

Crop Wild Relatives—Undervalued, Underutilized and under Threat?

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The world's wealth of plant genetic resources has much value for world food security, but these resources are under considerable threat. Crop improvement, particularly under climate change, depends on the genetic diversity of our plant genetic resources, which are arguably inadequately conserved and poorly used. There is wide recognition that the Convention on Biological Diversity's 2010 targets to reduce the loss of biodiversity have not been met. Biodiversity is at risk from multiple threats, including climate change, and the genetic diversity contained within plant genetic resources, particularly of species that are wild relatives of our crops, faces similar threats but is essential to our ability to respond to the new stresses in the agricultural environment resulting from climate change. It is important to consider the genetic value of these crop wild relatives, how they may be conserved, and what new technologies can be implemented to enhance their use.

Keywords: genetic resources, crop wild relatives, conservation, ecosystem services, climate change

Plant genetic resources are the “total genetic diversity of cultivated species and their wild relatives, much of which may be valuable to breeders” (Jackson and Ford-Lloyd 1990, p. 3) and *plant genetic resources for food and agriculture* (PGRFA) are those plant genetic resources most directly associated with human food production in agriculture. Conserved PGRFA represent a means of ensuring against future adverse changes in agricultural environments. Because human needs are constantly changing, genetic resources can provide important useful characteristics, such as resistance to new diseases or adaptability to changing climate conditions. PGRFA include breeding lines and genetic stocks, obsolete cultivars and landraces, and traditional or heritage varieties of crops. Importantly, they also include the wild plant species that are related to crop plants—*crop wild relatives* (CWR)—the possible progenitors of crops and species that can serve as gene donors to crops.

A CWR is therefore a “wild plant taxon that has an indirect use derived from its relatively close genetic relationship to a crop” (Maxted et al. 2008, p. 22). Historically, their potential as gene donors for crop improvement was clearly recognized by the renowned Russian plant geneticist Nicolai Vavilov in the 1920s and 1930s (Vavilov 1926). Since then, CWR's importance as a critical resource for future human well-being has not been fully recognized in the discussion of ecosystem services (Naidoo et al. 2008). They are in fact a natural resource and an important and deserved target for urgent and systematic conservation, as well as substantially expanded use.

The world food problem now

“We urge countries at the Copenhagen Conference to give due attention to crop diversity conservation and use” (www.croptrust.org/documents/Press%20Releases/statement%20English.pdf). This quotation formed part of a statement released by over 60 of the world's leading food security experts ahead of the United Nations Climate Change Conference in 2009. They called for the climate change negotiators to recognize the importance of crop diversity conservation and use as part of their commitments to climate change adaptation (www.croptrust.org/main/climatestatement.php).

Why did such food security experts make this proposal? Over the past four decades or so, the agricultural sectors in many countries have been transformed by crop genetic improvement. Billions of people can be fed today because of the Green Revolution, largely consisting of the release of modern varieties of crops, which predominantly resulted from the use of genetic resources available in national and international agricultural research programs in many parts of the world (Evenson 2005). In many cases, these programs were supplied with genetically diverse plant material because of work in Consultative Group on International Agricultural Research (CGIAR) centers (Evenson and Gollin 2001). In the latter part of these four decades, the Green Revolution has been succeeded by a gene revolution (Pingali and Raney 2005). The main focus of agricultural research and crop improvement has in fact switched from national programs to the private sector, especially in developed countries, where

significant trickle-down to developing countries is slow or is very inadequate in terms of meeting the current requirement for food security. Coupled with this focus, spending on agricultural research is only recently being acknowledged as needing a major boost (Pingali and Raney 2005, Breithaupt 2008) in order to cope with an escalating worldwide food-supply crisis (FAO 2008, Royal Society of London 2009, Tester and Langridge 2010) and because this research has suffered from major declines in funding since the 1990s.

