

A Case for Crop Wild Relative Preservation and Use in Potato

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ABSTRACT

Crop wild relatives (CWR) offer a critical resource to address food security needs by providing genetic diversity for crop improvement, leading to increased plasticity and productivity of farming systems. However, plant breeders typically have not developed systematic or comprehensive strategies for the characterization and use of CWR for cultivar improvement. Potato (*Solanum tuberosum* L.) provides an excellent case study for the use of CWR germplasm in addressing global food security needs. International cooperation and collaboration are critical to collect, characterize, and use CWR in anticipation of future production needs. Both ex situ and in situ preservation of wild potato species are essential to assure a comprehensive conservation plan. Top priorities include a coordinated inventory of gene bank holdings followed by re-collection of CWR and new collection where gaps exist. Access to CWR genetic diversity will continue to be critical as breeders face the challenge of developing cultivars that fit into new production systems, especially in response to climate change. With the advent of the genomics era, new visions of germplasm use strategies are emerging. In addition to filling gaps in collections, it will be important to expand efforts to characterize and use potato CWR. A systematic and integrated strategy is needed to evaluate CWR in gene banks for traits to continue breeding progress.

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Abbreviations: CWR, crop wild relatives; EBN, endosperm balance number; SGN, SOL Genomics Network.

THE PROBLEM

Environmental degradation and climate change pose a threat to global food security. Recent decades have brought crop failures, food shortages, reductions in crop productivity, food price increases, and economic crises, highlighting the vulnerability of global food production systems for sustaining an ever-growing human population (Miller et al., 2010). Estimates place 20% of all plant species in danger of extinction in the near future (Brummitt and Bachman, 2010). This number is likely to increase as a result of climate change and expanding urbanization and agricultural production. In addition, the geographic range of many plant species is expected to be reduced by half in the next 50 yr (Jarvis et al., 2008). Geographic range shifts for many species have already been documented at rates two to three times faster than previously thought (Chen et al., 2011).

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Table 1. Examples of major advances in potato cultivar development resulting from the introgression of crop wild relatives (CWR) germplasm.

Contribution	Clone	CWR donor	Reference
Late blight resistance	W races	<i>Solanum demissum</i>	Hawkes, 1945, 1958; Plaisted and Hoopes, 1989; Bradshaw, 2009
Potato virus Y resistance	MPI 61.303/34	<i>Solanum stoloniferum</i>	Bradshaw et al., 2006
Nematode resistance	Maria Huanca (CIP 279142-12)	<i>Solanum vernei</i>	Llontop et al., 1989; Brodie et al., 1991
Processing quality	Lenape	<i>Solanum chacoense</i>	Love et al., 1998

Crop wild relatives (CWR) offer a critical resource to address food security needs by providing genetic diversity for crop improvement, leading to increased plasticity, sustainability, and productivity of farming systems (Maxted et al., 2008). The value of CWR has historically been unappreciated by both agricultural scientists, who believe they are too wild to be useful, and conservation scientists, who often focus on rare plants without regard to potential economic value. The significance of the CWR resource is now becoming more apparent to policymakers. At the United Nations Climate Change Conference in 2009, the need for attention to the conservation and use of crop genetic diversity was emphasized. However, plant breeders typically have not developed systematic or comprehensive strategies for the characterization and use of CWR for cultivar improvement (Maxted et al., 2012). Consequently, the development of viable strategies for the conservation and sustainable use of CWR is required for germplasm enhancement of crop plants. In February, 2012, at the International Potato Center in Lima, Peru, the Global Crop Diversity Trust convened a meeting of potato CWR experts to discuss strategies for germplasm collection and use. The present review is a product of this meeting. It was developed to describe the current state of the potato germplasm resource and provide a plan for its preservation and use in the future.

