

The use of wild relatives in crop improvement: A survey of developments over the last 20 years

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Abstract The use of crop wild relatives (CWR) genes to improve crop performance is well established with important examples dating back more than 60 years. In this paper, we review available information on the presence of genes from CWR in released cultivars of 16 mandate crops of the CGIAR institutes, and some selected additional crops, focusing on the past 20 years—the period since a comprehensive review by Robert and Christine Prescott-Allen in 1986. It appears that there has been a steady increase in the rate of release of cultivars containing genes from CWR. While there continues to be a strong emphasis on using pest and disease resistance genes, a wider range of characteristics are being introduced than in the past. Those crops whose wild relatives have traditionally been used as sources of useful traits (e.g., wheat, tomato) continue to be most likely to include new genes from their wild relatives. CWR are continually gaining in importance and prevalence, but, we argue, their contributions to the

development of new cultivars remain less than might have been expected given improved procedures for intercrossing species from different gene pools, advances in molecular methods for managing backcrossing programmes, increased numbers of wild species accessions in gene banks, and the substantial literature on beneficial traits associated with wild relatives.

Keywords Crop wild relatives · Crop improvement · Introgression · Wild germplasm

Introduction

Crop wild relatives (CWR), which include the progenitors of crops as well as other species more or less closely related to them, have been undeniably beneficial to modern agriculture, providing plant breeders with a broad pool of potentially useful genetic resources. Wild relatives were used in crop improvement in sugar cane in the first half of the 20th century. Their utility was recognized in breeding programs of major crops in the 1940s and 1950s (Plucknett et al. 1987), and wild gene use in crop improvement gained in prominence by the 1970s and 1980s with their use being investigated in an increasing wide range of crops (Hoyt 1988). Although far from the first authors to recognize their growing importance, Prescott-Allen and Prescott-Allen (1986, 1988) reviewed in

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two publications the importance of CWR to the North American economy and crop production and compiled available information on the use of wild genes in cultivars at the time. They calculated that yield and quality contributions from CWR to US-grown or -imported crops amounted to over \$340 million a year (Prescott-Allen and Prescott-Allen 1986).

Significant advances have been made in the 20 years since the Prescott-Allens' study, both in the molecular technologies and hybridization procedures available for breeding and cultivar development that allow for the incorporation of more distantly-related taxa, and in our knowledge of the wild relatives available for use in these programs. Tanksley and McCouch (1997) pointed to the potential role of genome mapping in efficiently utilizing the genetic diversity of wild relatives, and suggested that the continued sampling of wild germplasm would result in new gene discoveries and use. While many articles have reported the importance or potential importance of wild species in providing beneficial traits to particular crops, information is lacking on the extent to which these are incorporated in new cultivars developed since the survey by Prescott-Allen and Prescott-Allen in the 1980s.

In this paper we describe the results of a survey of the introduction of genes from CWR into cultivars of crops of major importance to global food security. The survey concentrates on the period after the Prescott-Allen and Prescott-Allen reports of the mid-1980s to 2005.

Methods

Crop selection

While a large number of candidate crops could have been selected for this study, the scope was narrowed to the mandate crops of the Consultative Group on International Agricultural Research (www.cgiar.org) with three obvious additions. The reasons for this were the global importance of the crops in achieving food security, the expectation that these crops would enjoy a large portion of attention and resources dedicated to research, and the fact that the

research being carried out by the CGIAR centers would be accessible to the public. The following 16 of 19 mandate crops were the focus of the study: rice, wheat, maize, barley, sorghum, millet, cassava, potato, chickpea, cowpea, lentil, soybean, bean, pigeonpea, banana and groundnut. Sweet potato and yams were not included for lack of accessible information or responses from experts. Coconut belongs to a monospecific genus in which the wild relatives, if they exist, are not easily identified. In addition to these 16 crops, three non-mandate crops, namely tomato, sunflower and lettuce, were also studied, due to well-known cultivar improvements attributable to genes from wild relatives. To exclude the latter crops from the analysis would be disregarding a substantial portion of wild gene research and use. The information was collected and analyzed as part of the work of the project supported by the United Nations Environment Programme/Global Environment Facility (UNEP/GEF) and led by the Bioversity International (formerly International Plant Genetics Resources Institute), "In-situ Conservation of CWR through Enhanced Information Management and Field Application". The database will be made available through this project.

Defining improvements and prevalence

There is a broad spectrum as to what can be classified as an advance in the field of crop improvement, from simply characterizing more wild species through various stages of gene detection and characterization to the use of the genes in a crossing programme and release of new cultivars. In this paper we focus on the final step, that of the development of new cultivars. This is the defining test of usefulness and was also the approach adopted by Prescott-Allen and Prescott-Allen (1986, 1988).