It is widely recognized that food security is threatened by climate change, and indeed, there are already important examples of what consequences its effects could have. Although the problem is not directly attributable to climate change, in Australia, wheat, barley, and canola crop yields have been reduced by over 40% because of drought. Generally, rising temperatures and reduced precipitation will affect semiarid regions and reduce yields of maize, wheat, and rice over the next 20 years (Brown and Funk 2008, Lobell et al. 2008). "Adapting" agriculture is seen as a possibility to combat the problem, where shifting planting dates or switching to different crop varieties will have some benefit. However, it has been argued that the development of new crop varieties will provide the greatest benefits (Lobell et al. 2008), provided that this can be achieved in time. It will be a costly process that will require renewed investment in international agriculture, and new crop varieties demand new genes and gene sources. CWR need to be acknowledged as an important future source of those genes and their alleles, but this will only be possible if their future survival can be assured by effective conservation.

What genes are out there? Finding them and using them

Arguably, CWR form the most important component of PGRFA, because they hold so much potential for crop improvement (see supplementary table S1 online at [dx.doi.org/10.1525/bio.2011.61.7.10](https://doi.org/10.1525/bio.2011.61.7.10)). The Green Revolution of the 1960s and 1970s was largely dependent on the discovery of new genes in traditionally grown landraces that brought about highly significant increases in crop production. As an important component of PGRFA, landraces hold a vast wealth of genetic diversity yet to be exploited. However, given the current pressures on agricultural production and the need to provide new cultivars for the more marginal or extreme environments resulting from climate change, it is possible that more novel genes and gene systems of potentially greater use can be found in CWR, rather than in landraces (Breithaupt 2008). This has been strongly argued by Zamir (2001), who has made the case for using "exotic genetic libraries," in the form of wild species, to transfer sets of genes that control quantitative traits (see the discussion of minichromosomes below).

Using "conventional" biotechnology

Biotechnological approaches (Tester and Langridge 2010) can allow for the transfer of genes from more distantly

related CWR into breeding programs. CWR have already contributed significantly to improving food production (table S1), and their use in breeding programs has increased over time as technology has developed (Lobell et al. 2008). Asian rice is one of the clearest examples of the value of coupling wild species with biotechnological techniques for the genetic improvement of crops. Following the development of the rice variety IR8 in 1966, in the early 1970s over 7000 lines were screened to find one from wild *Oryza nivara* that possessed a resistance to the grassy stunt virus; this resistance can now be found in most rice crop germplasm emanating from the International Rice Research Institute in the Philippines. In 1990, the transfer from wild *Oryza longistaminata* of the *Xa21* gene for bacterial blight resistance really kick-started the systematic use of the wild rice gene pool: The IR72 variety out-yielded all other varieties after its release (Leung et al. 2002). The New Plant Type was initially formalized in 1989, with an aim to once again break the yield barrier in rice, but this has not yet happened, probably because of our lack of understanding of the primary physiological processes in plants. Nevertheless, new varieties are now being released that are based on the New Plant Type, which has been supplemented with genes from wide crossing involving hybrids with wild *O. longistaminata* and *Oryza rufipogon*.

How are these uses of wild species and interspecific crossing achieved? It is not an easy or quick process using conventional plant breeding, not least because undesirable traits can be transferred along with those that are desirable, and they then have to be selected out. Nevertheless, virtually all use has been based on conventional plant breeding but has been supplemented with newer processes involving chromosomal manipulation, embryo rescue, alien introgression lines, mapping populations, marker-assisted selection, and the use of doubled haploids to create inbred lines. Increasingly significant are genomic-based resources, map-based cloning, the analysis of quantitative trait loci, gene isolation, and genetic modification.

Greater exploitation of CWR through emerging biotechnologies

Much of the success of genetic engineering depends on locating useful genes to clone and then transferring those genes to genetic lines in a breeding program. In a sense, this is no different from conventional plant breeding, which also relies on finding the germplasm that contains the genes of interest. So what is needed is increased international collaboration for screening germplasm for useful genes. The increased use of information gained from model plant species will provide an important way forward. *Medicago truncatula* is one such model species with a relatively small genome (less than 500 mega base pairs) that has been fully sequenced. It is also a CWR closely related to alfalfa, an important polyploid crop species with twice the genome size.

