, Aman Verma, Sunil Kumar Singh and Rajwant Kaur Kalia*

ICAR-Central Arid Zone Research Institute, Jodhpur 342003, Rajasthan, India

*Corresponding author: Rajwant K Kalia; rajwant.kalia@icar.gov.in

Abstract

The increasing demand for food production with limited resources is creating a frightening situation to meet the hunger requirement of the world population. A range of biotic and abiotic stresses significantly affect crop productivity thereby widening the gap between demand and supply. Modern crop breeding involving the techniques and strategies of molecular biology has always been considered as one of the best approaches for creation of variability in the crop species to enhance the yield potentials. Transgenic techniques like gene introgression can supplement the conventional breeding methods for speedy development of desirable crop genotypes. Despite availability of modern techniques of plant improvement, identification and isolation of potential genes remains a major bottleneck. Crop genetic resources including wild relatives and landraces, which have survived all kinds of environmental challenges over centuries, can constitute a major reservoir of these potential genes/QTLs for creation of variability and enhance the yield potential of crops. Controlled inter-specific movement of genes has the potential to accelerate the pace of crop evolution by overcoming the limitations of conventional crossing like incompatibility issues and linkage drag.

The present paper reviews the utilization of crop genetic resources for gene introgression in different crops.

Key words: Introgression; adaptation; crop wild relatives; cereal; legume; tree

Introduction

Agriculture is the source of income to about 75 per cent population of the world. Therefore, improvement in the field of agriculture in terms of high-yielding and climate-resilient varieties is essential to enhance livelihood quality. The improvements in the field of agriculture could be possible due to the search of novel genes and potential populations having useful traits¹ along with their introgression. Introgression of beneficial characteristics into crop varieties has always been an important aspect of plant breeding, nevertheless, the magnitude and effect of natural or farmer-assisted introgression requires to be determined. The advancement in genomics and related techniques has opened new avenues to introgress the beneficial genes into the desired crops remained in the secondary/tertiary gene pools. Presence of diversity in the genetic material gives an opportunity to improve or develop novel varieties not only for improved productivity, adaptability, nutritional quality but also for providing resistance towards pests, diseases and abiotic stresses (FAO 2007)². Underutilized or neglected species, grown without any inputs on the marginal land, may also be encouraged for the creation of genetic amelioration³. These species may be exploited to assess their crossing compatibility, yield capability and genetic variability for the traits of agronomic importance.

Climate change has affected all the spheres of the earth including human health, agriculture, natural resources resulting into serious threat to economic development. The increase in temperature may enhance the CO₂ concentrations, incidence and severity of cyclones, rainfall, floods along with the occurrence of droughts⁴. When it has well established that changing environmental and climatic conditions may impose serious threats to the variability of cultivated crops as well as crop wild relatives (CWRs), it is essential to take up serious investigations in respect to the genetic makeup and or genetic erosion due to environmental aberrations. Crop genetic resources (CGRs) have the potential to face the challenges caused by climate change in terms of food security and sustainability (**Fig. 1**). Several underutilized plant species are having desired genes that may be utilized in crop improvement programmes and in the development of varieties having adaptation to varied climatic stresses. CWRs and landraces may be the probable basis for creation of resistance against several pathogens and pests⁵. Varieties and genetic materials having higher yield potentials and enhanced tolerance toward biotic and abiotic stresses has been developed over the period with the help of modern scientific interventions (**Fig. 1**); however, the climatic changes have imposed critical challenges for crop improvement programme and

requires extra attempts in terms of techniques and strategies to develop more adapted genetic resources for farmers⁶, particularly for the more susceptible regions of developing countries.

Problems associated with narrow genetic variability

There is a significant decline in the variability of agricultural plants. According to an estimate, out of thirty thousand edible plant species, merely 30 species including three major crops (*Zea mays*, *Triticum aestivum* and *Oryza sativa*) are used to fulfil the world's food requirement². The limited interspecific and intraspecific genetic variability within the crops may impose serious problems of insects, pests and diseases. Infestation caused by *Phytophthora infestans* in the *Solanum tuberosum* during 1845-1846 in the Western Europe, havoc created by *Bipolaris maydis* with maize crop during 1970 in the USA⁷, outbreak of blight caused by *Fusarium graminearum* in wheat and barley in Western USA during 1994-1996, are some of the examples of the serious problems caused due to lesser variability in the genetic materials. Besides these, susceptibility towards abiotic stress, quality concerns and male sterility^{8,9} are also some of the issues associated with the lack of genetic variability in the crops.