THE CURRENT SITUATION

Potato provides an excellent case study for the importance of CWR germplasm use in addressing global food security needs. It is the third most important food crop worldwide, behind rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.). In 2010, world potato production was 324 million t, with a value of nearly US\$56 billion (FAO, 2013). In addition, potato production in recent decades has increased steadily in developing countries due to its high yield of nutritious food. For example, China is the world's largest producer of potatoes and production is expanding to enhance food stability (Jansky et al., 2009a; Scott and Suarez, 2012). Potato CWR are abundant and most can be hybridized with the cultivated potato, either directly or by applying strategies that allow the circumvention of hybridization barriers (Hanneman, 1989; Camadro, 2010). In fact, potato CWR have made important contributions to disease resistance, enhanced yield,

and improved quality through plant breeding for over 150 yr (Hawkes, 1945, 1958; Rieman et al., 1954; Rudorf, 1958; Ross, 1966, 1979; Plaisted and Hoopes, 1989; Bradshaw and Ramsay, 2005; Bradshaw, 2009). Consequently, potato is acknowledged as a crop for which CWR have been prominently used (Maxted et al., 2012). Table 1 illustrates a few prominent contributions of CWR to improved potato cultivars. One of the earliest examples is the use of *Solanum demissum* Lindl. as a source of major genes for late blight resistance (Ross, 1966). While these genes were initially significant in controlling late blight, they were not durable. In contrast, major gene resistance for potato virus Y from *Solanum stoloniferum* Schldl. & Bouché has proven to be durable and is found in a number of European cultivars (Flis et al., 2005). Another notable success in the use of CWR in potato breeding is the Peruvian variety Maria Huanca, which has a complex pedigree containing *Solanum vernei* Bitter & Wittm. (Llontop et al., 1989). This cultivar is highly resistant to two races of the white cyst nematode *Globodera pallida*, potato virus X, and potato virus Y. The final example is the cultivar Lenape, which contains *Solanum chacoense* Bitter (Akeley et al., 1968). Lenape is in the pedigree of many modern chip cultivars and is credited with contributing to major advances in breeding for chip quality in the late 20th century (Love et al., 1998). Unfortunately, after its release, Lenape was removed from the market due to excessive levels of glycoalkaloids in its tubers, no doubt coming from *S. chacoense*, which is known for this characteristic (Zitnak and Johnston, 1970). This example illustrates the need for germplasm enhancement programs to carry out comprehensive evaluations of their products to avoid the inclusion of undesirable properties in eventual varieties.

During domestication, plant populations typically experience a severe genetic bottleneck (Feuillet et al., 2008). This so-called domestication bottleneck leaves behind much of the useful genetic diversity that could contribute to crop improvement. Potato provides a good illustration of the consequences of genetic bottlenecks. The cultivated potato originated in southern Peru about 10,000 yr ago and then spread both north and south while maintaining interactions with its wild relatives (Spooner et al., 2005). However, most commercial potato production today is concentrated in the temperate regions of North America, Europe, and Asia. These potatoes mainly

originated from a small set of clones brought to Europe in the latter half of the 1500s (Ames and Spooner, 2008). Presumably, many of the clones did not survive the passage from South America to Europe and others that arrived in Europe were lost due to poor adaptation and disease pressure. For over 300 yr, cultivated potatoes in these regions were grown with little or no influx of new genetic diversity. The potato famines of the 1840s resulted from the genetic susceptibility of the cultivars in Europe to *Phytophthora infestans*, the causal agent of late blight. The tremendous toll on human lives in the wake of these potato crop failures provided an impetus for breeders to search for new germplasm in an attempt to produce cultivars less vulnerable to disease (Ross, 1966). Since the mid 1800s, potato breeders have been experimenting with the introduction of CWR germplasm into their programs, with varying degrees of success. Nevertheless, the genetic diversity within and among major north temperate zone potato cultivars remains low (Mendoza and Haynes, 1974; Wang, 2011). While the introgression of specific genes from wild species has had a significant impact on cultivar development, only a few species have been used extensively (Bradshaw et al., 2006). Most breeding programs have not developed a systematic strategy to broadly incorporate CWR into advanced germplasm.

