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Enhancing Crop Gene Pools with Beneficial Traits Using Wild Relatives

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ABBREVIATIONS

AFLP	Amplified fragment length polymorphism
BC	Backcross
BLAST	Basic local alignment search tool
cDNA	Complementary deoxyribonucleic acid
CGIAR	Consultative Group on International Agricultural Research
C1AT	Centro International de Agricultura Tropical
CIMMYT	International Maize and Wheat Improvement Center
CMS	Cytoplasmic male sterility
CSSLs	Chromosomal segment substitution lines
DNA	Deoxyribonucleic aicd
EMBRAPA	Empress Brasileira de Pesquisa Agropecuaria
EBN	Endosperm balance number
FAO	Food and Agriculture Organization
GCP	Generation Challenge Programme
GP	Gene pool
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
MAAL	Monosomic alien addition lines
PGK	Plant genetic resources
QTL	Quantitative trait loci
rDNA	Recombinant deoxyribonucleic aicd
RFLP	Restriction fragment length polymorphism
RILs	Recombinant inbred lines
SNP	Single-nucleotide polymorphism
SSRs	Simple sequence repeats

I. INTRODUCTION

The Russian geneticist and plant explorer Nikolai Ivanovich Vavilov is known for his pioneering research on the phyto-geographic basis of plant breeding and the world centers of crop origin, the laws of homologous series in the inheritance of variability, and the study of immunity of plants from infectious diseases (Vavilov 1951). Vavilov also understood the role of wild species in the genetic enhancement of crops, as shown by his reports on the use of plant genetic resources in crop breeding. For example, after analyzing the interspecific constitution of bread wheat, Vavilov [1951) referred to the potential use of genera such as *Aegilops, Secale, Haynodia,* and *Agropyrum* in wheat improvement.

A crop wild relative is a wild plant taxon that has an indirect use derived from its relatively close genetic relationship to a crop (Maxted et al. 2006). An understanding of the taxonomic and evolutionary relationships between cultigens and their wild relatives is prerequisite for the exploitation of wild species in crop improvement (Hawkes 1977). Harlan and de Wet (1971) proposed the gene pool (GP) concept to define relationships among crop plants and related taxa that could be useful to plant breeders and geneticists wishing to make use of these resources in crop improvement. They assigned various genetic resources to the three GPs based on ease of hybridization: primary (GP-1), secondary (GP-2), and tertiary gene pool (GP-3). GP-1 includes germplasm that can be easily hybridized, for example, cultivars, land races, and elite germplasm. GP-2 consists of species that can be crossed with GP-1 without major problems of F_1 infertility, Gene transfer from species in GP-2 to cultivars is possible, but may be difficult to accomplish, GP-3 is the outer limit of potential genetic resources associated with cultivated species and hybrids between GP-1 and GP-3 species almost always require in vitro techniques for F_1 rescue due to lethality and physiological abnormality of complete sterility. In these cases, bridging species are often needed to effect gene transfer from the tertiary gene pool to the cultivated crop, but this is usually a laborious process, and selection for the desired gene can be very difficult. It is important to note that despite the problems of inter-gene pool hybridization, the need for these types of crosses is great, given that the cultivated gene pools of many food crops are narrow and genetic improvement is stifled by a lack of variability. Therefore, there is a need to broaden the basis of crop gene pools in order to enhance their genetic potentials and meet the growing food demands of the developing world,

The use of plant genetic resources (PGR) in crop improvement is one of the most sustainable methods to conserve valuable genetic resources for the future and simultaneously to increase agricultural production and food security. Haussmann et al. (2004) summarized issues related to use of PGR in crop improvement that include information resources on the Internet; documentation and evaluation of PGR; access to PGR, equitable sharing of profits, and material transfer agreements; impediments to the use of PGR in crop improvement; classical methods of using PGR in crop improvement; use of landraces in breeding for specific adaptation to stress environments; utility of molecular markers and genomic approaches for using PGR in crop improvement; and gene transfer. The greatest economic impacts of wild relatives in crop improvement to date have been in increasing disease and pest resistances in several crops (Harlan 1976; Stalker 1980; Goodman et al. 1987; Lenne and Wood 1991; Hoisington et al. 1999). The increases in annual crop yields from crop improvement since 1945 are worth approximately US $60 billion per year (USBC 1995), Assuming that contribution of genetic resources is responsible for 30% of yield increase and that much of this is from wide crosses with wild accessions, the introduction of new genes from wild relatives contributes per year approximately $20 billion toward increased crop yields in the United States and $115 billion worldwide (Pimentel et al. 1997). Wild relatives have also shown very high levels of resistance or tolerance to abiotic and biotic stresses in contrast to cultivated species. However, gene introgression from wild relatives to cultivars has been difficult due to cross incompatibility, hybrid sterility, and linkage drag (Stebbins 1958; Zeven et al. 1983).

This review documents the contributions of wild relatives to broadening the gene pools emphasizing selected cereal (wheat, rice, maize, barley, oat, sorghum, and pearl millet) and legume (soybean, common bean, chickpea, pigeonpea, cowpea, and peanut [groundnut]) crops found in the Food and Agriculture Organization (FAO)-mandated collections of the Consultative Group on International Agricultural Research (CGIAR). The institutes of the CGIAR have the responsibility to collect, preserve, characterize, evaluate, and document the genetic resources of the cultivated and wild relatives of these crops. Additionally, they have genetic improvement programs for their utilization. These gene banks have provided genetic resources to researchers around the world for use in crop improvement. Among the cereal and legume accessions preserved in the CGIAR collections, 17.4% (65,200) of the total collection (375,200) belong to wild relatives. Although this review concentrates on cereals and legumes, additional examples will be given from other crop species where they may serve as models for the use of germplasm for enhancing productivity to meet growing food demands.

II. GENETIC RESOURCES FROM WILD RELATIVES

Novel germplasm can be used in breeding programs to create new crops and new uses for existing crops, to meet breeding objectives for sustainability of crop production, and to ensure the entire world's people benefit from crop improvement through enhanced food security and quality (Heslop -Harrison 2002). The key to successful crop improvement is a continued supply of genetic variability and beneficial traits contained in this diversity. Most plant breeders/geneticists exploit variability only from the primary gene pool of a specific crop. However, variability for some traits of interest exists only in the secondary or tertiary gene pools. Novel germplasm that is available in species not currently used commercially can be expoited by domesticating them for direct use or introducing their genes into existing cultivars through conventional breeding, by use of in vitro technologies, or through use of genetic transformation. Molecular biology-based technologies such as marker-assisted selection now can assist in identifying and tracking allelic variants associated with beneficial traits and identifying desirable recombinant plants with the markers of interest. Alternately genes can be cloned from distantly related species or genera and introduced into existing crops. Indeed, gene technologies are now available to exploit species in the tertiary gene pool and even more distantly related taxa. As a result, the concept of gene pools is not static and shifts as new technologies become available to affect gene transfer. For example, a dominant gene for resistance to bacterial blight was cloned from a distantly related wild relative of rice [Song et al. 1995] and transferred into transgenic versions of commercial cultivars, of rice, which then showed the same level of resistance as observed in the wild relative from which the gene was cloned (Zhai et al. 2001]. Obviously, the potential for exploiting novel germplasm has greatly increased and will increase the potential of plant breeders to continue improving crops with high yields, better adaptation, and enhanced quality.

As part of this new paradigm for using genetic resources, the Generation Challenge Programme (GCP) (www.generationcp.org) was established with the objective of unlocking the genetic diversity existing in a wide spectrum of germplasm collections in order to solve some of the world's most serious agricultural arid food security issues. This program supports global competitively funded projects to (1) exploit natural genetic variation by developing genomic resources and introgression lines for four AA genome rice relatives; (2) enhance genetic diversity in wild relatives of peanut with genomic and genetic tools; and (3) discover genes in wild relatives of rice for tolerance of saline and phosphorus-deficient soils to enhance and sustain productivity on marginal lands. It is expected that the novel germplasm and associated technologies developed in these projects will be useful to applied breeding for improved adaptation of these crops to conditions in developing-country agriculture. Other examples of the exploitation of genetic resources from the secondary and tertiary gene pools (or even more distantly related species) and generation of novel cultivated germplasm exist for wheat, barley, and related small grains: *Hordeum bulbosum,* the only species belonging to secondary gene pool (Bothmer et al. 1995), contributing novel alleles for resistance to several leaf diseases to cultivated barley *(H. vulgore)* (Pickering and Johnston 2005); synthetic wheat with demonstrated potential to enhance grain yield and/or yield components (de Blanco et al. 2001); tritipyrum with high levels of salt tolerance (King et al. 1997b); and hexaploid tritordeum with high water-use and nitrogen-utilization efficiency and grain characteristics like bread wheat (Martin et al. 1999). However, brittle rachis in the hexaploid tritordeum is a serious limitation to threshing by mechanical harvester. To establish tritordeum as a new commercial cereal, Prieto et al. (2006) developed double disomic substitution lines, 2D($2H^{ch}$) and $3H^{v}$($3H^{ch}$), that possess nonbrittie rachis, tenacious glumes, and compact spikes (a character highly desirable for the improvement of tritordeum threshability), and these lines can be used for introgression to wheat or tritordeum background. Similarly in maize, exploitation of wild relative *Tripsacum* has the potential for fixing hybrid vigor through apomixes found in this species and contributing abiotic and biotic stress resistances not present in maize (Hoisington et al. 1999).

III. BARRIERS AND APPROACHES TO INTERSPECIFIC GENE TRANSFER

Barriers to interspecific hybridization are common among species. They can be caused by spatial or phonological differences in flowering, sexual incompatibility, and cytological abnormalities, or because they are genetically too distant to be compatible. Because plants that are being crossed are typically maintained in nurseries, sexual barriers are of most concern to the scientist. Reproductive barriers are differentiated by the time they occur, typically at pre- and postfertilization. Accessions within a species can be highly variable in their compatibility, and there are times when only a few accessions or cultivars within a species will serve as a parent in interspecific crosses, and often in only a unidirectional manner (Baum et al. 1992). Thus, it is important to attempt difficult crosses with a range of germplasm and in a range of environments. For example, hybrids with cultivated peanut and the related species *Arachis glabrata* must be made with the wild relative as a female parent and have only been successful in crosses made under natural sunlight to those in greenhouse. Interspecific crosses can also be enhanced or prevented by single genes (Fedak and Jui 1982; Laurie and Bennett 1989), and their effect on plant breeding is reviewed by Frankel and Galun (1977).