Sources of information

It was a substantial challenge to obtain records on CWR use in breeding programs. Little of this type of data exists in published papers and difficulties in ascertaining pedigrees of many crops prevented

us from relying only on germplasm registration records to any great extent.

Data was collected from published sources using different search procedures such as the CAB online database and appropriate sets of keywords and by specifically consulting journals such as *Crop Science* which are known to record some pedigree information in the form of germplasm registrations. Selected genebank managers and plant breeders were also consulted and asked a set of questions about the numbers of crop wild relative species that had been or were being used, the genes or characteristics sought and transferred and the numbers of cultivars released.

It should be noted that many of the breeders contacted noted the difficulties in keeping track of released cultivars and their genetic make-up, and several also commented on the difficulty in obtaining information on crop breeding in the private sector—one reason for focusing on advances made in the public domain. Thus the information gathered and statements made on trends are reflections of available published literature and the informal consensus opinion of several breeders. The results are therefore only semi-quantitative and may well be incomplete. However, the approach is comparable to that used by Prescott-Allen and Prescott-Allen (op. cit.). It is hoped that omissions will be identified by researchers in the field and can be added to the database created for the UNEP/GEF information project.

Results

This section reviews the information compiled in our survey, summarizing the wide variety of wild relative traits that have been incorporated into crops. Advances in crop improvement are grouped according to their main functional category: providing pest and/or disease resistance or abiotic stress tolerance, increasing yield, providing cytoplasmic male sterility or fertility restorers for use in producing hybrids, or improving quality traits of the crop.

Of the 19 crops reviewed here, examples of wild gene incorporation reaching the released cultivar stage were found in all but soybean,

pigeon pea, sorghum, lentil, *Phaseolus* beans and cowpea, although in at least *Phaseolus*, new cultivars incorporating genes from wild relatives were reported to be in the pipeline (see below). Over 60 wild species were identified to have been used for the remaining 13 crops, with over 100 beneficial traits having been derived from them (Table 1). As in the case of the earlier study by Prescott-Allen and Prescott-Allen (op. cit.) the most common use of wild relatives continues to be as a source of pest and disease resistance, although there have been many examples of gene introductions from CWR with other important characteristics such as drought and salt tolerance, improved quality and cytoplasmic male sterility.

Pest and disease resistance

Over 80% of the beneficial traits conferred by CWR genes in this survey involved pest and disease resistance. Breeders have exploited wild relatives for resistance to diseases for over a century (Prescott-Allen and Prescott-Allen 1986), and they continue to search extended gene pools for genes that convey resistance to major crop pests and diseases (e.g., Brar and Kush 1997; Rick and Chetelat 1995). Of the 13 crops with incorporated wild genes in released cultivars, all except barley and chickpea have cultivars with disease resistances derived from wild relative genes. However, only maize, banana and groundnut have disease resistance as the *only* beneficial trait derived from the wild.

Prior to the mid-1980s, stories about wild genes preventing devastation by pests and diseases were dominated by a handful of crop success stories. Most prominent among these were: *Oryza nivara* S.D.Sharma & Shastry providing resistance to grassy stunt virus in rice; *Solanum demissum* Lindl. providing resistance to potato late blight; the many tomato disease resistances introgressed from wild species, mostly from *Lycopersicon pimpinellifolium* Mill.; and, stem and leaf rust resistance from *Agropyron elongatum* Host ex. P.Beauv and *Aegilops umbellulata* Zhuck., respectively, in wheat (Prescott-Allen and Prescott-Allen 1986).

Since then, the discovery and use of new resistance genes from the wild have steadily

Table 1 Use of crop wild relatives in the past 20 years in released cultivars of 13 crops of international importance^a

Crop	Pest and disease resistance	Abiotic stress	Yield	Quality	Male sterility or fertility restoration	Total number of contributed traits
Cassava	+	–	–	+	–	3
Wheat	+++++	–	+	+	–	9
Millet	+	–	–	–	+	3
Rice	+++++	+++	+	–	+	12
Maize	+	–	–	–	–	2
Sunflower	+++	+	–	–	+	7
Lettuce	+++	–	–	–	–	2
Banana	++	–	–	–	–	2
Potato	+++++	–	–	–	–	12
Groundnut	+	–	–	–	–	1
Tomato	+++++	++	–	++	–	55
Barley	–	+	–	–	–	1
Chickpea	–	+	–	–	–	2