Crop genetic resources

CGRs are basically the genetic materials including new varieties, older genetic materials, landraces, wild or weedy species, elite line or mutants¹⁰. They may serve as the significant biological foundation for food security. Crop productivity has strong relations with the environment and genetic makeup. The CGRs and diversity therein need to be exploited properly to cope up with the future challenges². Genetic attrition is becoming one of the major problems associated with genetic resources. The issue has been globally recognized and efforts are being made to conserve the CGRs resulting into very good assemblage of genetic material however, some crops could not get proper attentions¹¹. CGRs having higher migration capabilities endure better as compared to those that have lower migration potentials¹². Due to lack of potential or new variants, secondary genepool denoted by the wild relatives of the crops open an avenue to offer genes of traits of importance¹³.

Availability of genetic information in respect to genetic resources is of prime importance. The comparative performance of genotypes differs from one environment to another and it can be articulated as a linear function of an environmental variable^{14,15}. Therefore, understanding of genotype and environmental (G×E) interactions is essential for the assessment of a variety for the desired trait. High-yielding stable varieties have great significance in several crops for cultivation under variable environmental conditions¹⁶⁻¹⁸.

Assessment of genetic response towards individual stress is more effective as compared to combined stresses¹⁹ as it is governed by multiple genes. The

search of climate resilient genetic material ends upon the CGRs. A combination of allele mining, gene prospecting and pre-breeding may be some of the better aspects to maximize the utilization of CGRs. Genetic improvement in several crops has been attributed to higher yields and simultaneously higher income to the stakeholders²⁰. Focused identification of germplasm strategy can be a better approach to identifying suitable genetic resources and detecting sources of resistance in various crops under the changing climatic scenario²¹. Besides this, the composite genetic combinations offer higher tolerance towards abiotic stresses²². The characteristics having resistance towards environmental aberrations may have positive impact on the enhancement of productivity of crops. It is evident from the facts that the short-growth habit traits obtained from the cultivars at farmers' field in Asia were incorporated with other potential traits to develop semi-dwarf varieties of cereals such as rice and wheat. The approach revealed great success in view of distinctively increased yield potential and led to the green revolution.

Crop wild relatives

With the due course of evolution, the plants showing higher yield potential and better characteristics became the choice of cultivation. CWRs are important genetic resources for climate change adaptation and provide genes having several important traits for biotic and abiotic resistance²³. Utilization of multiple genes from CWRs and several other organisms to acquire maximum climate resilience has always been considered complementary. CWRs are a wealth of beneficial genes but their utilization particularly associated with the tertiary gene pool is inadequate and if not managed, will face extinction²⁴. The same is the case with the landraces cultivated by the farmers. It may be due to cross incompatibility and or pairing limitation between the chromosomes of wild and domesticated species²⁵ leading to non-germination of pollen grains, non-fusion of male and female gametes or failure of pollen tube²⁶. Besides this, the alliance of unwanted genes with the desired genes also known as 'Linkage drag' is another major problem associated with the utilization of CWRs for gene introgression in domesticated species especially diploid crops²⁷. One of the best examples of genetic imbalance is the observation of negative impacts on the yield and quality of wheat²⁸ when genes other than desired gene (*Sr39* from *Aegilops speltoides* Tauschii) were introgressed to the foreign chromatin. In view of this, it was suggested to remove the extra chromatin of *A. speltoides* adjoining to *Sr39* gene to improve the potential of the gene to control the lineage (*Ug99*) of wheat stem rust²⁹.