It is beyond the scope of this review to provide in-depth discussion on the reproductive barriers and the technologies for circumventing these barriers that are published elsewhere (Liedl and Anderson 1993), A number of techniques have been used to either circumvent or overcome barriers to hybridization, A summary of these techniques is presented in two sections, depending on the timing of the barriers to hybridization, either before or after fertilization.

A. Prefertilization Barriers to Hybridization

Incompatability between the male and female parents can first occur in the stigma or stylar tissues before fertilization occurs. To overcome these incompatibilities, techniques can be employed, such as the use of (1) compatible pollen that is capable of germinating but with inactivated nuclei mixed with the pollen desired for crossing, or (2) mixtures of compatible and incompatible pollen with identification of hybrids versus selfs in the subsequent generation (Brown and Adiwilaga 1991). Other methods of overcoming stigma/style inhibitions include cutting part or all of the style tissue, thus removing the stigma and many of the inhibition factors that may be present (Wietsma et al. 1994), or heating styles before pollination to inactivate inhibition factors (Ascher and Peloquin 1968)- Alternatively, chemical applications of gibberellins or auxins and cytokinins to reproductive tissues can result in faster pollen tube growth and fertilization or enhanced fruit development (Dionne 1958; Larter and Chaubey 1965; Kruse 1974; Alonso and Kimber 1980; Sastri and Moss 1982). Immunosuppressants applied to floral tissues have also been used to enhance hybridization in cereals (Baker et al. 1975; Mujeeb-Kazi and Rodriguez 1980) and in legumes (Baker et al. 1975).

B. Post fertilization Barriers to Hybridization

Causes of postmating barriers include polyploidy differences between species, chromosome toss or rearrangements, cytoplasmic incompatibilities, physiological seed dormancy, apomixes, and hybrid breakdown resulting from lethals or low plant vigor in the first or subsequent generations. At least as important as producing hybrids is genetic recombination between the species to transfer the desired genes into the cultivated species genome. This is a straightforward event in some interspecies crosses, especially when the species are at the same ploidy level and have common genomes, but it can be an extremely rare event in other cross combinations. In other cases, apomixes but not recombination occurs after generation of the interspecific hybrid. When apomixes are present in one of two species to be crossed, interspecific crosses are made with the apomictic species as the male parent to avoid this trait. A more difficult circumstance occurs when it becomes necessary to cross two apomictic species because sexual hybridization is not possible. Although a limited number of sexual progenies develop even in apomictic species, large numbers of recombinants are usually required for intragenomic chromosome pairing to occur or to break up linkage groups associated with lethality.

After fertilization and gamete fusion and usually after a period of embryo growth, in vitro culture techniques are commonly used to recover young embryos from interspecific crosses before they abort (Williams et al. 1987). Ovule culture is more often used when embryo abortion occurs at a very early stage; alternately, sequential culturing of ovules and then embryos can be employed, as was done for interspecific hybrids of *Trifolium* (Przywara et al. 1989), In general legumes are more difficult than grasses to manipulate in vitro, but in either case, culturing procedures are not trivial exercises.

Another complexity occurs when cultivated and wild species are at different ploidy levels. This is important given that many cultivated species, including wheat, oat, sugarcane, peanut, cotton, and potato, are polyploids whereas related species for these crops are often at a different ploidy level. Genomic imbalances in hybrids between species with different chromosome numbers can be overcome by several approaches: First, direct crossing followed by chromosome doubling of the sterile hybrids can often restore fertility to the F_1 generation. Subsequently, the colchicines-treated plants can be either backcrossed with the cultivated species (as the recurrent parent) or they can be selfed in an effort to generate spontaneous chromosome reduction to the ploidy level of the cultivar, An example of this is interspecific hybridization between peanut ($2n$ = 40) and *A. cardenasii* (2n = 20), where the hybrids were initially triploid (2n = 30), but were treated with colchicines to double the number of chromosomes to the hexaploid level, followed by self-pollination for multiple generations to derive tetraploid progenies (Company et al. 1982). Although time-consuming and unpredictable, the advantage of the selfing approach is the increased number of generations in which recombination can occur between the chromosomes of different genomes. A second method of overcoming ploidy differences is to raise the chromosome number of the species at the lower ploidy level to that of the species at higher ploidy level, which is usually the cultivar prior to making pollinations between species. For cultivars that are autopolyploid, this has been highly successful, but in allopolyploid species, there remains a considerable amount of sterility in F_1 hybrid or later generations. To partially circumvent this type of genomic sterility, bridging species at the lower ploidy level and chromosome doubling can be used to make the desired interspecific hybrid with the respective cultivated species (Simpson 1991). Some species can be manipulated to lower the chromosome number of the higher-ploidy species. For example, Voigt (1971) reported a diploid sexual plant in the tetraploid apomictic grass species *Eragrostis curvula,* in tobacco where tetraploid *Nicotiana tabacum* can be hybridized as females with *N. afracana* to generate maternally derived haploids (Burk et al. 1979), or by reduced parthenogenesis in species of *Solarium* (Peloquin and Ortiz 1992), Polyploids can then be resynthesized to equal the chromosome number of the higher-ploidy species. In wheat, techniques have been used for nearly a half century to induce translocations or create chromosome addition or substitution lines with these methods (Khush 1973). Although not a cereal, *Saccharum* is one of the easiest genera to manipulate, in large part because of its high ploidy level, and it has been possible to introgress partial or complete genomes from wild species into *S. officinarum* L. (2n = 80), creating modern cultivars that vary in number but all of which have more than 100 chromosomes.

Ploidy manipulations with haploids, *2n* gametes, and use of wild species remain as impressive and exciting crop germplasm enhancement methods that have developed from cytogenetic research (Ortiz et al. 2006). Professor Stanley J. Peloquin (University of Wisconsin, Madison, USA) and his associates were able to develop new potato genotypes that combine high and stable yield with disease or pest resistance, which allow potato to be grown in areas previously unsuitable for this crop (Ortiz et al, 2005). The genetic enhancement of potato germplasm often involves the use of species that are the source of genetic diversity, haploids that provide a method for utilizing this diversity, and *2n* gametes with the endosperm balance number (EBN) that provide an effective method for transmitting the diversity into cultivars. There are two main methods for ploidy manipulations in potato: unilateral sexual polyploidization (*4x-n* gametes x *2x-2n* gametes or vice versa) and bilateral sexual polyploidization (ensuing from crosses between *2x-2n* gametes producing parents) (Ortiz 1998).

For these breeding schemes, the diploid progenitors ensue from crosses between potato haploids and tuber-bearing diploid species. Maternal haploids are easily extracted through parthenogenesis from most tetraploid potato cultivars, and they can be crossed with diploid species. The locally adapted haploid-species hybrids are used for selection because they possess *2n* gametes, acceptable tuber characteristics, and additional desired attributes (e.g., disease or pest resistance). Polyploids can then be resynthesized because most of the hybrids ensuing from sexual polyploidization in potato are tetraploids (due to a strong triploid block in potato).

Other difficulties in transferring genes from wild to cultivated species are: (1) nonflowering of hybrids; (2) selective chromosome elimination of the donor parent; (3) hybrid breakdown due to hybrid lethality or low vigor; and (4) physiological seed dormancy of the hybrid (Baum et al. 1992). Unfortunately, options to circumvent these problems do not exist for crop improvement.

Biotechnology is increasingly being utilized for interspecific hybridization efforts. Although marker-assisted selection is useful both for identifying and following genes of interest in wild species crosses (Tanksley and McCouch 1997), it is not useful for overcoming barriers per se. Transformation technologies, however, are useful for overcoming these barriers because in many cases a single gene is desired from the wild species parent and can be more precisely moved through genetic engineering rather than genetic crosses. This is true in the case of monogenic resistance to plant pathogens, as discussed in Section V.B. It is worth keeping in mind, however, the large amount of research involved in identification and cloning of specific genes from a wild relative, as well as their transformation into the genome of the cultivated species and selection for stable expression. As more genomes are fully characterized, gene cloning and transformation methodologies will become more useful and common techniques for gene introgression will be available.

IV. BENEFICIAL TRAITS FROM WILD RELATIVES CONTRIBUTING TO CROP GENE POOLS

A. Resistance to Biotic Stresses

Pests and diseases are the major causes of low productivity in cultivated plants. For biotic stresses, resistance is either not available in cultivated species or is available only at very low levels. In contrast, very high levels of resistance to pests and diseases have been reported in many wild relatives of cultivated species, and in some case attempts to transfer this resistance have been successful (Table 3.1), Examples of successful gene transfer include resistance to bacterial blight *(Xanthomonas oryzae pv. Oryzae),* blast *(Magnaporthe grisea),* sheath blight *(Rhizoctonia solani),* brown plant hopper *(Nilaparvata lugens),* white-backed plant hopper *(Sogatella furcifera),* yellow stem borer *[Scirpophaga ineertulas),* and grassy stunt virus in rice; leaf rust *[Puccinia triticina),* yellow rust (also known as stripe rust) *(Puccinia striiformis f. sp. tritici),* stem rust *(Puccinia graminis),* karnal bunt *(Tilletia indica),* powdery mildew *(Erysiphe graminis),* common root rot *(Cochliobolus sativus),* fusarium head blight (*Fusarium graminearum),* hessian fly *(Mayetiola destructor),* green bug *(Schizaphis graminum),* root-knot nematode *(Meloidogyne naasi),* and soil-born mosaic and spindle-streak mosaic viruses in wheat; leaf blight *(Bipolaris maydis)* in maize; and powdery mildew *(Bulmeria graminis f. sp. hordei),* septoria speckled leaf blotch *(Septoria passerinii),* leaf rust *(Puccinia hordei),* scald *(Rhynchosporium secalis),* and barley mild mosaic and barley yellow mosaic viruses in barley. Unlike cereals, the contribution of wild relatives to legumes has been limited to a few pests and fungal or bacterial diseases that include resistance to nematodes *(Heterodera* spp.) in chickpea and soybean; to common bacterial blight *(Xanthomonas axonopodis pv, phaseoli),* fusarium root rot *(Fusarium solani* f. sp. *phaseoli),* white mold *(Sclerotinia sclerotiorum),* and bruchid *(Zabrotes subfasciatus)* in common bean; and to rust *(Puccinia arachidis),* early leaf spot *(Cercospora arachidicola),* late leaf spot *(Phaseoisariopsis personata),* nematodes *(Meloidogyne* spp.*)*, southern corn rootworm *(Diobrotica undecimpunctata howardi),* corn earworm *(Heliothis zea), Spodoptera (Spodoptera spp.),* and velvetbean caterpillar *(Anticarsia gemmatalis)* in peanut (Dwivedi et al. 2005),

B. Tolerance to Abiotic Stresses

Drought, salinity, acidic soils, phosphorous deficiency, and variation in temperature are the major abiotic stresses contributing to the substantial loss of production in cereal and legume crops. Many wild relatives have shown high levels of tolerance to these stresses, and some genes conferring these stress tolerances have been successfully transferred into cultivated species (Table 3.2). Examples include tolerance to acidic soils and aluminum toxicity in rice; drought and salinity tolerance in wheat; and drought tolerance in barley. Interspecific progenies in chickpea have shown tolerance to drought and cold temperature. Unlike cereals, this is the only example of gene transfer for abiotic stress tolerance from wild to cultivated legumes.