^a Plus signs indicate number of wild relatives that have contributed beneficial traits to crop varieties in each category of traits. Minus sign indicates wild relatives have not contributed beneficial traits in that category. Total number of individual traits obtained from wild species are indicated in the last column for each crop

increased in these crops and others. Resistances found in tomato wild relatives have been reported at a rate of about one per year since 1982 (Rick and Chetelat 1995), with virtually all disease resistance genes currently in commercial cultivars having been bred from wild genetic resources (D. Zamir, personal communication). Over 40 resistance genes have been derived from *Lycopersicon peruvianum* (L.) Mill., *L. cheesmanii* Riley, *L. pennellii* (Correll) D'Arcy, and several other wild relatives (Rick and Chetelat 1995).

In rice, *Oryza nivara* genes still provide strong and extensive resistance to grassy stunt virus on millions of hectares of rice fields in south and south-east Asia (Barclay 2004), and resistance to at least six other major diseases in rice have been obtained from different wild species (Brar and Kush 1997; D. Brar, personal communication). In potatoes, besides several new resistances from other wild relatives, resistance to potato late blight obtained from *Solanum demissum* and *S. stoloniferum* Schltld. and Bché continues to be effective in some areas, and currently 40% of the total area of the most popular potato cultivars in the United States have *S. demissum* in their ancestry (National Potato Council 2003), a considerable increase from 11% of the total area in 1986. Along with these wild relatives, *S. chacoense* Bitt., *S. acaule* Bitt., *S. vernei* Bitt. and Wittm., and *S. spegazzinii* Bitt. have provided

resistance to several viruses and pests (Love 1999; Ross 1986).

Breeders continue to isolate and introgress genes from wheat wild relatives for resistance to leaf and stem rust (Hoisington et al. 1999; H. Bariana, personal communication; R. Koebner, personal communication), yellow dwarf virus, root lesion nematode (H. Bariana, personal communication), powdery mildew and wheat streak mosaic virus (Hoisington et al. 1999). Spring wheat germplasm lines derived from *Aegilops tauschii* Coss. for resistance to Hessian fly, a major insect pest causing multi-million dollar crop losses in the US, have recently become available to breeders (Suszkiw 2005).

The prevalence of wild genes in providing pest and disease resistance has increased in many other crops as well (see Table 1). Disease resistances in wild sunflowers have been exploited for decades, with multiple sources of genetic resistance to all the known races of downy mildew, as well as rust, verticillium wilt, and broomrape, continually being transferred from wild *Helianthus annuus* L. and *H. praecox* Engelm. & A.Gray into new sunflower hybrids (J. Robinson, personal communication; G. Seiler, personal communication). Resistance to new strains of downy mildew continue to be found in the wild relative, with several of these resistant cultivars having been released in 2005

alone (G. Seiler, personal communication). The most recent trait from wild *H. annuus* L. is herbicide resistance to *imidazolinone* and *sulfonylurea* chemicals used to control broomrape (Seiler and Gulya 2004). These resistance genes have been transferred into cultivated hybrids under the trade name ‘Clearfield’, and are expected to be worth millions of dollars globally (G. Seiler, personal communication).

Less well known are the Tropical Manioc Selection (TMS) cassava cultivars, developed by the International Institute for Tropical Agriculture using crosses with *Manihot glaziovii* Müll.Arg., and adopted by a number of African countries in combating the devastation caused by cassava mosaic disease and bacterial blight. Disease resistance derived from the wild relative has contributed to a 40% yield increase in Nigeria (Nweke 2004), and has led to a gain in popularity for these cultivars in neighboring countries, with, for example, 25% of Western Kenyan households planting one of the cultivars. The cultivars are now planted on an estimated 2 million hectares (N. Nassar, personal communication).

In millets, rust and *Pyricularia grisea* resistances were introgressed from wild relatives. Although the rust resistance was overcome quickly, *Pyricularia* resistance is still effective (Wilson et al. 1991; Wilson and Gates 1993). *Striga* resistance has been identified in millet’s primary gene pool (Wilson et al. 2000), but the work remains at the early stages of gene transfer (J. Wilson, personal communication). In sorghum, recent success in hybridization between *Sorghum macrospermum* and *S. bicolor* promises to help in introducing several pest and disease resistance traits to cultivars (Price et al. 2005).