Next-generation sequencing: An important way forward for allele mining. With the complete genome sequence for soybean already published, scientists have now started the process of high-throughput resequencing of related genomes (Lam et al. 2010). Seventeen whole-genome sequences of CWR of soybean have been produced, and of particular note, they have found greater allelic diversity among the wild soybean species (CWR) than among the cultivated species. So, we are now at a point in technological development that will allow us to screen CWR for important genetic diversity much more efficiently and in greater volume than before. Next-generation sequencing promises, by way of this high-throughput, targeted resequencing (focused on specific genes rather than on whole genomes), a way of screening thousands of samples of germplasm for interesting gene variants and making them available for use in conventional breeding. There are now many candidate genes—shown to be involved in some way in drought tolerance, for instance—and large-scale resequencing will allow us to identify these genes and all the variants that can be found in the CWR related to many crops. Researchers in the Generation Challenge Programme (www.generationcp.org) have identified allelic diversity in candidate genes for drought tolerance in cereal crops, and a group of hormone-related genes for stress and ripening have proven to be of particular interest. Similar approaches for targeting pest resistance and drought tolerance pinpoint CWR as being important in the development of “green super rice”—one possible answer to climate change challenges (Zhang 2007). However, although the discovery of useful gene variants may be speeded up substantially, a note of caution is needed, because even with a genetically modified approach, new varieties of crops cannot be produced over a short term. Substantial conventional breeding is still involved and takes several years to complete, and it is only just becoming apparent that there is a clear shortage of conventionally trained plant breeders, at least within Europe, the United States, and Africa. This raises a major concern: New plant breeders are not born overnight, and neither are new varieties of crops; neither can really happen quickly enough to keep up with climate change.

Modifying genetic recombination: Releasing new gene combinations. Plant breeding is dependent on meiotic recombination for the generation of new genotypes that can be selected for improved phenotypes. Meiotic recombination itself is nonrandom, and the low-frequency and often uneven distribution of meiotic crossing over has been a major constraint to efficient and timely crop improvement, with large parts of genomes remaining completely immune to genetic recombination and effectively immune from exploitation. For example, recent work in cereals has demonstrated that the recombination rate is not linearly related to gene distribution and that very large linkage blocks of genes—up to half in barley (Künzel et al. 2000)—rarely undergo recombination. Using wild species for the transfer of advantageous genes in crop improvement programs inevitably either requires

many years of backcrossing (time that we can ill afford to waste) in attempts to break up the transfer of deleterious genes carried along by linkage drag or requires the use of novel and more immediate methods for manipulating the recombination frequency and distribution in these hybrids. The need for the transfer of basic knowledge in model organisms such as *Arabidopsis thaliana* to crops has been recognized by the Biotechnology and Biological Sciences Research Council in the UK (www.bbsrc.ac.uk/organisation/policies/reviews/scientific_areas/0404_crop_science.html). A comprehensive understanding of the genes that control the frequency and distribution of genetic crossovers during meiosis in *Arabidopsis* will allow us to manipulate those genes in wild-species–crop hybrids. This will allow us to increase genetic recombination and to release new genetic variation when and where it is required. It will enable us to create new breeding lines with very novel combinations of alleles originating from CWR.

Transferring multiple traits with minichromosomes. If the future use of genes from CWR depends on biotechnology, new opportunities may already exist that will assist in the transfer of sets of genes or even complexes of genes conferring tolerance to drought, salt, and temperature from CWR, rather than just that of individual genes. It has been possible for some time to construct autonomous minichromosomes in yeast. These DNA fragments behave as chromosomes in a normal way and, by way of segregation at meiosis, deliver multiple genes to daughter cells. This has been achieved in maize (Carlson et al. 2007, Yu et al. 2007, Sabelli et al. 2009) and presents the exciting possibility of engineering plant processes—the ability to select segments of the genome from a CWR known to influence disease resistance or drought tolerance and to transfer them directly into breeding material.

For how long will CWR be available? Threats and the need for conservation

Global changes could mean irretrievable losses: How will the continued existence of CWR be threatened in the future, and what, therefore, needs to be done to conserve them? One of the first threats to PGRFA to be described occurred at the same time as, and because of, the Green Revolution in the 1960s and 1970s. Agricultural scientists and plant geneticists recognized that if and when the Green Revolution modern cultivars became successful and were taken up by farmers on a large scale, these modern varieties would rapidly replace the genetically rich traditional landraces that had existed for centuries. This has quite clearly happened between then and now and would have resulted in serious loss of the genetic diversity of traditional varieties had not genetic resources conservation in gene banks been implemented. In fact, the CGIAR established the International Board for Plant Genetic Resources (now Bioversity International) to coordinate collection efforts at a global level and to arrange for the long-term conservation of agricultural plant genetic resources, and the Global Crop Trust was recently

established to reinvigorate the *ex situ* conservation priority. But although the conservation of these resources was kick-started because of the perceived threat of landrace replacement by Green Revolution varieties, CWR did not play a significant role in the early days of germplasm collection and gene bank conservation. So what about CWR conservation in the present day?