Table 3.1. Wild relatives contributing resistance to pests and diseases in barley, chickpea, common bean, maize, oat, peanut, rice, soybean, and wheat.

Pest/Disease	Wild Relatives Contributing Genes for Resistance to Biotic Stresses	Reference
Barley (*Hordeum vulgare)*		
BaMMV and BaYMV	*H. bulbosum* contributed gene, *RYM16*^{Hb}, conferring resistance against all European viruses of soil-borne virus complex (BaMMV, barley mild mosaic virus; BaYMV, barley yellow mosaic virus (BaMMV, BaYMV-1, -2)) in *H. vulgare.*	Ruge-Wehling et al. 2006
	H. bulbosum contributed gene, *Rym14*^{HB}, for resistance to BaMMV and BaYMV in *H. vulgare.*	Ruge et al. 2003
Leaf rust	Resistance to rust *(Puccinia hordei)* transferred from *H. bulbosum* to *H. vulgare.*	Zhang et al. 2001
Leaf rust and mosaic viruses	Resistance to all leaf rust and mosaic viruses transferred into winter *H. vulgare* from *H. bulbosum.*	Walther et al. 2000
Multiple resistance	*H. bulbosum* contributed genes for resistance to leaf rust, powdery mildew *(Bulmeria graminis* f. sp. *hordei)*, scald *(Rhynchosporium secalis)*, septoria speckled leaf blotch *(Septoria passerinii)*, and BaYMV/BaMMV in *H. vulgare.*	Pickering and Johnston 2005
Powdery mildew	*H. bulbosum* contributed gene for resistance to powdery mildew in *H. vulgare.*	Xu and Kasha 1992; Pickering et al. 1995
Powdery mildew, leaf rust, and scald	*H. vulgare* asp. *spontaneum* contributed genes for resistance to powdery mildew, leaf rust, and scald in *H. vulgare.*	von Korff et al. 2005
Septoria speckled leaf blotch (SSLB)	Resistance to SSLB *(Septoria passerinii)* transferred into barley from *H. bulbosum.*	Toubia-Rahme et al. 2003
Chickpea (Cicer arietinum)		
Cyst nematode	Resistance to cyst nematodes *(Heterodera ciceri* and *H.* rosii*)* transferred from C. *reticulatum* and C. *echinospermum* to C. *arietintim.*	Malhotra et al. 2003
Wilt, foot rot, and root rot	Inter-specific derivatives involving C. *reticulatum* showed resistance to wilt (Fusarium *oxysporum* f. sp. *ciceris),* foot rot *(Phacidiopycnis padwickii),* and root rot *(Fusarium spp.* and *Rhizoctania solani)* diseases.	Singh et al. 2005

Common Bean *(Phaseolus vulgaris)*		
Bruchid	Monogenic arcelin-based weevil resistance against the bruchid *(Zabrotes subfasciatus)* transferred from wild common bean to ClAT breeding lines.	Kornegay et al. 1993
	Resistance to bruchid from wild bean populations from highlands of Mexico transferred to P. *vulgaris.*	Cardona and Kornegay 1989, 1999
Common bacterial blight (CBB)	Resistance to CBB *(Xanthomonas axonopodis* pv. *phaseoli)* transferred from tepary bean to P. *vulgaris.*	Singh and Munoz 1999
CBB, fusarium root rot, and white mold	Moderate resistance from *P. coccineus* to CBB, fusarium root rot *(Fusarium solani* f. sp. *phaseoli),* and white mold *(Sclerotinia sclerotionim)* introgressed to dry/snap beans.	Singh 2001
Maize *(Zea mays)*		
Leaf blight	Resistance to northern corn leaf blight *(Bipolaris maydis)* transferred from *Tripsacum dactyloides* to maize.	Goodman et al. 1987
Oat (Avena sativa)		
Powdery mildew	*A. macrostachya* contributed gene for resistance to powdery mildew *(Erysiphe graminis)* in oat.	Herrmann 2006
Peanut *(Arachis hypogaea)*		
Nematodes and insect pests	Wild *Arachis* species contributed resistance to nematodes (*Meloidogyne spp.),* *Spodoptera (S. frugiperda* and S. *litura),* corn earworm (*Heliothis zea),* southern corn rootworm *(Diobwtica undecimpunctata howardi),* velvetbean caterpillar *(Anticarsia gemmatalis),* and Jassids *(Empoasca* ssp*)* to *A. hypogaea.*	Stalker et al. 2002a; Stalker and Lynch 2002; Dwivedi et al. 2003; Mallikarjuna et al. 2004
Rust and leaf spots	Wild *Arachis* species contributed resistance to rust *(Puccinia arachidis),* early leaf spot (*Cercospora arachidicola),* and late leaf spot *(Phaeoisariopsis personata)* to *A. hypogaea.*	Stalker et al. 2002b; Dwivedi et al. 2003; Mallikarjuna et al. 2004
Rice *(Oryza sativa)*		
Bacterial blight (BB)	A dominant gene for resistance to BB *(Xanthomonas oryzae pv. Pryzae)* transferred from *O. longistaminata* to *0. sativa*. Several introgression lines resistant to BB developed by crossing IR 56 with 0. *brachyantha.*	Khush et al. 1990 Brar et al. 1996
Blast (Bl) and BB	Resistance to Bl *(Magrtaporthe grisea)* and BB transferred from O. *minuta* to O. *sativa.*	Amante-Bordeos et al. 1992

(continues)

Table 3.1. (continued)

Pest/Disease	Wild Relatives Contributing Genes for Resistance to Biotic Stresses	Reference
Brown plant hopper (BPH)	Resistance to three biotypes of BPH (*Nilapavata lugens)* transferred from *O. officinalis* to *O. sativa.*	Jena and Khush 1990
	An introgression line resistant to BPH selected from BC_2F_4 population of *O. australiensis* x *O. sativa.*	Ishii et al. 1993
Grassy stunt virus (GSV)	A gene for resistance to GSV transferred from *O. nivara* to *O. sativa.*	Khush et al. 1977
Rice stripe necrosis virus (RSNV)	Tolerance to RSNV transferred into double haploid progenies involving Caiapo and *O. rufipogon.*	www.ciat.cgiar.org/riceweb/pdfs/poster_alleles-pdf
Soil-borne diseases	Interspecific progenies, involving improved varieties and *O. rufipogon,* showed good tolerance to *Rhizoctonia solani, Sarocladium oryzae,* and *Bipolaris oryzae.*	www.ciat.cgiar.org/riceweb/pdfs/poster_alleles.pdf
Tungro virus, yellow stem borer, and sheath blight	Resistance to tungro virus from *O. rufipogon,* to yellow stem borer *(Scirpophaga incertulas)* from O. *longistaminata,* and to sheath blight *(Rhizoctonia solani)* from *O. minuta* transferred to *O. sativa.*	Brar and Khush 1997
White-backed plant hopper (WPH), BPH, and BB	Resistance to WPH (*Sogatella furcifera),* BPH, and BB from O. *officinalis* transferred into elite breeding lines.	Jena and Khush 1990
	Resistance to BPH and/or BB from *O. australiensis* transferred into elite breeding lines.	Multani et al. 1994
Soybean (Glycine *max)*		
Soybean cyst nematode	Resistance to cyst nematode (*Heterodera glycines)* introgressed from *G. tomentella* to *G. max.*	Riggs et al. 1998
Wheat (*Triticum* aestivum)		
Barley yellow dwarf virus (BYDV) and/or wheat streak mosaic virus (WSMV)	*Thinopyrum intermedium* and *Th. ponticum* contributed genes for resistance to BYDV and WSMV to *T. aestivum.*	Sharma et al. 1995; Fedak et al. 2001; Jiang et al. 2005
Common root rot	*Aegilops ovata* contributed resistance to common root rot *(Cochliobolus sativus)* in T. *aestivum.*	Bailey et al. 1993
Fusarium head blight	Resistance to fusarium head blight (*Fusarium graminearum)* transferred from *T. dicoccoides, T. timopheevi, T. monococcum,* and *Ae. speltoides* to *T. aestivum.*	Cai et al. 2005
Hessian fly	Resistance to hessian fly (*Mayetiola destructor)* from *Aegilops* species *(Ae. geniculate, Ae. triaristata, Ae. squarrosa,* and Ae. *ventricosa)* transferred to T. *aestivum/T. durum.*	El Khlifi et al. 2004