In bananas, ‘Calcutta 4’ (*Musa acuminata* Colla), a wild, non-edible diploid banana has been used as a source of resistance in banana hybrids to black Sigatoka, the most serious constraint to banana production globally caused by the fungus *Mycosphaerella fijiensis* (Escalant et al. 2002). The new generations of these hybrids, distributed since the 1990s, are resistant to black Sigatoka and Fusarium wilt (Vuylsteke et al. 1993). However, resistance to black Sigatoka has been overcome in the Pacific, and breeders have once again turned to wild

M. acuminata for more resistance genes (Escalant et al. 2002).

The vast majority of modern lettuce cultivars have benefited from wild relatives. All lettuce downy mildew, *Bremia lactucae*, and lettuce aphid, *Nasonovia* spp., resistance is derived from the wild (Crute 1992; Eenink et al. 1982). For downy mildew, cultivars with resistance derived from wild germplasm have been released regularly since the 1980s. Fungicides have limited effectiveness against the pathogen, thus without the introduced genes it would not be possible to grow lettuce in many parts of Europe. However, resistance genes appear to be overcome rapidly, and breeders are constantly returning to wild germplasm for new resistance genes (Crute 1992; D. Pink, personal communication).

The use of wild genes in groundnut and maize has not been as successful so far. Groundnut cultivars with root knot nematode resistance derived from *Arachis cardenasii* Krapov. & W.C. Greg. (Simpson and Starr 2001) were released, but were never grown on a significant area because of a lack of resistance to tomato spotted wilt (C. Simpson, personal communication). Introgression of genes from *Tripsacum* L. into maize cultivars has not had any successes since cultivars released between the 1950s and 1980s with resistance to *Helminthosporium* and *Puccinia* (A. Blakey, personal communication). However, both these crops have cultivars in the pipeline, with wild-derived disease resistant groundnut germplasm available to breeders (Rao et al. 2003), and rootworm resistant, drought and aluminum-tolerant, nutritionally-enhanced maize cultivars with *Tripsacum* gene introgression currently being field tested, expecting to be released in 2007 (M. Eubanks, personal communication).

We could not identify cultivars released after the mid 1980s that have incorporated disease resistance from wild relatives in soybean, chickpea, or beans, as was also the case for Prescott-Allen and Prescott-Allen (op. cit.). Soybean cyst nematode resistance has been successfully transferred from wild perennial soybean, *Glycine tomentella* Hayata. (Riggs et al. 1998), but cultivars are still in an experimental stage (T. Hymowitz, personal communication). Unsuccessful attempts have

been made to transfer resistance to Maruca pod borer to cultivated cowpea from crosses with *Vigna vexillata* (L.) A. Rich (B.B. Singh, personal communication). Chickpea lines derived from *Cicer reticulatum* Ladizinsky and *C. echinospermum* P.H. Davis are currently being developed for resistance to root lesion nematodes and *Phytophthora* root rot, but these are still undergoing backcrossing programs to recover the domesticated phenotype (T. Knights, personal communication). *Phaseolus* wild relatives are currently being screened for resistances to web blight, rust, white mold, bean golden yellow mosaic, bruchids, and seed storage insects (Singh 2001; Gallepo 1988; J. Beaver, personal communication; S. Beebe, personal communication; D. Debouck, personal communication).

Abiotic stress tolerance

Only a handful of examples of wild relatives contributing genetic resistance to abiotic stresses in crops have reached the stage of cultivar release although many wild relatives with potential have been described (e.g., Shannon 1997). Important recent advances in this field include the release of a chickpea cultivar with introgressed wild genes in 2004. Developed by the India Agricultural Research Institute, 'BG1103' drought and temperature tolerance are derived from *Cicer reticulatum*, and is already a leading cultivar in Northern India (S. Yadav, personal communication). Also in 2004, six barley cultivars with drought tolerance derived from *Hordeum spontaneum* K. Koch were released for use in Syria by the International Center for Agricultural Research in Dry Areas (S. Ceccarelli, personal communication). *Oryza rufipogon* Griff. genes have been exploited for tolerance of soils with high acidic-sulfate content in Vietnam (Nguyen et al. 2003), and *O. longistaminata* A.Chev. & Roehrich genes for drought tolerance (Brar 2005) in cultivars in the Philippines, allowing the spread of rice production to previously unusable lands (D. Brar, personal communication). In tomatoes, *L. chilense* and *L. pennellii* genes have been used to increase drought and salinity tolerance (Rick and Chetelat 1995).

Sunflower and bean cultivars with genes from CWR will soon be released. Salt tolerant sunflower hybrids, which promise to yield 25% more in salt-impacted soils, are still under development (Lexer et al. 2004; G. Seiler, personal communication) although maintainer lines have already been released (Miller and Seiler 2003). Bean cultivars with tolerance to low temperatures and salinity derived from wild *Phaseolus* are in the pipeline (Bayuelo-Jimenez et al. 2002; D. Debouck, personal communication).