Estimates of the number of species in taxonomic groups containing tuber-bearing *Solanum* species (section *Petota*) have varied considerably over time and by taxonomist (Ovchinnikova et al., 2011). The number has been reduced in recent years and section *Petota* is currently considered to encompass four cultivated (Spooner et al., 2007) and approximately 110 wild tuber-bearing *Solanum* species (Spooner, 2009). These species are distributed among 16 countries from the United States through Central and South America to Chile and Argentina (Spooner and Salas, 2006). Wild potatoes grow from sea level to 4300 m but are most commonly found at altitudes of 2000 to 4000 m. Crop wild relatives of potato are adapted to a much wider range of habitats than the cultivated potato. They are found in a diverse array of environments, including the cold high grasslands of the Andes, hot semidesert and seasonally dry habitats, humid subtropical to temperate mountain rain forests, cultivated fields, and even as epiphytes in trees (Hawkes, 1990; Ochoa, 1990). Approximately 70% of wild potato relatives are diploid. Cultivars in major potato production regions of the world are typically tetraploid while landraces still grown as staple crops in South America may be diploid, triploid, tetraploid, or pentaploid (Ochoa, 1990).

The ecosystems in which CWR grow are becoming unstable due to climate change, poor land management practices, urbanization, and infrastructure expansion such as road development (Maxted et al., 2012). For potato, climate change scenarios predict that increasing

temperatures and decreasing water availability will result in a substantial worldwide yield reduction of up to 32% by 2050 (Schafleitner et al., 2011). Severe threats in the Andes and Mexico, where most wild potato species are found, include mining, overgrazing, expansion of exogenous livestock (such as pig [*Sus domesticus*] and goat [*Capra aegagrus hircus*]), deforestation, expanding agriculture, and habitat loss in general. The regions under greatest threat to crops and their wild relatives overall include the tropical highlands of South America, Asia, and Africa and parts of southern Africa.

Crop wild relatives are often classified according to the gene pool concept developed by Harlan and De Wet (1971). Priority crop gene pools for CWR conservation are typically GP1B (wild relatives directly crossable to cultivars) and GP2 (wild relatives crossable with some manipulations) (Maxted et al., 2012). These germplasm resources are the most likely to be introgressed into cultivars via conventional breeding methods. Wild and cultivated potato species are found in a ploidy series ranging from diploid to hexaploid. One determinant of interspecific hybridization success in potato is endosperm balance number (EBN) (Johnston et al., 1980). Species with matching EBN values, regardless of ploidy, will hybridize as long as other barriers are absent. Ploidy and EBN values of wild relatives of potato include 6x (4EBN), 4x (4EBN), 4x (2EBN), 2x (2EBN), and 2x (1EBN). The application of the gene pool concept to potato would place the 6x (4EBN), 4x (4EBN), 4x (2EBN), and 2x (2EBN) species in GP1B and the 2x (1EBN) species in GP2. There are two diploid non-tuber bearing *Solanum* species, which would be in GP3 (not directly crossable to cultivated potato). Since they cannot be hybridized with potato, they have not been assigned an EBN value. Ploidy and EBN values of wild *Solanum* species are provided by Spooner and Hijmans (2001). In addition to EBN, numerous other pre- and postzygotic barriers to hybridization are common in *Solanum* interspecific crosses (Fritz and Hanneman, 1989; Camadro et al., 1998, 2004, 2012; Jackson and Hanneman, 1999; Chen et al., 2004; Weber et al., 2012). These barriers confound attempts to apply the gene pool concept to potato.

Many of the wild and cultivated relatives of potato are represented in gene banks throughout the world. These facilities provide access to CWR for research and breeding activities. Potato gene banks include the International Potato Center (CIP) (Lima, Perú), United States Potato Introduction Project (National Research Support Program [NRSP]-6) (Sturgeon Bay, WI), Dutch–German Potato Collection (Center for Genetic Resources, The Netherlands [CGN], Wageningen, The Netherlands, and Braunschweig Genetic Resources Collection [BGRC], Braunschweig, Germany), Institute of Plant Genetics and Crop Plant Research (The Groß Lüsewitz Potato

Collection [GLKS], Groß Lüsewitz, Germany), Commonwealth Potato Collection (CPC) (Dundee, Scotland), N.I. Vavilov Institute (VIR) (St. Petersburg, Russia), the Instituto Nacional de Tecnología Agropecuaria (INTA) (Balcarce, Argentina), and Centro Nacional de Pesquisa de Recursos Genéticos e Biotecnologia (CENARGEN) (Empresa Brasileira de Pesquisa Agropecuária [Embrapa], Brasília, Brazil). An inter-gene bank potato database contains records from seven of these gene banks (Huaman et al., 2000). The database is hosted by CIP and can be found online at <http://germplasmbd.cip.cgiar.org> (accessed 18 Oct. 2012). However, it is not currently updated on a regular basis. The lack of stable funding for the maintenance of scientific databases is a serious problem (Baker, 2012). The Global Crop Diversity Trust has, however, committed to multiyear support for the Genesys database (<http://www.genesys-pgr.org/> [accessed 28 Oct. 2012]). This system focuses on collecting accession level data from gene banks worldwide.