Hessian fly, green bug, and rust	*Ae. squarrosa* contributed resistance to hessian fly, green bug *(Sckizaphis graminum),* and leaf rust *(Puccinia triticina)* to *T. aestivum.*	Gill and Raupp 1987
Hessian fly, leaf rust, and soilborne-mosaic virus	*Ae. squarrosa* contributed genes for resistance to hessian fly, leaf rust, and soil-borne mosaic virus to *T. aestivum.*	Cox et al. 1990
Karnal bunt	Resistance to karnal bunt *(Tilletia indica)* transferred from *T. tauschii* to *T. aestivum.*	Villareal et al. 1995
Leaf rust	Resistant to leaf rust race 5 transferred from *Ae. speltoides* to *T. aestivum.*	Dvorak 1977
Powdery mildew	Resistance to powdery mildew *(Blumeria graminis)* transferred from *Ae. variabilis* to *T. aestivum.*	Spetsov et al. 1997
	T. turgidum var *dicoccoides* contributed gene for resistance to powdery mildew, *Pm 26,* in *T. aestivum.*	Rong et al. 2000
	Resistance to powdery mildew transferred from *T. urartu* into *T. aestivum.*	Qiu et al.. 2005
Root-knot nematode	*Ae. variabilis* contributed resistance to root-knot nematode *(Meloidogyne naasi)* to *T. aestivum.*	Yu et al. 1990; Barloy et al. 2000
Rust	*Lr32* from T. *tauschii* transferred to *T. aestivum.*	Kerber 1987
	Rust-resistant genes Lr41, *Lr 42,* and *Lr 43* from T. *tauschii* introgressed to *T. aestivum.*	Cox et al. 1994
Rust, WSMV, and WSSMV	Resistance to rust, WSMV (wheat soil-borne mosaic virus), and WSSMV (wheat spindle-streak mosaic virus) transferred from *T. tauschii* to T. aestivum.	Cox et al. 1995
Stem rust	Resistance to stem rust *(Puccinia graminis)* transferred from *T. turgidum L.* ssp. *dicoccum* to *T. aestivum.*	McFadden 1930
	Resistance to stem rust transferred from *T. monococcum* to *T. aestivum* via *T.* durum.	Kerber and Dyck 1973
Yellow rust and leaf rust	*T. turgidum* and *T. tauschii* contributed genes for resistance to yellow rust in synthetic hexaploid wheat.	Ma et al 1995
	Triticum spp. and *Ae. speltoides* contributed genes for resistance to yellow rust and *T. baeoticum* and *Ae. speltoides* to leaf rust to T. *durum.*	Valkoun 2001
Yellow rust (stripe rust), stem rust, and leaf rust	Resistance to yellow rust *(Puccinia striiformis)* from *Ae. comosa;* to stem rust from *Ae. speltoides, T. monococcum,* and *T. timopheevi;* to leaf rust from *A. squarrosa, A. umbellulata,* and *A. elogatum* transferred to *T. aestivum.*	Goodman et al. 1987

Table 3.2. Wild relatives contributing resistance/tolerance to abiotic stresses in barley, chickpea, rice, and wheat.

Trait	Wild Relatives Contributing Gene(s) for Abiotic Stress Tolerance	Reference
Barley (*Hordeum vulgare)*		
Drought	Some progenies involving *H. vulgare* ssp. *spontaneum* and *H. vulgare* ssp. *agriocrithon* with *H. vulgare* ssp. *vulgare* outyielded control variety by 13-22% under dry Mediterranean environments.	Hadjichristodoulou 1993
	Recombinant inbred lines (Arta x *H. spontaneum* 41-1) produced higher grain yield under drought-stress conditions.	Baum et al. 2003
	Tolerance to drought selected from the BG_1F_2 population *(H. vulgare x H. spontaneum).*	Forster et al. 2004
	Progenies involving Barke and wild barley (HOR11508) produced greater yield under varying water availability.	Talame et al. 2004
Drought and cold	*H. spontaneum* 41-1 contributed tolerance to drought and cold to *H. vulgare.*	Baum et al. 2003
Chickpea *(Cicer arietinum)*		
Drought and cold	*C. reticulatum* and *C. echinospemum* contributed tolerance to drought and cold to *C. arietinum.*	Malhotra et al. 2003
Rice *(Oryza Sativa)*		
Acidic sulphate soils and aluminium toxicity	Tolerance to acidic sulfate soils and toxicity to iron and aluminum transferred from *O. rufipogon* (AA genome) to *O. sativa.*	Brar and Khush 1997; Nguyen et al. 2003
Wheat *(Triticum aestivum)*		
Drought	Drought tolerance from *Agropyron elongation* incorporated to *T.* aestivum.	Goodman et al. 1987
	Traits related to drought tolerance from *T. urartu, T. baeoticum, Aegilops speltoides,* and *Ae. tauschii* transferred to *T. dicoccoides.*	Valkoun 2001
	T. tauschii contributed genes for traits related to drought tolerance in T. *aestivum.*	Gororo et al, 2002
Salinity	Salt tolerance from *Ae. cylindrica* and *Thinopyrum junceum* transferred to *T. aestivum.*	Farooq et al. 1992, 1995; Wang et al. 2003
	Amphidiploids from T. *turgidum* and Ae. *Speltoides* showed greater salinity tolerance than either parent.	Noori 2005

C. Cytoplasmic Male Sterility

Cytoplasmic male sterility (CMS) is a maternally inherited trait that prevents plants from producing normal pollen and is used as a tool to produce large-scale commercial F_1 hybrid seeds in many crops. This system has been more frequently used for developing commercial hybrids in cross-pollinated crops (maize, sorghum, and pearl millet) than to inbreeders (with exception in rice and pigeonpea) to exploit hybrid vigor, largely because the flower structure of inbreeders does not permit an economical large-scale hybrid seed production. Although many CMS sources and fertility restorer genes are known in these crops, additional CMS sources and fertility restorer genes have been desirable since the Southern corn leaf blight *(Bipolaris maydis)* disease epidemic of the 1970s, which was precipitated by the wide-scale use of cms-T cytoplasm in the United States (Holley and Goodman 1989). Compared to the contribution of wild relatives in terms of abiotic/biotic resistance or tolerance genes, only a few examples exist that demonstrate the potential of wild relatives as sources of cytoplasmic male sterility and nuclear restorer genes (Table 3.3), "CMS lines having cytoplasm from the wild relative *Oryza sativa f. spontanea* have been used extensively for production of commercial hybrids in China (Yuan 1993)". New and stable CMS cytoplasm from "A" genome species has also been developed. In legumes, interspecific crosses between *Glycine max* and *G. soja* have given rise to a cytoplasmic-nuclear male sterile line and its maintainer; while crosses involving *C. cajan* with wild relatives gave to four sources of cytoplasmic nuclear male sterility in pigeonpea. Additionally, C, *acutifolius* contributed nuclear genes that interact with cytoplasm C. *cajan* to produce cytoplasmic nuclear male sterility system in pigeonpea.

D. Yield, Nutritional Quality, and Adaptation Traits

Wild relatives are usually substantially inferior to modern cultivars with respect to agronomic and seed quality traits as well as yield; however, evidence suggests that wild accessions can contribute useful alleles for improvement of these traits if the appropriate breeding technique is used. It is worth noting that the favorable alleles found in wild relatives are often masked by deleterious genes that have been difficult to eliminate through conventional breeding techniques. Pioneering work in this regard was first reported in tomato, where Rick (1974) produced a high-soluble solid genotype from a green-fruited wild species, *Lycopersicon pimpinellifolium.* Other successful examples in tomato include the use of *L. chmielewskii, L. hirsutum, L. peruvianum,*

Table 3.3. Wild relatives as a source of cytoplasmic male sterility (CMS) and/or fertility restorer gene in pigeonpea, rice, and soybean.

Cms Reported from Wild Species	Reference
Pigeonpea (Cajanus *cajan)*	
Four CMS sources, A_1 from *C. sericeus*, A_2 from C. *Scarabaeoides*, A_3 from *C. volubilis* and A_4 from *C. cajanifolious*, developed.	Ariyanayagam et al. 1995; Wanjari et al. 2001; Saxena and Kumar 2003; Saxena et al. 2005
Cytoplasmic nuclear male sterility system developed involving cytoplasm from cultivated pigeonpea and nuclear genes from wild relative, C. *acutifolius*.	Mallikarjuna and Saxena 2005
Rice (O*ryza sativa)*	
Wild abortive (WA) type that has cytoplasm of O. *sativa* L. f. *spontanea*, and nuclear genome of *O. sativa*.	Lin and Yuan 1980
IR66707A has cytoplasm of O. *parennis* and the nuclear genome of 1R 64.	Dalmacio et al. 1995
IR69700A has cytoplasm of O. *glumaepatula* and nuclear genome of IR64.	Dalmacio et al. 1996
CMS lines containing cytoplasm of either O. *rufipogon* or O. *nivara* developed.	Hoan et al. 1997
Soybean (*Glycine* max)	
A CMS line developed from wild soybean accession 035.	Sun et al. 1994
A cytoplasmic nuclear male sterile line (cms A) and its maintainer (B line) developed from an interspecific cross involving *G. max* and *G. soza*.	Sun at al. 1997
A male sterile cytoplasm discovered from wild soybean accession N23168.	Zhao and Gai 2006

L. piminellifolium, and *L. pennellii* to improve fruit yield and processing quality traits, such as fruit size, color, firmness, soluble solids content, glucose and fructose concentration, and viscosity (de Vicente and Tanksley 1993; Fulton et al. 1997; Bernacchi et al. 1998a, b; Fridman et al. 2000; Yousef and Juvik 2001).

Among cereals, there have been a number of studies reporting the successful introgression of genes from wild relatives for improved agronomic and seed quality traits (Tables 3.4 and 3.5). In oat, *Avena sterilis* and *A. sativa* crosses produced progenies with up to 30% increased grain yield over control due to increased growth rate from the wild accession. In sorghum, yield- and seed quality-enhancing traits were found in *Sorghum virgatum* and *S. verticilliflorum* and incorporated into cultivated genotypes. Similarly successful examples occur in pearl millet, rice, bread wheat, and barley.

In contrast to cereals, wild species have been less utilized for agronomic and grain quality trait breeding in legumes. The few examples include *Glycine soja* used to increase grain yield and protein content in soybean; *Cicer reticulatum* and *C. echinospernum* for increased yield in chickpea; wild *Phaseolus vulgaris* to improve an Andean common bean cultivars; and *Cajanus scarabaeoides* for high protein content in pigeonpea. Halward et al. (1991) also reported yield increases in cultivated peanut from genes derived from *Arachis cardenasii.* Clearly, these gains demonstrate that wild species of legumes do contain gene(s) for agronomic and/or seed quality traits that can be exploited toward increased productivity through appropriate breeding strategy.