Yield increase

Wild relatives have poor agronomic performance and it is therefore not surprising to find very few examples of wild genes being used to enhance yield in modern cultivars. In this study, reported yield improvements of the selected crop cultivars have mostly been associated with other beneficial traits, namely biotic or abiotic stress tolerance, provided by the wild relatives. For example, chickpea cultivar 'BG1103' (see above) yields approximately 40% more than competing cultivars (S. Yadav, personal communication), but this increase is due to wild genes conveying increased drought and temperature tolerance, rather than specifically targeting yield. Similarly the TMS line of cassava, derived from an initial cross with a wild relative, gives a 40% yield increase (Nweke 2004), although this is mostly a result of disease resistance provided by the wild genes.

Of our target crops, we have found only one example of a released cultivar using wild germplasm to specifically increase yield: rice cultivar NSICRc112 released in the Philippines in 2002 from the cross of *Oryza sativa* and *O. longistaminata* is known to be high yielding (Brar 2005; D. Brar, personal communication).

Nevertheless, there are an increasing number of cases of high-yielding derivatives of hybrids created with the use of wild relatives, of which synthetic hexaploid wheats are a good example. Produced by the International Maize and Wheat Improvement Center (CIMMYT), synthetic hexaploid (SH) wheats are a cross between durum wheat and the wild relative *Aegilops tauschii* that has undergone artificial chromosome doubling to

produce a hexaploid with A,B, and D genomes (Mujeeb-Kazi et al. 1996). These lines are then back-crossed to elite bread wheat cultivars, to produce wheats with superior quality, disease resistance and yield. In 2003, 'Chuanmai 42', a cross between an SH wheat and a local cultivar, was released in China, producing 20–35% higher yields (CIMMYT 2004). 600 SH lines with a wide range of positive traits are currently being tested and crossed (CIMMYT 2004), including water-logging tolerance (Villareal et al. 2001), spot blotch (*Cochliobolus sativus*) resistance or karnal bunt (*Neovossia indica*) resistance (Mujeeb-Kazi et al. 2001).

The use of wild relatives of sorghum has potential to increase yields in the crop (Wayne Smith and Frederiksen 2000). *Sorghum arundinaceum* Roem. & Schult. and other wild sorghum have proved to be sources of useful genes for improving grain yield in hybrid grain sorghum (Jordan et al. 2004), and work at Texas A&M University on sorghum cultivars derived from wild *S. propinquum* (Kunth) Hitchcock has produced cultivars with early maturity and good yields but these have yet to be released (W. Rooney, personal communication). Yield-enhancing quantitative trait loci (QTLs) have been identified in populations derived from crosses with *O. rufipogon* (Xiao et al. 1996; Moncada et al. 2001), but we are not aware of any cultivars so far resulting from this research. Breeding programmes designed to increase yields and make use of wild germplasm in *Phaseolus* have been proposed (Kelly et al. 1998) and cultivars with increased yield derived from a Colombian wild bean are in the pipeline (D. Debouck, personal communication). In a recent study, pyramiding of three independent yield-promoting genomic regions introduced from *Solanum pennellii*, a green-fruited wild relative of tomato, has led to hybrids with a 50% increased yield over a leading variety (Gur and Zamir 2004).

High-yielding hybrid derivatives created with the use of cytoplasmic male sterility (CMS) derived from wild relatives have also gained in prominence. This will be addressed in the following section.

Cytoplasmic male sterility and fertility restorers

A major advantage of producing F1 hybrids is fixing heterosis in the population, often resulting in higher yields, frequently through the use of male sterility. Cytoplasmic male sterility has been found in an increasing number of wild species, resulting in much hybrid research and a few released cultivars.

CMS based on using wild *Helianthus annuus* and *H. petiolaris* Nutt. has been used in high-yielding commercial sunflower hybrids since 1972, significantly expanding the sunflower industry (Prescott-Allen and Prescott-Allen 1986). Currently, 100% of sunflower production in the US, and approximately 60–70% of production worldwide is estimated to be from these hybrids (G. Seiler, personal communication). With rice, 95% of hybrids grown in China are derived from crosses using CMS from wild *Oryza sativa* f. *spontanea* L. (Virmani and Shinjo 1988). Released in 1976, these hybrids are currently planted on approximately 45% of China's rice-planting area (T. Dayun, personal communication). More recently, CMS found in wild millet has been used to produce popular high-yielding and disease-resistant hybrids. CMS and fertility restorer lines derived from *Pennisetum purpureum* Schum. were used in the first pearl millet grain hybrids and commercial forage hybrids (Hanna 1989; W. Hanna, personal communication) and the Tifleaf series derived from these are the mostly widely cultivated in North America, popular as far down as Brazil (J. Wilson, personal communication). The latest in the Tifleaf series, Tifleaf 3, released in 1997 (Hanna et al. 1997), produces 20% more forage than the disease susceptible hybrids it replaced (W. Hanna, personal communication). Production of pigeon pea hybrids using CMS found in five different wild relatives is ongoing (e.g., Saxena and Kumar 2003), but no cultivars have been released so far (K.B. Saxena, personal communication).