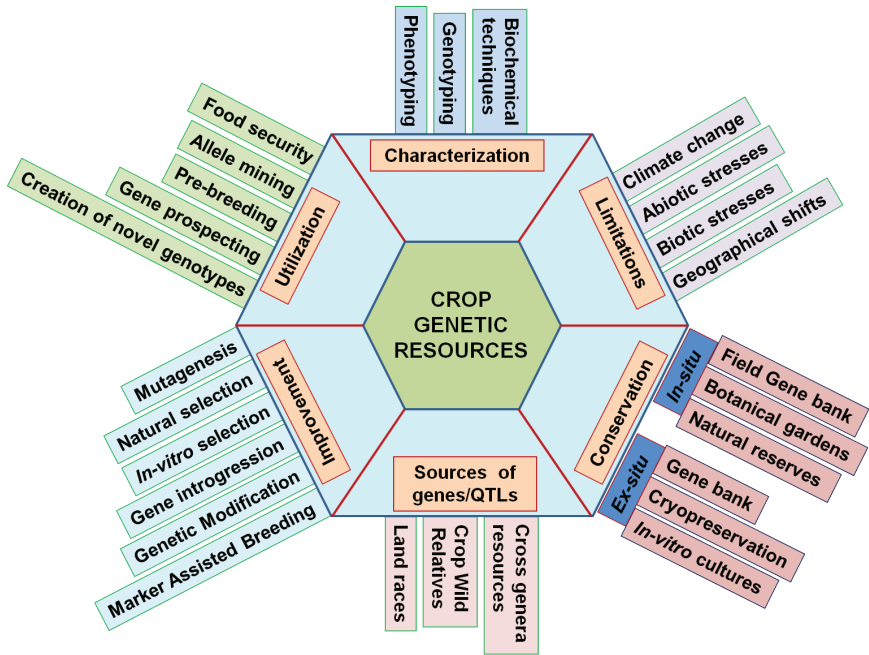


Figure 1: Crop genetic resources, their utilization and applications in agriculture

Management of CGRs and genetic tools

Conservation and management of genetic resources have been a common practice followed by mankind for centuries. The changing climatic conditions may impose serious threats to the CGRs and therefore, their management requires a systematic approach. On-farm conservation of CGRs having variable crops, landraces or traditionally grown materials by the farmers is one of the best management practices of CGRs³⁰, which permits the incorporation of both natural and artificial selections in agriculture. *In-situ* conservation harbours the maximum genetic diversity of plants and is the best source for initially domesticated crops. The *ex-situ* conservation possesses higher quantities of genetic material that may include improved germplasms, CWRs, landraces etc²⁰.

Genomic studies provide an important insight with respect to finding the stress response of a particular crop and also help in searching the genes/alleles/QTLs within CWRs that may be exploited for creation of variability in the cultivated crops. Transfer of important genes in a crop through genetic manipulation has always been a debatable issue but development in the field of plant genomics provides better insight for crop improvement through identification of the presence of diversity at species as well as gene level^{31,32}. DNA fingerprinting, mapping of genes, QTLs and evolutionary data are the tools that provide better understanding for the identification of a specific trait³³.

With the developments in next-generation sequencing, a higher number of genetic markers including single nucleotide polymorphisms (SNPs), insertion-deletion-substitution etc. has been identified even in several neglected crops³⁴. The next-generation sequencing along with the genome-wide association studies provides better insight with respect to the location of desired genes, alleles and or QTLs³⁵. Several new genes have evolved naturally over the period and that have been rearranged according to the environmental conditions, CWRs are the best examples in this context. With the help of genomic tools, the desired gene can be identified and also can be incorporated into the subjected germplasm leading to the development of improved genetic material having enhanced potential over the environment. Genetic amalgamation from varied sources in view of abiotic stresses may be more beneficial in the coming days²². For example, traits incorporated from wild species of rice (*Oryza rufipogon*) to cultivated rice varieties exhibited higher survival potential in the submergence of plants under deep water or under a flooded environment for a longer period.

Gene introgression in plants

Plant hybridization has always been a subject of great interest for geneticists and it has occupied a huge space in the literature from the start of the 20th century. Introgression was discussed initially by DuRietz³⁶ and Marsden-Jones³⁷. The term 'Introgression' coined by Anderson and Hubricht³⁸ is the incorporation of genes from one species to another species by means of frequent crossing between hybrid and parental species. Despite a few bottlenecks like linkage drag, inadequate complementation etc. introgression breeding has been looked at as a potential method in the widening of genetic variability of the genetic resources. Renaissance of the work done by Mendel and its utilization in plant breeding facilitated the process of introgression of genes in a more systematic, rather more controlled way. The introgression of genes leads to genetic diversity and encourages the species to acquire or develop adaptation in the particular environment³⁹. However, there was a contradictory suggestion at that time that the progenies that resulted by the hybrids were limited and or likely to be temporary. Therefore, in the absence of adequate confirmation in respect to plant evolution, introgression or hybridization was considered doubtful⁴⁰. With the advent of molecular techniques, issues related to inherited genes, their detection and quantification could be possible and our understanding with respect to introgression has been improved¹³⁰.