V. BIOTECHNOLOGICAL APPROACHES TO ENHANCE UTILIZATION OF WILD RELATIVES IN CROP IMPROVEMENT

A. Chromosome-Mediated Alien Gene Transfer

The wheat tribe *Triticeae* includes wheat, barley, rye *(Secale cereale),* triticale *(Triticosecale),* and their wild relatives. Bread wheat *(Triticum aestivum)* is an allohexaploid (2n = 42) composed of A, B, and D genomes from *Triticum urartu* (Nishikawa 1983), *Aegilops speltoides (*Sarkar and Stebbins 1956; Dvorak and Zhang 1990), and *Aegilops squarrosa* (Pathak 1940), respectively. Durum wheat is an allotetraploid (2n = 28) with A and B genomes. The 21 chromosomes of wheat fall into seven groups of three chromosomes each, and the corresponding chromosomes of the A, B, and D genomes are homoeologues (Sears 1966). Ph_1 gene on the long arm of chromosome 5B suppresses pairing

Table 3.4. Wild relatives contributing genes for agronomic and/or grain quality traits transferred in chickpea, oat, pearlmillet, pigeonpea, sorghum, soybean, and wheat using conventional backcrossing and selection.

Trait or	Wild Relatives Contributing Gene(s) for Enhanced Yield and/ Seed Quality Traits	Reference
Chickpea *(Cicer arietmum)*		
Yield	Few F_6 lines *(ILC* 482 x *C. echnospernum)* outyielded ILC 482 by 39% and free from undesirable traits found in wild relatives.	Singh end Ocampo 1997
	Interspecific progenies involving *C. reticulatu*m and *C. echinospermum* with chickpea produced greater biomass, more number of branches, and were earlier in maturity.	Malhotra et al. 2003
	Four desi and kabuli lines involving C. *reticulatum* with chickpea produced 6-17% increased seed yield over best control.	Singh et al. 2005
Oat (Avena sativa)		
Yield	Introgressed lines from *A. sativa* x *A. sterilis* recorded up to 30% grain yield advantage but with growth duration and harvest index similar to the A. *sativa.*	Frey 1976; Takeda and Frey 1976
Pearlmillet *(Pennisetum glaucum)*		
Yield	The introgressed progenies involving weedy and wild pearlmillet *(P. americanum* ssp. *monodii)* with *P. typhoid* produced segregants with increased growth rate and grain yield.	Bramel-Cox et al. 1986

Pigeonpea *(Cajanus cajan)*		
Protein	HPL# 2, 7, 40, and 51 with high protein content were selected from a cross between *A. scarabaeoides* and *C. cajan.*	Reddy et al. 1979
Sorghum *(Sorghum bicolor)*		
Yield	Backcrossed derived lines involving *virgatum* and *verticilliflorum* with S. *bicolor* produced on average 13.5% greater grain yield than control cultivar.	Cox et al. 1984
Soybean (Glycine max)		
Protein content	High grain protein content from *G. sofa* transferred to *G. max.*	Diers et al. 1992
Wheat *(Triticum aestivum)*		
Agronomic traits	Synthetic hexaploid from Huarani x *Aegilops tauschii* produced backcrossed progenies with short plant stature, early maturity, high productive tillering, high spike productivity, and drought tolerance.	Valkoun 2001
Grain protein and/or grain weight	Gene(s) for higher grain weight and protein content incorporated from *T. turgidum* var. *dicoccoides* to T. *aestivum.*	Kushnir and Halloran 1984
	A genomic region from T. *turgidum* var. *dicoccoides* associated with high grain protein content introgressed to *T. aestivum.*	Mesfin et al. 1999; 2000
	A gene for high protein content from *T. turgidum* var. *dicoccoides* transferred to *T. aestivum.*	Khan et al. 2000

Table 3.5. Wild relatives contributing quantitative trait loci (QTL) associated with beneficial traits into progenies of the wild x cultivated species crosses in barley, common bean, rice, sorghum, soybean, and wheat.

Trait	Wild Relatives Contributing Chromosomal Regions (Qtl) Containing Beneficial Alleles	Reference
Barley (*Hordeum vulgare)*		
Drought and cold	*H. spontaneum* 41-1 when crossed with Arta contributed positive alleles for days to heading, plant height, tiller number, and tolerance to drought and cold.	Baum et al. 2003
Yield and yield components; malting quality traits	In BC_2F_2 population *[H vulgare (Hv)* x *H. spontaneum (Hsp)]* detected 29 favorable effects QTL from the Hsp. Lines homozygous for *Hsp* alleles were associated with 7.7% increased grain yield over *Hv* alleles.	Pillen et al. 2003
	H. vulgare subsp. *spontaneum,* despite its overall inferior phenotypes, contributed favorable alleles for higher seeds per head, 1000-kernel weight, grain protein content, diastatic power, and β-glucan.	Matus et al, 2003
	In another BC_2F_2 population (*H vulgare [Hv]* x ISR 101-23 *[H. spontaneum [Hsp]),* 52 QTL with favorable effects identified from *Hsp.* The *Hsp* QTL allele at EBmac0679$_{[4H]}$ was associated with 5.9% increase in yield across 6 environments.	Pillen et al. 2004
	Wild barley accession 1SR42-8 contributed several positive alleles associated with improved agronomic performance in *H. vulgare:* alleles on 4HL improved yield by 7.1% while allele on 2HS increased number of ears m^2 by 16.4% and 1000-grain weight by 3.2%.	von Korff et al. 2006
Common Bean *(Phaseolas vulgaris)*		
Yield and yield components	Wild *P. vulgaris* contributed 3 QTLs for increased yield to a Colombian variety of cultivated common bean using an advanced backcross breeding strategy.	Blair et al. 2003
	A total of 13 QTLs for plant height, yield, and yield components along with a single QTL for seed size showed positive alleles from the wild parent, G24404, in $BC_2F_{3:5}$ introgression lines.	Blair et al. 2006
Rice *(Oryza sativa)*		
Aluminum toxicity	Relative root length (RRL) exerts significance influence on plants' ability to tolerate aluminum toxicity in rice, *0. rufipogon* contributed favorable QTL alleles for RRL, a primary parameter for A1 tolerance.	Nguyen et al. 2003

Drought	*O. rufipogon* contributed 2 QTLs, *qSDT2-1* and *qSDT2-2*. associated with drought tolerance in rice.	Zhang et al. 2006
Grain quality	*O. glandiglumis* contributed alleles at the locus RM290 on chromosome 2 that increased grain weight, width, and thickness, and grain yield but decreased panicle length, while alleles at locus RM144 on chromosome 11 decreased the grain weight grain width, and grain thickness but increased panicle numbers.	Yoon et al. 2005
	Advanced lines with long, slender, and translucent grains were selected from BC_2F_2 population (Bg90-2 x O. *rufipogon),* and O. *rufipogon* contributed alleles associated with superior grain quality.	www.ciat.cgiar.erg/riceweb pdfs/poster_alleles.pdf
Stem elongation	Gene(s) for increased stem elongation ability transferred from *O. rufipogon* into rice.	Brar and Khush 1997
Yield and yield components	O. *rufipogon* alleles at marker loci RMS on chromosome 1 and RG256 on chromosome 2 were associated with enhanced grain yield in backcross progenies involving O. *rufipogon,* V20A (CMS), and V20B (maintainor), showing 1.1 to 1.2 t ha^{-1} superiority for the lines carrying *O. rufipogon* alleles at these loci.	Xiao et al. 1996, 1998
	O. *rufipogon* contributed 13 QTLs for yield components, 4 for maturity, and 6 for plant height in a backcross population involving Caiapo, an upland *japonica* cultivar from Brazil.	Moncada et al. 2001
	O. *glumaepatula* contributed beneficial QTLs associated with increased tillering and panicle number, known to substantially affect plant architecture.	Brondani et al. 2002
	O. rufipogon contributed gene(s) for increased panicle length, panicles per plant, percentage of seed set, grains per plant, grain weight and yield while reducing the duration into IRM genetic background.	Septiningsih et al. 2003
	O. rufipogon contributed favorable alleles for yield, grains per panicle, panicle length, and grain weight in advanced backcross lines (*O. rufipogon* x Jefferson).	Thomson et al. 2003
	O. rufipogon contains 2 yield-enhancing QTLs, *yld1.1* on chromosome 1 and *yld2.1* on chromosome 2, capable of improving the yield of hybrid rice by 18 and 17%, respectively. BC_3F_1 (9311 x O. *rufipogon)* produced lines that produced 24% to 43% greater yield over control.	Liang et al. 2004
	O. rufipogon contributed favorable alleles for days to heading, culm length, panicle exertion, panicle length, spikelets per panicle, and leaf discoloration associated with cold tolerance in RILs.	Lee et al. 2004; 2005

(continues)

Table 3.5. (continued)

Trait	Wild Relatives Contributing Chromosomal Regions (Qtl) Containing Beneficial Alleles	Reference
	O. rufipogon alleles had a beneficial effect on 74% of the 39 QTL associated with yield and yield related traits in interspecific BC_2 progenies.	Marri et al. 2005
	O. *grandiglumis* contributed positive alleles for days to heading, spikelets per panicle, and grain shape traits into *japonica* cv. Hwaseongbyeo background.	Yoon et al. 2006
	0. rufipogon contributed a QTL, *gpa7,* with pleiotropic effect on panicle structure in rice.	Tian et al. 2006
Sorghum *[Sorghum bicolor]*		
Grain yield	Chromosome regions associated with enhanced grain yield from *S. artindnaceum* identified and transferred to BC_1F_4 progenies involving *S. bicolor.*	Jordan et al. 2004
Soybean (*Glycine max)*		
Seed protein content	G. *soja* contributed 2 major QTL alleles that increased protein, content in backcross progenies involving *G. soja* and *G. max.*	Sebolt et al. 2000
Yield	*G. soja* contributed yield-enhancing QTL alleles that demonstrated 9% yield advantage in backcross progenies.	Concibido et al. 2003
Wheat (*Triticum aestivum)*		
Yield and yield components	A synthetic wheat W-7984 when crossed with Prinz contributed beneficial alleles for grain yield and yield components in progenies.	Huang et al. 2003
	A synthetic wheat line XX86 when crossed with Flair contributed 24 QTL with positive effects on 1000-grain weight and grain weight per ear.	Huang et al. 2004
	Aegilops tauschii contributed positive alleles for earliness, short stature, ear length, grain weight, and spikelet number in *T. aestivum.*	Pests ova et al. 2006