Improved quality

Tomatoes have provided many classic examples of improved quality traits from wild genes, from

increased soluble solid content, fruit color, and adaptation to harvesting. These improvements are reviewed in the Prescott-Allen and Prescott-Allen study (1986). Since then, QTL mapping and analysis has aided the discovery of useful quality-controlling genes, such as fruit size, in unlikely candidates such as the small-fruited tomato ancestor *L. pimpinellifolium* (Tanksley and McCouch 1997).

A handful of other advances in quality traits can be attributed to wild relatives: a doubling of protein content in a Brazilian cassava cultivar, ICB 300, derived from *Manihot oligantha* Pax. & K.Hoffm. (Nassar 2003; N. Nassar, personal communication); and increased protein content in wheat cultivars derived from *Triticum dicoccoides* (Körnicke) G.Schweinfurth (Hoisington et al. 1999). The Prescott-Allen and Prescott-Allen study reported on the increased alpha acid content of a cultivar of hops derived from wild hops, but this cultivar has since been discarded due to adverse aroma components that had a severe negative impact on beer flavour (A. Haunold, personal communication).

Better grain quality synthetic hexaploid wheat cultivar 'Carmona' has been released in Spain, and future releases of synthetic hexaploid wheats with higher content of essential minerals such as iron or zinc are expected (CIMMYT 2004).

Discussion

How far have we come?

The use of wild relatives has continued to increase in the 20 years since the Prescott-Allen and Prescott-Allen studies (1986, 1988), in terms of the number of crops with cultivars containing genes from wild relatives, the number of wild species used to provide genes, and the range of traits obtained from wild relatives. Thus, approximately double the number of wild species reported by Prescott-Allen and Prescott-Allen were identified in our survey as having been used for nine of the crops common to our survey and the previous study and over a 100 traits were identified as having been transferred.

Those crops where use of wild relatives was well established in the 1980s continue to be dominant in terms of numbers of species used and numbers of traits transferred, namely, tomato, wheat, rice, potato, and sunflower. Nonetheless, novel traits are continually being incorporated from new wild relatives in most of these and other crops, with more promised in the pipeline. Pest and disease resistance is still the leading reason why breeders look to the wild, resulting predictably in a dominance of pest and disease-related wild gene introgressions. Yet since the 1986 study, when a third of crops reviewed had *only* pest and disease resistance derived from wild relatives, approximately 80% of the 14 crops reviewed here with released cultivars have more than just biotic stress tolerance traits incorporated from wild relatives, with most also incorporating abiotic stress tolerance or enhanced yield and quality traits.

Respondents to our enquiries frequently reported cultivars in the pipeline, often at advanced stages of field-testing. In addition, many more germplasm lines with beneficial wild genes are being made available to both private and public sectors. In communications with several crop breeders, we were given the impression that a sharp increase in released cultivars in the coming years in novel crops or locations is to be expected. Some examples include: 200 lines of rice derived from a cross with *O. glumaepatula* Steud. will be released in the next 2 years in Brazil, where previously there has been no use of wild relatives (C. Brondani, personal communication); after a two-decade slump in work on *Tripsacum*-derived lines, *Tripsacum*-derived maize cultivars will be ready in 2007 (C.A. Blakey, personal communication); and pigeonpea, sorghum, and soybean breeders seem to be at the cusp of producing successful cultivars and hybrids. It remains to be seen whether these and other advances will indeed result in an increased rate of release of cultivars with new genes from CWRs.

Despite the continuing steady increase in use of CWR since the 1980s, a number of factors might lead one to expect a greater increase than seems to have occurred. These include increased knowledge of the occurrence and genetics of

desired traits, increased availability of wild relatives in genebanks, improved inter-specific hybridization capabilities and advances in molecular technologies. It is worth considering the effects of these and the factors that still constrain the use of wild relatives.