Mutagenesis has been widely applied for the creation of required genetic variability in crops⁴¹. Presently, targeted mutagenesis is induced with the help of gene editing tools like zinc finger nucleases⁴², transcription activator-like effector nucleases⁴³, engineered homing endonucleases or meganucleases⁴⁴, clustered regularly interspaced short palindromic repeats (CRISPR), CRISPR-associated⁴⁵. Various advantages and disadvantages in terms of efficiency of targeting, ease of

construction, cost etc. have been ascertained for each technique⁴⁶. Genome editing has been successfully demonstrated in different plant species such as rice, wheat etc.⁴⁷. Genome engineering is getting more importance parallel to the conventional plant breeding and transgenic approaches to improve several characteristics for sustainable agriculture⁴⁷. Introgression using molecular techniques has been attempted in different crops such as *Brassica*⁴⁸, *Zea*⁴⁹, *Oryza*⁵⁰, Potato⁵¹ and Sunflower⁵². Genes or QTLs introgressed for different potential characteristics in different cereal crops are presented in **Table 1**.

Table 1: Genes/QTLs introgressed for different potential characteristics in different cereal crops

Crop	Gene/QTL	Target trait	References
Wheat	Sr31/Yr9/Lr26/Pm9	Resistance against fungal disease	53
	LrM	Leaf rust resistance	54
	Ug99 Linage	Resistance against all stem rusts	55
	CDH gene, BADH	Tolerance to salt, drought and cold	56
	TaPIMP1	Resistance to the fungal pathogen and drought stresses	57
	TiMYB2R-1	Resistance to the take-all disease	58
	Ta-Mlo RC24	Resistance to powdery mildew and stripe rust disease	59
	SN1	Resistance to take-all pathogen	60
	KN2	Tolerance to freezing stress	61
	TaERF3	Adaptation towards salt and drought stresses	62
	Mildew-resistance locus gene	Resistance to powdery mildew	63
Nib8 gene	Resistance to wheat yellow mosaic virus	64	
Rice	Sub1	Survivability under submergence	65
	Dro-1	Drought tolerance	66
	GSV strain1	Grassy stunt virus	67
	Pi-b and Pi-kh	Blast resistance	68
Millet	SiDREB2	Drought resistance	69
Maize	acetyl-CoA carboxylase (ACC1)	herbicide resistance	70
	o2 gene	Quality protein maize (QPM)	71
	Phol1, 2a	Nutrition	72
	o1, Orp2, Sbe1, Ss5, Su4	Grain development	73

Gene introgression in legumes

Legumes are generally grown on marginal lands with limited inputs and are, therefore, more prone to climatic changes in comparison to other crops. In view of this, gene introgression has got significant success in the field of legume breeding. The CWRs, landraces and non-native genotypes provide immense opportunities for introgression of variability and broadening of the genetic base in the available genetic materials of legumes. Gene introgression from wild relatives has been effectively utilized in several legumes *viz.*, *Cicer arietinum*, *Cajanus cajan*, *Arachis hypogaea*, *Lens culinaris*, *Vigna radiata*, *V. mungo*, *Phaseolus vulgaris* etc. for development of better genetic materials and to improve their performance. In chickpeas, crosses between *C. arietinum* and *C. echinospermum* were performed⁷⁴ and their diversity has been exploited to transfer beneficial characteristics such as disease resistance, cold tolerance in the domesticated chickpea^{75,76}. Interspecific crosses have effectively been performed in several species of chickpea using *C. arietinum*⁷⁷. These exhibited effective introgression of beneficial genes into *Cicer* species. Interspecific hybridization of *Phaseolus vulgaris* was performed with the wild species of *Phaseolus* and white mold-resistant line was developed from *P. costaricensis*. Several germplasm lines were developed by different workers⁷⁸ by crossing the domesticated and wild-type bean germplasm.