(Sears 1976). This gene also suppresses pairing between wheat chromosomes and alien chromosomes of donor species, thereby restricting the incorporation of alien genes into wheat. However, there are methods that eliminate or suppress the activity of *Ph1* to promote pairing between alien and wheat chromosomes, thus accelerating gene transfer from alien species to wheat. The methods to promote homoeologous chromosome pairing include use of (1) *Phlb/ph2b* and *ph1c* mutants (Ceoloni et al. 1986), (2) 5-B deficient genetic stocks (Jauhar and Almouslem 1998), and (3) alien species that inactivate *Ph1* (Sears 1976; Jauhar 1992). Using the above-mentioned approaches, transfer of several alien genes possessing beneficial traits has been effected into durum and bread wheat (Jauhar and Chibbar 1999), However use of homoeologous chromosome pairing has also its own limitations as the recombination between homoelogous chromosomes of wheat and related species is either absent or drastically reduced in the proximal regions of chromosome arms, making it difficult to transfer a target gene from these regions (Lukaszewski 1995). In such cases, radiation followed by strong selection for the recovery of compensating translocations might prove an effective strategy (Sears 1993),

B. Using Cloned Genes from Wild Relatives to Produce Transgenics

As discussed, many wild species with desirable genes are either totally cross-in compatible with cultivated species or require complex bridge crossing and/or embryo rescue techniques for crosses to be successful. In practice this results in a long struggle to incorporate and retain desirable genes while eliminating linkage drag and deleterious genes from the wild accession. Traditional backcross breeding can be used for this process but is generally a tedious, time-consuming, and inefficient task even when marker-assisted selection is utilized (Tanksley et al. 1989). Molecular cloning and subsequent transfer through transformation has been suggested as the method of choice to overcome the problems associated with direct introgression through sexual crossing and selection although few examples of this approach exist to date.

One notable transfer of a wild species gene through transgenesis to a set of cultivars is for bacterial blight, which is one of the most destructive diseases of rice. In this case, the broad-spectrum resistance gene *Xa21* from *Oryza longistaminata* (Khush et al. 1990) was cloned through a map-based approach (Song et al 1995) and transferred through *Agrobacterium*-mediated transformation to five rice cultivars (Zhai et al, 2000) and a widely used hybrid restorer line in China (Zhai et al. 2001). In both cases the transgenic lines and derived hybrids displayed high levels of broad-spectrum resistance to the disease and maintained elite agronomic traits of the parents. This approach has also been used to clone *Hs1*^{pro1} from wild sugarbeet *(B. procumbens)* and *Rpi-blb1* from wild potato *(S. bulbocastanum);* and after being transferred to cultivated sugarbeet and potato, respectively, progenies showed high levels of resistance to nematode (*Heterodera schachii)* in sugarbeet and late blight *(Phytophthora infestans)* in potato (Cai et al. 1997; van der Vossen et al. 2003]. Finally, for the legumes there is promise in the work of Bhattarai and Fettig (2005), who isolated a drought- and salinity-induced dehydrin gene, *cpdhn1,* from a cDNA from ripening seeds of *Cicer pinnatifidum,* a wild relative of chickpeas, which may be used for the transformation of commercial cultivars to create more stress-resistant chickpeas. *C. reticulatum,* another wild relative of chickpea, is also tolerant to drought (Singh et al. 1994) and could be used for studying the dehydrin genes (Thomashow 1993). Clearly, the transgenic approach can accelerate the introgression of the new alleles from wild relatives to crop species compared to conventional breeding, which in many cases can be a slower and less precise method due to linkage drag. The use of transgenic transfer of wild species genes could therefore increase the genetic diversity available for crop improvement.

C. Developing Transgenics with Large-Scale Transfer of Exogenous DNA from Distant Relatives

It has been difficult to produce hybrids between rice and some of its distant relatives from the tertiary gene pool even with marker-assisted selection and embryo rescue techniques; therefore, other methods of gene transfer are needed. One option is the use of microparticle bombardment with the unfractionated genomic DNA (Abedinia et al, 2000), which was used to introgress genes from *Zizania palustris,* a wild rice from North America that is adapted to extreme cold conditions (Oelke et al. 1997). In that study, transgenic plants were recovered with grain characteristics from wild rice, and AFLP analysis revealed that a significant amount of DNA from *Zizania palustris* was introduced. This method is not without drawbacks. Liu et al. (2004) found that alien DNA introgression into a plant genome could induce extensive alternations in DNA methylation and transcription of both cellular genes and transposable elements in a genotype-independent manner. *Zizania latifolia* possesses resistance to diseases and insects, cold and flood tolerance, and good grain quality. Using repeated pollination, Liu et al. (1999) produced a set of introgression lines with introgressed DNA segments from *Z. latifolia* that exhibited a high level of resistance to blast and bacterial blight- Wang et al. (2005) studied the impact of alien gene introgression on a recipient plant genome by examining 6,000 unbiased genomic loci of three stable recombinant inbred lines (RILs) derived from intergeneric hybridization between 'Matsumae' and the wild relative *Zizania latifolia.* Although the lines each contained less than 0.1% of the wild species genome, they had extensive and genome-wide *de novo* variations with up to 30% of the analyzed loci for the three lines studied Further analysis using BLAST (Basic Local Alignment Search Tool) revealed that the genomic variations occurred in diverse sequences, including protein-coding genes, transposable elements, and sequences of unknown functions. Pair-wise sequence comparison of selected loci showed that the variation represented either base substitutions or small insertion/deletions, On the positive side, the same authors report the generation of new diversity with some of the introgression lines showing increased biomass, tolerance to low temperature and plant submergence, and immunity or high levels of resistances to several major rice diseases, It is evident that alien introgression can be highly mutagenic to a recipient plant genome. More recently, Chen et al, (2006) isolated eight resistance-gene analogs from *Z. latifolia* by using introgression lines and subsequently classified them into six distinct groups.

Another method for creating interspecies transgenic hybrids was developed by Zhao et al. (1998), who used a "spike-stalk injection" method to transfer exogenous genomic DNA from wild rice, maize, sorghum, *Echinochloa crusgalli,* and *Panicum maximum* into the uppermost stem internode at the position just under the panicle base of recipient rice plants at flowering. Xing et al. (2004) developed many useful lines of the hybrid rice with this approach, including the restorer line RB207 with a 40% increase in the number of spikelets per panicle and 1000-grain weight and the maintainer line Yewei B with better tolerance to high temperature. These studies demonstrated that direct introduction of genomic DNA of distant relatives can be an effective approach for creating new rice germplasm and potentially for enhancing other crops with genes from wild relatives in species where highly efficient transformation methods are available,

D. Marker-Aided Introgression

Molecular marker-based genetic linkage maps have provided a method to monitor and facilitate interspecific gene transfer and to mitigate linkage drag, thus improving the prospects for successful introgression of desirable genes from wild species (Tanksley et al 1989; Young and Tanksley 1989; Tanksley and McCouch 1997). An early combination of genetic mapping and wild species crosses was reported on by de Vicente and Tanksley (1993), who found that *Lycopersicon pennellii* could contribute quantitative trait loci (QTL) alleles.for yield in cultivated tomato even though it did not display high yield itself. Using a RFLP-based genetic linkage map, they detected at least one QTL from L. *pennellii* that had an allelic effect opposite of what would be expected based on the phenotype of the wild plant. They concluded that by combining wild species crosses with molecular genetic linkage maps, it could be possible to identify and selectively introgress new alleles from wild species that normally were not considered to be sources of useful variation. Expanding on this, Tanksley and Nelson (1996) proposed advanced backcross QTL analysis as an efficient breeding methodology for the simultaneous discovery and transfer of valuable QTL from unadapted germplasm into elite breeding lines. In this method, compared to previous QTL analysis with the F_2 or BC_1 derived populations, QTL analysis is conducted in the BC_2 or BC_3 generation, and negative selection is practiced to reduce the frequency of deleterious donor alleles. Using this breeding scheme, unique wild gene introgressions for improved fruit yield, size, weight, shape, and firmness were transferred into cultivated tomato (Fulton et al. 1997, 2000; Bernacchi et al. 1998a, b).

Among the legumes and cereals, advanced backcrossing and QTL analysis has been applied to successfully introgress higher yield from wild relatives into cultivated rice, wheat, barley, sorghum, common bean, and soybean (Table 3.5). The above-mentioned examples clearly demonstrate that wild relatives contain desirable alleles for agronomic traits even though their effect is phenotypically not evident in wild relatives. In future years there should be more successful exploitation of wild relatives as we progress toward saturating genetic linkage maps with user-friendly markers, such as SSRs and SNPs, and the technological cost of applying the marker technology is substantially reduced.

E. Resynthesizing the Crop Progenitors to Capture Variability Lost During Crop Evolution and Domestication

Polyploidization, a common event in the evolution of crop and noncrop plants alike, usually results in speciation and reproductive isolation and a genetic bottleneck between the new polyploid and its progenitor or related species. In spite of this, the existence of numerous wild polyploids and the frequent association of plant domestication with polyploidization testify that the polyploidy state must bring some significant selective advantages. Notable polyploids include such crops as wheat, rapeseed, peanut, and potato; furthermore, many crop species that were until recently considered typical diploids are, in fact, ancient polyploids that have undergone one or more rounds of chromosome doubling during their evolution but nevertheless behave cytologically as diploids (Leitch and Bennett 1997; Wolfe 2001). The duplication of genomes, either from the same species (autopolyploidy) or more frequently from divergent species (allopolyploidy or amphiploidy), is therefore a major force of evolution in plants, affecting genome size and gene copy numbers (Soltis and Soltis 2000; Wendel 2000).

The narrow genetic base of many polyploid crop plants presents difficulties to the plant breeder trying to cope with evolving disease and insect pressures and variations in environmental stresses. This is compounded by the problems inherent in introducing novel alleles from nonpolyploid relatives to the polyploid crop as discussed earlier. This has led to the suggestion of "resynthesizing" polyploids to generate additional diversity and as a mechanism for gene introgression, The "resynthesis" pathway has, in some cases, proven a useful way to overcome the difficulties in breeding polyploids using genes from wild relatives. This pathway essentially attempts to artificially re-create evolutionary events similar to those that gave rise to the evolutionary speciation of the crop species.