CWR are, just like any other wild plant species, subject to an increasing range of global threats. The major driving forces behind the erosion of CWR plant biodiversity are land-use change; climate change; nitrogen deposition; and biotic exchange, including alien invasive species. The fourth report of the Intergovernmental Panel on Climate Change, published in 2007, confirmed that the global climate is changing. The International Union for the Conservation of Nature Red List criteria have been applied to projections for species distributions in Europe under different climate change scenarios (Thuiller et al. 2005), which showed that many European plant species could become severely threatened. Half of the species studied could be vulnerable or threatened by 2080. The species studied were wild species, but not specifically CWR.

Other studies on CWR indicate how susceptible they could be to climate change. The answer is very worrying, according to recent research that indicates that wild peanut species in South America, wild cowpeas in Africa, and wild potatoes in Central and South America will lose half their current geographic ranges and that between 16% and 22% of these species will go extinct (Jarvis et al. 2008). Furthermore, Jarvis and colleagues (2008) found that the results varied among the three crop complexes. The most deleterious impact will be on *Arachis*, in which between 24 and 31 (out of 50) species are likely to go extinct; of the remaining species, their ranges are likely to decrease by 85%–94%. So it is not just that climate change will have significant impact; it will have different impacts on different CWR groups, and thus far, it is difficult to predict which species of CWR will be most affected.

There are many other threats to the survival of CWR. These threats are exemplified by genetic erosion caused by land use change, such as major hydroelectric dam construction on the Nu River in China (Stone 2008). The expansion of rubber plantations and the promotion of biofuel crops (Sims et al. 2006), such as jatropha (*Jatropha curcas*), could similarly threaten CWR in China. In southern Yunnan's Xishuangbanna region, two-thirds of a unique rainforest have been lost during the last 30 years, largely to rubber plantations. Other threats include the reclamation of wasteland, the development of aquaculture, overgrazing, urbanization, and pollution.

How can we ensure survival—through sustainable conservation? First, we need to gain acceptance of the idea that CWR can make a major contribution to ecosystem services and are therefore worth preserving. For many, the fundamental reasons for biodiversity conservation are taken for granted. Increasingly, however, conservationists have become

interested in the goods and services that can be derived from ecological systems that benefit people in a material way (Naidoo et al. 2008). Setting conservation priorities has now started to involve the assessment of the extent to which conservation can improve—for example, carbon sequestration, carbon storage, grassland production for livestock, and water provision. So why are CWR and the contribution that they can make to the improvement of crops and to world food security not routinely considered in the same way when national conservation priorities are formulated?

Second, given the growing problem of global food insecurity and the global interdependence of nations with regards to food security, a coordinated global approach is required for CWR conservation (Maxted and Kell 2009). Large steps forward have been achieved in documenting those species that are CWR in Europe and the Mediterranean, so that conservation can be objectively and systematically planned (Kell et al. 2008). At least in this region, we now know which wild species of plants can be screened as sources of useful genes in the future, and we are moving forward to determine which ones are most under threat (Maxted et al. 2008) and in need of urgent conservation action. The United Kingdom remains an isolated example where a national CWR conservation strategy has been developed (Maxted et al. 2007), yet even in the United Kingdom, where the sites to focus *in situ* CWR conservation have been identified, the sites themselves have yet to be formally established and protected by legislation as part of the national protected-area policy. In contrast, of the large number of flowering plants in China, we are currently largely unaware of those that will be of the most value to us in a biotechnological sense—those that are CWR. By adopting the protocols and models that were developed in Europe to produce the CWR Catalogue for Europe and the Mediterranean (www.pgrforum.org/cwr/cwr.asp), this should be achievable in a short amount of time. However, designing and implementing the necessary conservation actions to secure the CWR currently under threat will be a major task, both in Europe and in the rest of the world. The most exciting aspect to this task is that positive action resulting from European, Chinese, and South East Asian collaboration—triggered by projects such as DIVERSEEDS (www.diverseeds.eu) that supported networking on conservation and the use of plant genetic resources in Europe and Asia—would be an excellent demonstration of what could be achieved worldwide.