Drivers and constraints

Historically, a major limiting factor has been difficulties with interspecific crossability. However, using embryo rescue and other techniques to overcome inter-specific crossing barriers, it has been possible to make new hybrid combinations involving different species and to transfer many new traits. There are many examples, such as the transfer of cassava mosaic virus resistance as a result of the development of hybrids between cassava and *Manihot glaziovii* (Akano et al. 2002) and the production of hybrids between cultivated chickpea and *C. pinnatifidum* Jaub. & Spach, with resistance to asochyta blight (Mallikarjuna 1999). As far as we are aware no cultivars have been released so far in these two cases but they are expected in the near future. The survey confirms the impression from the literature that improved interspecific hybridization techniques have led to an increase in use of secondary and tertiary gene pools of many crops over the last 20 years.

However, biological constraints still prevent successful use of wild relatives in a number of crops, where blocks to hybridization and hybrid sterility have not yet been overcome. Crossing difficulties are the main reason why *Cicer* wild relatives are not more prevalent in modern cultivars, with only two species, *C. echinospermum* and *C. reticulatum*, easily crossed with the cultivar (Rao et al. 2003). Crosses between soybean and *Glycine* species were unsuccessful in the 1970s (Ladizinsky et al. 1979), taking one lab 17 years to work out a successful hybridization methodology between *Glycine tomentella* and soybean cultivars (T. Hymowitz, personal communication). Unsuccessful crosses with *Vigna vexillata* have limited work with cowpea wild relatives (Fatokun 2002).

Regardless of interspecific crossability, retention of undesirable agronomic traits remains a prominent technical limitation to using wild

germplasm. Crosses with wild relatives usually produce lines that have poor agronomic performance, and often the undesirable traits cannot be eliminated. Some examples of these problems reported during our survey included: crosses of cowpea cultivars with *Vigna unguiculata* (L.) Walp subsp. *dekindiana* and *pubescens* which failed to produce any breeding lines with high agronomic performance or better quality traits (B.B. Singh, personal communication); lines with spider mite resistance from wild hops which were abandoned because of extreme hairiness of the leaves and strobiles of breeding populations (A. Haunold, personal communication); and chickpea breeding lines developed from a cross between *C. arietinum* L. and *C. reticulatum* by the Haryana Agricultural University, India, which were not promoted to advanced variety trials due to poor yield (P. Gauer, personal communication). Efforts to reduce deleterious effects of cross breeding with wild relatives through backcrossing are costly and time-consuming, and will no doubt effect the speed with which new cultivars are released. Molecular techniques offer a partial solution but there will likely continue to be cases where pleiotropic effects limit the use of genes from wild relatives.

In a 1983 report, the International Board for Plant Genetic Resources placed special emphasis on the need for wild species collections in their future collection missions (IBPGR 1983), and indeed since then the number of wild species accessions in public gene banks worldwide has been increasing. A search on the SINGER database of CG gene banks shows that since Plucknett et al.'s 1987 study documenting wild accessions in international agricultural research centers, absolute numbers of wild accessions, as well as the percent of wild species accessions per crop, have increased substantially for many of the crops reviewed here (Hodgkin and Hajjar 2007). Almost all of the crops reviewed here have hundreds, or thousands, of wild species accessions held just in the international genebanks of the CGIAR and many more accessions are often held in national genebanks. Thus, it does not seem to be the case that supplies of CWR are limited or that limitations in supply are restricting the use of these species. Indeed, some crops, such as barley

and cowpea, are abundant in the CG gene banks, with accessions numbering over a thousand each, yet few to no cultivars have been released containing traits obtained from wild germplasm.

Improvements derived from wild species in many crops have enticed crop breeders and researchers to further explore wild genomes in search of beneficial traits. This is easily demonstrated by the literature currently available on work discussing the myriad of beneficial traits of wild relatives and the importance of broadening our crop gene pools. Queries on a literature search database, CAB Direct, were conducted, in search of articles on wild relatives of crops from our survey. Keywords such as the crop generic name or scientific name preceded by “wild”, or scientific names of individual wild species, resulted in dozens and even hundreds of hits for many crops, most of which have to do with the availability and benefits of the wild germplasm. Articles on many crops date as far back as the database’s records go, the 1970s, and references for most crops appear in the database steadily throughout the following decades. A query for “wild barley” resulted in over 300 references, dating back to 1974, yet only one successful wild-derived cultivar has been released from research within the CGIAR. Similarly, “wild *Arachis*” and “wild soybean” searches produced dozens of hits, yet neither wild relative genes are prominent in released cultivars. It appears that significant research on useful traits in wild relatives is not sufficient by itself to lead to significantly increased use of these species if other barriers (crossing problems, associated agronomic problems) also need to be addressed.