The most notable resynthesized crops have been the synthetic hexaploid wheat, produced by crossing durum wheat (2n = 28, AB genomes) with *Aegilops tauschii* (2n = 14, D genome). These hybrids have been used as an intermediary for transferring resistance/tolerance to many biotic and abiotic stresses as well as adding substantial variability for morphophysiological and reproductive traits to wheat (Fernandes et al. 2000; del Blanco et al. 2001 and references therein). A major program was developed at CIMMYT to create more than 1,000 synthetic wheats that could be used to broaden the genetic diversity of the modern wheat. Some of these or their derivatives have been recently released as cultivars ('Chuanmai 42' in China and 'Carmoona' in Spain) (www.cimmyt.org/english/wps/news/wild_wht.htrn). Another wheat strain developed by CIMMYT produces between 20 and 40% more grains under dry conditions than traditional wheat (www.nature.com/news/2006).

Synthetic polyploids have also been successful at generating new diversity in *Brassicaceae*, For example, resistance to *Plasmodiophora brassicae* (Diederichsen and Sacristan 1996), *Leptosphaeria maculans* (Crouch et al. 1994), and pod shattering (Summers et al. 2003), and variation in flowering time (Schranz and Osborn 2000; Pires et al. 2004) and oil quality (Lu et al. 2001) has been introduced into cultivated rapeseed *(Brassica napus)* germplasm. Using AFLP analysis, Seyis et al. (2003) showed that resynthesis generates an increase in genotypic variation caused by frequent intergenomic recombinatons between the diploid genome chromosomes in early generations of resynthesis.

In legumes, polyploidization has been rarely associated with domestication. Two notable exceptions are the autopolyploid *Medicago saliva* and the amphiploid peanut, which originated via hybridization of two wild species with contrasting genomes that were possibly brought together through cultivation by humans. In the case of peanut, this hybrid would have been sterile, but would have regained fertility by a spontaneous duplication of the original number of chromosomes. As is the case with most amphiploids, the new amphiploid would have been reproductively isolated from its diploid relatives due to the differences in chromosome number between their genomes. As a result, the genetic variability of cultivated peanut is very low, and all cultivated germplasm is thought to be derived from only one or a few amphiploid plants, facts that hamper the efforts of plant breeders and limit the development of peanut genetics. In contrast, wild *Arachis* species are very diverse genetically (Halward et al. 1992; Galgaro et al. 1997; Moretzsohn et al. 2004) and have been selected during evolution in a range of environments ranging from marsh to semiarid, rocky terrain providing a rich source of variation for resistance to many biotic and abiotic stresses (Stalker and Moss 1987). It has been clear for some time that the introduction of wild genes into cultivated germplasm would present new possibilities for the crop. Various attempts to do this have been made, but until now, the most productive was through a cross that we now know approximates resynthesis (Simpson et al. 1993). In this cross a hybrid AA genome donor *(A. cardenasii x A. diogoi)* was crossed with a BB genome species *A. batizocoi*, and the resultant sterile hybrid was treated with colchicine to double the chromosome number and regain fertility. Crosses and backcrosses of this synthetic amphiploid (named T x AG-6) with peanut have resulted in the release of two peanut cultivars (Coan and NemaTAM) with wild genes for root-knot nematode *(Meloidogyne arenaria* (race 1) resistance (Simpson and Starr 2001; Simspon et al, 2003). In addition, it was the genetic variation of this amphiploid that allowed the construction of the only tetraploid peanut map available to date (Burow et al. 2001). Although hybrids of T x AG-6 with peanut showed high fertility, meiosis was not totally normal, and there was substantial segregation distortion of about 25% in the backcrossed population used for making the tetraploid map. This is consistent with evidence, from both molecular and cytogenetic characterization, that none of the wild species used for the creation of

T x AG-6 is ancestral to *A. hypogaea.* In particular, the genome of A. *batizocoi* is very distinct cytogenetically, differing from the BB genome of *A. hypogaea* in the locations of one of its 18S-25S rDNA sites and of its centromeric heterochromatic bands in 9 of the 10 chromosome pairs, The most likely donor of the AA genome was probably *A. duranensis* and of the BB genome, *A. ipaensis* (Seijo et ah 2004). Recently an amphidiploid constructed from these two species has been shown to produce very fertile hybrids with *A. hypogaea* (Favero et al. 2006), Preliminary mapping data indicates diploid genetics and a very low level of marker segregation distortion in an F_2 population derived from a cross of this amphidiploid with *A. hypogaea.* This very strongly suggests that this amphidiploid is a genuine resynthesis of peanut.

Clearly, resynthesis of *A. hypogaea* using ancestral and related species is an effective strategy for the introduction of new genes into the peanut crop while minimizing the problems of sterility and suppression of recombination, both major constraints in the utilization of wild species in breeding. Our understanding of the relationships of the wild genomes is improving in such a way that a routine resynthesis with a range of species now seems feasible. In parallel, advances in genetic mapping have been made that will allow plant breeders to work with complex hybrids more efficiently, Recently the first microsatellite-based genetic map of *Arachis* was published (Moretzsohn et ah 2005), which will allow the construction of a consensus map for Arachis in the future. New peanut cultivars incorporating wild *Arachis* genes promise improved resistance to biotic stresses and tolerance to abiotic stresses together with allelic combinations for enhanced yield potential and increased quality profiles that would never have been possible through conventional approaches.

F. Developing Exotic Genetic Libraries

Another approach for the enhanced utilization of wild relatives in crop improvement was suggested by Eshed and Zamir (1994) based on the development of exotic genetic libraries (also known as introgression lines) consisting of marker-defined genomic regions taken from wild species and introgressed onto the background of elite crop lines. In addition to providing a resource for the discovery and characterization of genes that underlie traits of agricultural value, Zamir (2001) emphasized the immediate utility of the introgression lines for the improvement of agricultural productivity of modern crop varieties and that the exotic libraries should consist of a set of lines, each of which carries a single, defined chromosome segment that originates from a donor species in an otherwise uniform elite genetic background and that provides systematic coverage of the entire genome. Once such permanent genetic resources have been generated for diverse donor accessions, they can be screened for multiple phenotypic characteristics to identify alleles of economic importance, Materials are readily available to other researchers interested in using the exotic genetic libraries in applied genomics and plant breeding,

Development of introgression lines, more specifically called chromosome segment substitution lines (CSSLs), also known as contig lines or exotic genetic libraries, offers several advantages over conventional populations: (1) they provide useful stocks for highly efficient QTL or gene identification and fine mapping of these; (2) they can contribute-to the detection of epistatic interactions between QTLs; and (3) they can be used to map new region-specific DNA markers (Eshed and Zamir 1995; Fridman et al. 2004), Crosses between the exotic genetic stocks can also enhance their trait value through pyramidization of beneficial loci and fixation of positive epistasis. For example, when tomato introgressed lines carrying three independent yield-promoting genomic regions were pyramided, lines produced more than 50% greater yields compared to controls under both wet and dry field conditions (Gur and Zamir 2004), Thus, surpassing yield barriers provides a rationale for implementing similar strategies in other crops that are important for global food security. In addition to the CSSLs developed in tomato (Eshed and Zamir 1995), there are CSSLs in rice (www.ciat.cgiar.org/riceweb/pdfs/rice_2004_executive_surrimary.pdf; Sobrizal et al. 1999; Tan et al. 2005), wheat (Pestsova et al. 2001, 2002, 2003, 2006; Liu et al. 2006), and barley (Pickering 1992; Matus et al. 2003; von Korff et al. 2004).

Fewer CSSL stocks have been developed for legumes, perhaps due to the greater difficulty of generating interspecific crosses compared to the cereals. One exception was the development of monosomic alien addition lines (MAAL) by Singh et al. (1998) from *Glycine max* by *G. tomentella* crosses in soybean. *Glycine tomentolla* belongs to tertiary gene pool of soybean and contains genes for resistance to rust *(Phakopsora pachyrhizi Sydow)* and cyst nematode *(Heterodera glycines Ichinohe)* as well as salt and drought tolerance. In that study, Singh et al, (1998) developed a total of 22 MAAL lines each with the addition of an extra chromosome of *G. tomentella* to the diploid complement of soybean. The MAAL lines presented new morphological traits and were favorable for broadening the narrow genetic base of cultivated soybean, demonstrating how exotic germplasm that had not been utilizable in the past could be incorporated into breeding programs.

VI. OUTCOMES OF WILD RELATIVES USE IN GENETIC ENHANCEMENT OF CROPS

Crop wild relatives have had important impacts on improving agricultural productivity. Their impact has been greater in cereals as compared to legumes as measured by germplasm and cultivar releases of genotypes with wild ancestry (Table 3.6). To date the largest number and greatest extent of production of wild-derived cultivars is found for rice with commercially grown rice cultivars possessing gene(s) for resistance to grassy stunt and tungro virus, brown plant hopper, and bacterial wilt and tolerance to acid soils in Asia. Indeed, the gene for grassy stunt virus is now routinely incorporated in all new cultivars of rice grown across more than 1 million square kilometers of rice production area. Chinese researchers have exploited yield-enhancing QTL from wild relatives to increase the yield potentials of the hybrids by approximately 1 T ha^{-1}, and these are now commercially grown in China (Xiao et al. 1998). In wheat meanwhile, four fusarium head blight or rust-resistant wild-derived cultivars ('Steele', 'Hope', 'H44-24' and 'Marquillo'), and one high-protein cultivar ('Glupro') have been released in the United States. 'Sunnan' wheat containing a rust-resistant gene from a wild relative has been released in Sweden. Similarly in barley, two cultivars with wild ancestory, 'Athene' and 'Birgit', were released in Germany. In peanut, four cultivars containing at least one wild *Arachis* species in their pedigrees have been released in the United States: 'Spancross', 'Tamnut 74', 'Coan', and 'NemaTam'; the latter two resistant to nematode. 'ICGV SM 86715' with resistance to foliar disease was released in Mauritius. Nematode resistance has helped U.S. peanut growers save US $100 million annually (www.unep.org/documents/default.asp?documentID=399&article). In common bean, a number of interspecific derived lines from crosses with *Phaseolus acutifolius* have been released in the United States ('Tara' and 'Jules' and derivates) and Canada ('OAC Rex'), primarily for their high levels of common bacterial blight resistance.