Conservation of CWR has started to be addressed by various national and international initiatives, including the International Union for Conservation of Nature's Crop Wild Relative Specialist Group (www.cwrsg.org), a Global Environment Framework project (“*In situ* conservation of crop wild relatives through enhanced information management and field application”; www.cropwildrelatives.org/index.php?id=3261), the recently inaugurated CWR global portal, the Food and Agriculture Organization of the United Nations' initiative to establish a global network for the *in situ* conservation of CWR diversity (Maxted and Kell 2009),

and the European Union–funded European Crop Wild Relative Diversity Assessment and Conservation Forum (www.pgrforum.org). This latter initiative published a catalog containing 25,687 crop and CWR species known to exist in Europe and the Mediterranean, indicating that approximately 80% of the Euro-Mediterranean flora consists of crop species and their wild relatives; in other words, more than three-quarters of the plant species in the region have a current or potential direct use to humankind. An analysis of the catalog data revealed some useful statistics for regional conservation planning, and data can also be extracted to form the basis of national CWR inventories. But although we now have a good basis for CWR conservation planning in Europe, these baseline data are not readily available for other regions; therefore, our knowledge of the CWR flora of the entire world is still far from complete. However, we do know that 17.5% of the worldwide vascular plant genera contain food and agricultural crops and that there are probably at least 60,000 crop and CWR species worldwide (Maxted and Kell 2009). Most important in terms of food security, there are 10,739 crop and CWR species within the world's 77 genera that contain food crops, and of these, around 700 species are of a high value in terms of their potential use in plant breeding programs.

The conservation of CWR has historically been focused almost entirely on the *ex situ* collection and storage of seeds in gene banks. An analysis of European gene bank holdings recorded in the EURISCO catalog of *ex situ* plant genetic resource accessions (http://eurisco.ecpgr.org/home_page/home.php) revealed that CWR account for only 5.6% of the total germplasm holdings in European *ex situ* collections (Maxted and Kell 2009). Furthermore, when compared with the European CWR flora data, the catalog was found to contain 24,448 accessions of 1,095 species from 462 CWR genera out of a total of 436,436 European accessions. The 1,095 CWR species included represent only 6% of the 17,495 CWR species found in Europe, which means that 94% of European CWR species are not conserved in *ex situ* collections. Even the world's most important crops—the wild relatives of *Triticum* and *Aegilops*—are poorly represented in gene banks, and wild rice accessions consist of only 10% of the total gene bank entries worldwide (Tankley and McCouch 1997). The national Chinese soybean collection, located in the Chinese Academy of Agricultural Sciences, has the world's largest collection of wild soybean (*Glycine soja*), comprising 6000 accessions (Zhao et al. 2005), but other soybean CWR are poorly represented or absent. Other gene banks are only starting to develop prioritization schemes for agricultural plant genetic resource *ex situ* collections that include CWR. The recently inaugurated Israel Plant Gene Bank has prioritized 323 plant species for collection in readiness for *ex situ* conservation, including many Israeli CWR (Barazani et al. 2008).

In situ conservation within protected areas—specifically, CWR genetic reserves—offers a complementary approach to gene bank conservation, but one that has yet to be systematically applied. There is very sound knowledge of *ex situ*

conservation techniques, and substantial progress has been made in drafting the necessary protocols for *in situ* CWR conservation (Iriando et al. 2008), as well as in identifying high-priority species and sites for the conservation of wild relatives of globally important food crops.