Traits of interest including disease resistance and tolerance towards salinity have been identified in wild soybean species. QTL analysis in wild relatives of soybean revealed that it has the potential to increase protein content in cultivated soybean⁷⁹. Lentil CWRs have been exploited in the breeding programme and early maturing and biofortified lines of lentil was developed⁸⁰. The hybrids developed with the crossing of cultivated lentils and *Lens ervoides* resulted into the introgression of resistance in the domesticated species against *Orobanche crenata* and anthracnose⁸¹. *L. orientalis* and *L. ervoides* have been successfully utilized for the introgression of several agronomically important characteristics along with disease resistance and biofortification in the pre-bred lines. These lines exhibited higher micronutrient content and early maturity⁸². In pigeonpea, seven cytoplasmic male sterility (CMS) systems have been developed and out of these, six were developed using the wild species of secondary gene pool while 7th system was developed using a member (*Cajanus platycarpus*) of tertiary gene pool⁸³. Hybridization between mung bean and urd bean showed tolerance against biotic and abiotic stresses, non-shattering of pods, synchronicity in podding etc.⁸⁴. Hybridization between *V. radiata* and *V. umbellata* was performed and hybrids having transitional morphological traits along with resistance against MYMV were obtained. Some of the early maturing varieties in mung bean as well as in Urd bean are the important outcome of hybridization between mung bean and Urd bean⁸⁵.

An important gene having heat and drought resistance potential has been reported in *P. vulgaris*⁸⁶. Several genetic maps based on intra and interspecific distance have been constructed for chickpea⁸⁷. Besides this, regions of the genome that are accountable for biotic⁸⁸, abiotic stresses⁸⁹ and several agronomically important characteristics⁹⁰ has also been identified in chickpea. Several QTLs in peanut having tolerance against abiotic stresses⁹¹, disease resistance⁹² and better oil quality⁹³ have been recognized. The available genetic information and resources may be exploited in the crop improvement with the help of introgression of genes in the breeding programme. Potential wild species selected for gene introgression have been listed in **Table 2**.

Table 2: Potential wild species for gene introgression in legumes

Crop	Species	Target trait	References
	<i>C. echinospermum</i>	Ascochyta blight	94
	<i>C. judaicum</i>	Ascochyta blight	94
	<i>C. reticulatum</i>	<i>Pratylenchus thornei</i>	95
	<i>C. echinospermum</i> ; <i>C. oxyodon</i>	Drought	94
	<i>C. yamashitae</i>	Drought	96
	<i>C. echinospermum</i>	Phytophthora root rot	97
Lentil	<i>L. culinaris ssp. orientalis</i> , <i>L. ervoides</i>	Fusarium wilt	98
	<i>L. culinaris</i> Medikus subsp. <i>orientalis</i> , <i>L. nigricans</i> , <i>L. lamottei</i>	Bruchids	99
	<i>L. ervoides</i>	Powdery mildew and Fusarium wilt	98
Several <i>Vigna</i> species	<i>V. angularis</i>	<i>Heterodera glycines</i>	100
	<i>V. luteola</i> , <i>V. marina</i> , <i>V. vexillata</i> , <i>V. riukiensis</i> , <i>V. trilobata</i> , <i>V. vexillata</i> , <i>V. marina</i> subsp. <i>oblonga</i> , <i>V. luteola</i> , <i>V. unguiculata</i> , <i>V. nakashimae</i> , and <i>V. marina</i>	Salt stress	101-104
Field pea	<i>P. sativum</i> subsp. <i>elatius</i>	Seed protease inhibitors	105
	<i>P. elatius</i> ; <i>P. fulvum</i>	Pulse beetle	106

Crop	Species	Target trait	References
Pigeonpea	<i>C. acutifolius</i> , <i>C. cinereus</i> , <i>C. lanceolatus</i> , <i>C. latisepalus</i>	Heat, drought	107
	<i>C. confertiflorus</i> , <i>C. mollis</i> , <i>C. platycarpus</i> , <i>C. trinervius</i>	Cold	107
	<i>C. sericeus</i> , <i>C. lineatus</i>	High precipitation, waterlogging	107
	<i>C. scarabaeoides</i>	Insect resistance	108
	<i>C. sericeus</i>	Pod fly	109
Common bean	<i>P. acutifolius</i>	Abiotic stresses	110, 111
Cowpea	<i>V. unguiculata</i> group <i>sesquipedalis</i>	Heat and salinity	103

Gene introgression in tree species

Trees are perennials that survive for a longer period compared to cereals and legumes. The dispersal of tree species is anticipated to change due to the effect of climate change, biotic and abiotic stresses. Gene introgression plays an important role in the novel genetic modification that helps the tree species to survive under the changed environmental conditions. However, its understandings with respect to plant species are comparatively less. Efforts in terms of domestication and breeding in tree species are lesser as compared to other agricultural crops. The interspecific hybridization offers a base for the genetic variability by the mean of introgression of genes/alleles between inter-fertile species¹¹² and the development of more potential species¹¹³.