Genes from wild relatives have also been used to improve grain quality. For example, lines containing yield- and/or seed quality-enhancing alleles from wild relatives have been developed in rice, wheat, barley, soybean, and pigeonpea. The greatest amount of introgression has occurred in wheat with approximately 100 genes including traits for resistance to biotic and abiotic stresses and value-added products introgressed into this crop. The species contributing the largest numbers of these resistance genes are *Thinopyrum intermedium, Lophopyrum elongatum, Aegilops squarossa, Ae. speltoides, Ae. umbellulata, Triticum monococcum,* and *T. timopheevii* (Fedak 1999).

Table 3.6. Elite germplasm/cultivars developed from interspecific crosses in barley, chickpea, common bean, oat, peanut, rice, soybean, and wheat.

Elite Germplasm/Cultivars Containing Gene(s) from Wild Relatives	Reference
Barley ***(Hordeum vulgare)***	
North Dakota (ND) 497 and ND 586, the former involving H. *bulbosum* and the later H. *brachyantherum* and H. *bogdanii*, released as germplasm because of tolerance to barley yellow dwarf virus.	Schooler and Franckowiak 1981
2 cultivate, Athene and Birgit, released in Germany had ssp. *spontaneum* as one of the parents in. their pedigrees.	Arias et al. 1983
81882 derived from Vada x *H. bulbosum* cross possess resistance to both powdery mildew and leaf rust.	Pickering et al. 1998
72 agronomically useful recombinant inbred lines containing H. *bulbosum* chromosome segments associated with resistance to several leaf diseases developed.	Pickering and Johnston 2005
Chickpea (*Cicer* ***arietinum)***	
BG 1100, BG 1101, and BG 1103, involving C. *reticulatum* and *C. arietinum*, produced 20% higher seed yield than the best-adapted cultivars and resistant to fusarium wilt *(Fusarium oxysporum* f. *ciceri).*	Yadav et al. 2004
Common Bean (*Phaseolus vulgaris)*	
Tara and Jules released in USA	Munoz et al. 2004
Resistance to common bacterial blight (CBB) transferred from tepary bean, a wild relative of common bean, into a line XAN1S9 and then into navy bean breeding lines HR67 and HR45.Another CBB resistance gene transferred from **a** different tepary bean into OAC Rex.	www.manitobapulse.ca/Pulse%20Media/PulseBeatmag/PB_winter-0405_web.pdfwww.ontariobeans.on.ca/OACRex.html
Oat ***(Avena*** *sativa)*	
Rapida and Sierra oats, adapted to arid regions and involving *A. fatua* in their pedigrees, have been released for cultivation in USA.	Suneson 1967a, b
Peanut ***[Arachis hypogaea]***	
Spancross and Tamnut 74 with increased yield and good pod/seed characteristics released in USA.	Hammons 1970; Simpson and Smith 1975
ICGV 86699 and ICGV87165, possessing resistance to rust and late leaf spot, elite germplasm developed.	Reddy et al. 1996; Moss et al. 1997
A foliar disease-variety, ICGV SM 86715, released in Mauritius.	Moss et al. 1998
Coan and NemaTAM with resistance to nematode released in USA.	Simpson and Starr 2001; Simpson et al. 2003

11 interspecific derivatives possessing resistance to early leaf spot, root-knot nematode, southern com rootworm, corn earworm, fell armyworm, and velbetbean caterpillar released as improved germplasm.	Stalker and Lynch 2002: Stalker et al. 2002 a, b
Advanced lines selected from interspecific crosses possessing resistance to root-knot nematode and tomato spotted wilt virus in *A. hypogaea.*	Holbrook et al. 2003
5 rust and late leafspot-resistant peanut germplasm developed	Singh et al. 2003
Rice (*oryza sativa)*	
IR28, IR29, IR30, IR32, IR34, and IR36, containing gene for grassy stunt virus, released for cultivation in many countries.	Brar and Khush 1997
IR2701-625-3, a sister selection of IR36, resistant to grassy stunt virus, released in Kerala, India.	Brar and Khush 1997
MTL98, MTL103, and MTL105, all containing gene(s) for brown plant hopper, released in Vietnam.	Brar and Khush 1997
Tong 31 and Tong 35, containing genes from *Zizania latifolia,* with improved grain quality and resistance to blast and sheeth blight, are grown in more than 600,000 ha in China.	Liu et al. 1999
O. ru*fipogon* contributed genes for cold tolerance and other abiotic stresses in well-known Chinese cultivar, Zhongshan No. 1.	Songet al. 2005
IL23 containing genes for drought tolerance from *Oryza rufipogon* developed.	Zhang et al. 2006
An introgression line. HG101, a backcross derivative involving *japonica* cv. Hweseongbyeo and *O. grandiglumis,* outperformed Hwaseongbyeo for a few grain characterstics.	Yoon et al. 2006
IR 73678-6-9-B released as AS996 for cultivation under acid sulfate soils in Vietnam.	www.irri.org/media/hotline/hljun2003
A tungro virus-resistant cultivar, Matatag 9, released in Philippines.	www.irri.org/publications/today/pdfs/3-l/feral.pdf
Soybean (*Glycine max)*	
SS201 and SS202, involving wild species *G. soja,* released as special purpose cultivars for the production of soy sprouts and Japanese fermented product natto.	Fehr et al. 1990a, b
Bean 13, selected for strong rooting capacity and tolerance to drought from an intergeric cross, released in Korea	Li 1990
Pearl soybean, involving unknown wild relative in its pedigree, released as a special-purpose cultivar for the development of Japanese fermented product natto.	Carter Jr et al. 1995
Wheat (*Triticum aestivum)*	
A hexaploid wheat cultivar, Hope, was developed that contain *Sr2* for resistance to stem rust from T. *turgidum* spp. *dicoccum.*	McFadden 1930

(continues)

Table 3.6. (continued)

Elite Germplasm/Cultivars Containing Gene(s) from Wild Relatives	Reference
A hard red winter wheat cultivar, Plainsman V released in USA, has high protein content probably transferred from *Aegilops ovata*.	Sharma and Gill 1983
A wheat cultivar, Amigo, contains both wheat-rye and wheat-Aegilops *elongatum* translocations in its pedigree.	Cai 1994
4 synthetic hexaploid wheat germplasm lines derived from T. *tauschii* and *T. turgidum* possess immunity to karnal bunt.	Villareal et al. 1996
A new salt-tolerant cereal, containing salt-tolerant gene from *Thinopyrum bessarabicum*, performed much better at 150 mol m^{-3} concentration.	King et al. 1997a, b
An amphidiploid, OK 7211542, derived from hybrids of wheat with *Th. intermedium* or *T. ponticum,* is immune to BYDV, a serious disease that has *no* source of resistance in wheat primary gene pool.	Ayala et al, 2001
Swedish wheat cultivar, Sunnan, contain a translocation from *Th. ponticum* with leaf rust-resistant gene *Lr19;* Marquillo and H 44-24, both released in USA, contain T. *dicoccoides* in their pedigrees.	Bartos et al. 2002
An agronomically useful wheat-Ae. *geniculata* line, 2K-11-1, possesses resistance to leaf and stripe rust.	Aghaee-Sarbarzeh et al. 2002
Crossing the substitution line LDN (DIC-3A) to 4 T. *tauschii* accessions developed 4 synthetic hexaploid wheat germplasm lines resistant to fusarium head blight.	Berzonsky et al. 2004
Several wheat-alien species derivatives exhibited resistance to fusarium head blight (FHB) as that of Sumani 3.	Oliver et al. 2005
A hard red spring wheat cultivar, Steele-ND, resistant to fusarium head blight, released in USA.	Mergoum et al. 2005
Kansas State University released 30 hard red winter wheat or durum wheat germplasm possessing resistance to hessian fly; green bug; soil-borne mosaic and spindle streak mosaic virus; leaf, stem, and stripe rust; powdery mildew; tan spot; and fusarium head blight, all derived from crosses involving wild relatives.	www.k-state.edu/wgrc/ germplasm/grmplasm.html
Plainsman V has *Aegilops ovata* and Agent has *Agtopyron elongatum* in their pedigrees, both released in USA.	www.oznet.ksu.edu/library/ crpsl2/sTll26.pdf
The 3n chromosome carrying aluminium-tolerant gene from *Ae. uniaristata* transferred into a model wheat cultivar "Chinese Spring" with no undesirable trait (spike neck break) from Ae. *uniaristata.*	www.dfid-psp.org/ccstudio/ publicatians/annualreport/ 2004_aluminium.pdf
Chuanmai 42, a derivative from synthetic wheat and local wheat, released in China. A synthetic wheat derivative, Carmona, that has better grain quality, resistance to foliar diseases, and adapted to zero tillage, released in Spain.	www.cimmyt.org/english/ wps/news/wildWht.htm

Wild relatives have contributed in development of cytoplasmic male sterility sources and/or fertility restoration systems that have been widely used in the production of hybrids in rice and pigeonpea. Similarly, genes for promiscuous nodulation and seed longevity, which led to the success of soybean cultivars in West Africa, were introgressed from wild sprawling soybean accessions mostly from Indonesia (Ortiz 2004).

VII. FUTURE OUTLOOK

Wild relatives have been extensively used to transfer resistance to many pests and diseases in agriculturally important crops. Furthermore, exploitation of wild relatives in rice, wheat, barley, oat, sorghum, common bean, soybean, potato, and tomato have demonstrated that although wild ancestors may be phenotypically inferior to modern-day cultivars, they harbor genes that can contribute to increased yield and/or seed quality traits. The demand for food will continue to increase as the world population approaches 7.5 billion people in 2020 (Pinstrup-Anderson et al. 1999). As gains from conventional breeding are gradually exhausted, further yield growth will be generated by the combination of conventional breeding with wide crossing, genomics, and transgenic technologies to tailor better-adapted crop cultivars to diverse growing conditions (Rosegrant et al. 1995). With the development of user-friendly markers and availability of saturated genetic linkage maps in crop species, it is likely that there will be greater exploitation of wild relatives to identify the alleles associated with yield-enhancing traits. When these genes are introgressed/pyramided into new genetic backgrounds, they could bring large increases in yield, as already demonstrated in pioneering studies with tomato. It is essential that CGIAR institutes concentrate on developing chromosome segment substitution lines targeting chromosomal introgressions from wild relatives that can be provided to plant breeders as a resource for the discovery and utilization of genes associated with improved agronomic traits. In conclusion, wild species germplasm holds great promise both for broadening the genetic base of many crops and for enhancing sustainable crop production.

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