Interdependence: The need for more intense international collaboration

Today, the agriculture of virtually every country is heavily dependent on a supply of genetic resources from other parts of the world (FAO 2010). The United States and Australia, for example, place considerable reliance on species originating in other regions of the world for their major food and industrial crops. Sub-Saharan Africa is estimated to be 87% dependent on other parts of the world for the plant genetic resources that it needs, and the figure is estimated to be 90% in Europe and 62% in East and Southeast Asia (www.fao.org/ag/AGP/AGPS/PGRFA/pdf/swrfull.pdf). Many countries hold a significant amount of plant genetic diversity for food and agriculture in their gene banks, farmers' fields, and natural habitats. In the medium to long term, however, these countries are likely to require access to additional diversity from the crop species' centers of diversity, the majority of which are restricted to eight crop diversity hotspots identified early in the last century (Vavilov 1926) and located in resource-starved developing countries. Germplasm, CWR, and the genes that they possess will therefore need to be moved around the world more than ever before in order to facilitate the process of agricultural adaptation as a response to changing climate.

Although developing countries contain the Vavilov centers of crop diversity and therefore possess much of the world's genetic resources, they struggle to conserve these resources, and they may lack the technologies—in particular, the more advanced molecular and genomic tools—and the corresponding expertise to use the genetic wealth for their own benefit. The onus is therefore on developed countries to work with those developing countries to conserve agricultural plant genetic resources, including CWR diversity. Improving the collaboration between genetic resource-rich developing countries and technologically advanced developed countries—as has been the goal of the European Union funded DIVERSEEDS project (www.diverseeds.eu)—seems to be a prerequisite to unlocking the full genetic potential of CWR. There is a real need to promote awareness of the value of the link between CWR conservation and their use. This holds true between scientists in developed countries who can provide the tools for the conservation and sustainable use of CWR on one hand and scientists and stakeholders working in the centers of origin and diversity of CWR on the other. Only in this way will our responses to a rapidly changing climate be able to sustain agricultural biodiversity on one hand and global food production on the other.

Setting priorities for the future

The world is facing growing global food insecurity and interdependence for food supplies, which is at least partially

a consequence of climate change on agricultural production. A step change in crop improvement through plant breeding is needed in order to combat the problem, and this could be achieved by a concerted effort to more fully exploit the potential of CWR, currently very much an underutilized resource. Maximizing the use of newly emerging biotechnological tools is imperative, but it will not be possible if the sustained conservation of CWR is not addressed with some urgency.

It is now important that national, regional, and global strategies for complementary CWR *in situ* and *ex situ* conservation be developed and implemented; that priority CWR taxa and sites containing these CWR taxa be identified; and that genetic reserves be established, which will require the protected area and PGREF communities in different world regions to work more closely together than they have in the past. *In situ* CWR conservation will require the use of local-scale climate change models. The conservation of CWR will be boosted substantially if they are recognized as being major contributors to ecosystem services and are valued in that context. There is an urgent need to increase the use of plant genetic resources—especially CWR—through conventional, novel, and emerging approaches; combinations of technologies need to be fully exploited in order to increase the rate of gene discovery within naturally occurring genetic variation, followed by their introduction into new varieties of crops with novel combinations of genes. This will have the dual effect of contributing to enhanced food production and to the conservation of CWR.

Food security is a global issue, so improved cooperation is important—on one hand, to fight current pest and disease outbreaks and, on the other, to address national skill shortages that hinder the setting up of CWR conservation sites, effective *ex situ* conservation, and the sustainable use of CWR using state-of-the-art biotechnological methods coupled with more traditional plant breeding. Improving cooperation requires not only the exchange of technical expertise, but also the willingness of scientists from developed and developing countries to establish and develop their professional relationships, with international funding schemes providing the necessary support. As one scientist rhetorically asked in one of the DIVERSEEDS Euro-Asian plant genetic resources meetings, “Biology doesn’t know political borders, so why should we have such borders in our work?”

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2011 Tyler Prize



Dr. May R. Berenbaum

Swanlund Professor and
Head of the Department of Entomology
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The Tyler Prize Executive Committee announces the awarding of the 2011 Tyler Prize for Environmental Achievement on its thirty-eighth anniversary to Professor May R. Berenbaum. Dr. May Berenbaum is recognized for her scientific contributions in understanding the coevolution of herbivorous insects and plants, elucidating the physiological and genetic basis for coevolution, for her application of these concepts to agricultural practices, and for sharing her insights on the role of insects in our ecosystems.

www.life.illinois.edu/entomology/faculty/berenbaum.html

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