The inter-species introgression is often observed in sympatric tree species that influence the addition, substitution and deletion of bases in the DNA fragments and may stimulate the adoption process of the species. Evidence of natural hybridization has been reported in the genus *Eriobotrya* suggesting that *E. prinoidea* var. *Daduheensis* is the outcome of hybridization between *E. japonica* and *E. prinoidea*¹¹⁴. Similarly, the genetic material of the natural hybrid poplar *Populus × Jrtyschensis* was reported to be influenced by two distantly related species *P. nigra* and *P. laurifolia*¹¹⁵. The species *Juglans regia* and *J. cathayensis* exhibited resilient reproductive isolation along with exceptional occurrence of gene introgression¹¹⁶.

Two (PjMT1, PjMT2) metallothionein (MT) genes were isolated from *Prosopis juliflora*. The genes were cloned on pCAMBIA1301 and after cloning, gene introgression was done in tobacco to study the tolerance against heavy metals. The study revealed nine times and five times higher cadmium accretions in the transgenic plants of tobacco developed by PjMT1 and PjMT2 genes, respectively as compared to non-transgenic tobacco plants along with higher accumulation of

chlorophyll content¹¹⁷. An example of ancient gene introgression between two conifers (*Cupressus gigantea* to its relative species *C. duclouxiana*) was presented by Ma *et al.*¹¹⁸. Cross genera transferability of microsatellite markers from *Incarville asinensis*, *I. mairei*, *Jacaranda copaia*, *Tabebuia aurea* and *Arrabidaea chica* to *Tecomella undulata* was undertaken^{119,120} and about 40.58 per cent transferability was recorded. The study revealed that the transferability of SSR motifs having dinucleotide repeats, trinucleotide repeats and complex nucleotide sequences were higher than the penta-nucleotide-based or hexa-nucleotide-based repeats. Utilization of genetic resources from con-familiar species may be useful for the assessment of genetic diversity and preparation of genetic maps in tree species. Plant growth regulators were also utilized to induce genetic diversity, especially in fruit trees¹²¹.

Genetic as well as morphological diversity of different *Sorbus* species comprising of *S. aria* (domesticated species), *S. intermedia* (foreign species) and *S. carpatica* (hybrid species) was assessed¹²² and hybridization between tested species were recorded with the confirmation of its hybrid species (*S. carpatica*). Oaks are exploited to understand the adoption mechanism and gene introgression. Hybridization and introgression in the populations of oak species were studied¹²³ and 361 alleles in all the species were identified. A better understanding of life antiquity and reproductive mechanism may be an important factor for the determination of gene introgression in tree species.

Conclusions

CGRs are the fundamental material for sustainable development in agriculture. Parents having variable and improved characteristics are utilized for enhancing the potential of desired traits^{124,125}. Genomics-aided approaches for the development of genotypes may considerably help in the reduction of the negative effects of climate change on agriculture^{126,127}. Advancements in the technologies such as transgene-based, molecular breeding or genomic-assisted breeding have expedited the development of potential crops for crop improvement^{128,129}. Several underutilized or neglected plant species have been reported with useful genes/QTLs. The genes associated with the desired traits in these plant species may be decoded and introgressed in the domesticated plant species. The genetic base of domesticated varieties should be widened in such a way that they can acquire more resistance toward abiotic and biotic stresses, seed quality and higher yields. DNA sequencing and genomic tools may be useful for the detection of desired genes and or governing regions with respect to higher yields as well as stress resilience. Hybridization and utilization of exotic germplasms and CWRs may be utilized in the improvement of several crops. Increasing the pervasive crossing between domesticated species and their wild relatives may provide improved and precise introgression of genes/alleles of choice. Introgression of genes from wild genetic resources has been fruitful in

several cereals and legumes and resulted in the development of several varieties, breeding and male sterile lines that may be exploited in the planning of breeding programmes.

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