The number of references increases greatly for queries on wild wheats or tomatoes. Yet some tomato scientists, working on the crop that arguably has the most incorporation of wild genes, continue to perceive this as insufficient, and blame “a lack of appreciation and inadequate screening” for neglect of the astonishing extent of variation in the wild (Rick and Chetelat 1995). Relative to the amount of ongoing research in crop improvement in general, soybean researcher Ted Hymowitz noted that wild relatives occupy a comparatively small part of the literature and budget; funding agencies focus their attention on

one to two year applied soybean breeding problems, rather than on basic research problems such as wide hybridization methodologies (T. Hymowitz, personal communication). This is part of a much more general phenomenon noted by others (Knight 2003) that funding for the kind of long term research needed to study, conserve and use CWR in plant breeding has been reduced.

Perhaps most promising in their potential to increase the use of wild relative genes are the advancements in the field of genomics. While introgression was not easily detectable with the genetic tools of a few decades ago, recent use of DNA markers and sequencing has helped in isolating beneficial genes and in selecting for traits which are difficult to detect based on phenotype. Marker-assisted selection is not only cost-effective and efficient, it is also amenable to automation and high throughput (Gupta et al. 2001), allowing for screening of whole collections of CWR. Marker-assisted selection can also be increasingly applied for the maintenance of recessive alleles in backcrossing pedigrees and for pyramiding of resistance genes (Koebner and Summers 2002). The use of SNP (single nucleotide polymorphism) technology has enormous potential as the next generation of molecular marker, in that it offers a high density of markers and because SNP assays are not dependent on the rate-limiting step of electrophoresis (Koebner and Summers 2002). Genetic engineering has allowed for the introduction of new traits by overcoming crossing barriers between non-sexually compatible individuals, and these methods might be expected to increase the use of CWR. However, it has been noted that the speed of introduction of new genes by genetic engineering, as compared to classical breeding, is overstated (Gepts 2002), due to the lack of precision in the integration point of the introduced gene requiring extensive testing of progeny, and the additional backcrossing programmes that oftentimes follow successful transformation in order to introduce the transgene into the desirable genetic background (Gepts 2002; Zhong 2001).

Breeders have been predicting accelerated introductions of desirable characteristics to crop plants through the development of molecular

genetic techniques for more than a decade (Appels and Lagudah 1990). However, while these introductions have increased greatly in number, the dramatic rate of increase predicted is not yet apparent.

Future prospects

In this paper we have described the continuing increase in the use of CWR for the production of new cultivars over the last 20 years. Nearly 10 years ago, Tanksley and McCouch (1997) argued that breeders were relying on the old paradigm of searching for beneficial traits associated with wild relatives, rather than searching for beneficial genes. Considering that phenotypically most wild relatives have poor yield or quality traits, they are rarely sought for contributions of these traits. Tanksley and McCouch argued that, as a consequence, there has been an overrepresentation of single-gene controlled traits such as disease resistance that can be ascertained phenotypically from wild relatives through standard screening exercises. Despite a growth in the literature on traits controlled by quantitative trait loci in wild relatives (e.g., Bernacchi et al. 1998; Huang et al. 2003; Nguyen et al. 2003; Sebolt et al. 2000; Tanksley et al. 1996; Xiao et al. 1998), results of the present study suggest that, so far, the potential of new molecular technologies have yet to be fully realized in ways that result in a significant increase in the rate of production of new cultivars carrying genes from CWR.

Despite the limited evidence of a new paradigm to date, plant breeding is a fairly long-term endeavour and the impact, like many of the cultivars, is likely to be still in the pipeline. Improving molecular technologies, interspecific hybridization techniques and genetic knowledge will continue to increase the capacity to use the valuable traits found in CWR. Problems associated with crossing barriers and associated undesirable agronomic traits will probably remain in a number of cases, but in many crops they will be overcome. As a result, the numbers of cultivars containing crop wild relative genes is likely to increase and wild relatives are likely to continue to grow in importance for plant breeders and for improved agricultural productivity. In these

circumstances, it will become increasingly important to conserve a broad enough range of diversity of these species for breeders, and their effective conservation in situ and ex situ will also increase in importance (Meilleur and Hodgkin 2004). However, realizing the full potential of the genes present in CWR will ultimately depend on the availability of resources to support the pre-breeding programmes necessary to deploy the kind of techniques proposed by Tanksley and McCouch (1997) over the long term.

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