CALL FOR ACTION

International cooperation and collaboration are critical to collect, characterize, and use CWR in anticipation of future potato production needs. First, an inventory must be made of existing CWR in their natural environments and in gene banks. Based on well-defined habitat threat levels, endemism, distribution range, characterization data, conservation efforts, and use value, among other factors, a systematic approach to in situ conservation should be promoted in centers of CWR diversity. In addition, collection and preservation priorities must be developed. High priority collections would be those at threatened sites and for species that are underrepresented in gene banks. At the same time, systematic and comprehensive efforts must be made to develop and implement the most effective strategies for the characterization, documentation, and incorporation of CWR germplasm into potato breeding populations for cultivar development.

Geographic information systems technologies have enabled a better understanding of potato species distributions based on passport data from gene bank collections (Hijmans and Spooner, 2001; Hijmans et al., 2002). However, in recent decades, no field level research has been conducted on habitat shifts and conservation status in situ. Our understanding of the population ecology and dynamics of potato wild relatives is generally very poor. Several biases in gene bank collections have been documented and must be addressed in efforts to fill gaps in ex situ germplasm resources (Hijmans et al., 2012).

A gap analysis will help to determine the extent to which CWR resources are assembled and conserved in gene banks. This analysis compares the natural range of CWR with that documented in gene bank inventories. Results of the gap analysis provide direction for efforts to

expand collections of CWR that are underrepresented in ex situ gene banks (Maxted et al., 2008; Ramírez-Villegas et al., 2010). A team at the International Center for Tropical Agriculture (CIAT) (Cali, Colombia) is working on a gap analysis for potato CWR in coordination with CIP and the Global Crop Diversity Trust. When the results of this project are available they will be displayed here: <http://www.cwrdiversity.org/conservation-gaps/> (accessed 24 Oct. 2012). Additional collection priority criteria, such as threats to wild populations (for example, mining, urbanization, overgrazing, climate change) and degree of relatedness of taxa to cultivated species, may also be included in the analysis when data are available. To include a more complete picture, the method should ideally be coupled with an assessment of perceived in situ conservation status, for example, in parks and other protected areas.

In addition to those determined by the gap analysis, collecting priorities may focus on GP1 and GP2 species, which are most easily introgressed into the cultivated potato. However, most CWR in potato fall into this category, so additional complementary criteria are needed if priorities are to be set. Alternatively, an argument can be made that GP3 species should receive priority because they have the potential to contribute unique genes for traits not currently considered to be important to breeders but that may be in the future. For example, novel phytonutrients and starch properties have been found in GP3 species (Navarre et al., 2011; Fajardo and Jansky, 2012). Among priority taxa, those with the most urgent need for conservation typically have a limited geographic range (Maxted et al., 2012). While collecting expeditions should focus on adding to the genetic diversity that is already found in current germplasm collections, re-collection of populations held in gene banks would provide an opportunity to assess genetic erosion in the field and genetic drift in gene bank collections. Field and laboratory studies, including genetic and population analyses, are recommended to guide germplasm collection and conservation strategies and to inform breeders on effective approaches to crop improvement (Del Rio et al., 1997, 2001; Del Rio and Bamberg, 2003; Bamberg and Del Rio, 2006; Bamberg et al., 2009; Camadro, 2012).

A considerable challenge to the collection of potato wild relatives is that they are often found in sympatric associations where they hybridize readily. Species boundaries can easily become blurred as a result (Masuelli et al., 2009; Camadro et al., 2012). Transgressive segregation in these hybrid populations may allow them to survive in habitats that are more extreme than those of either of their parents. It is important then to include naturally occurring hybrids when collecting but to keep them separate and, when possible, clearly label them as such. Descriptive information on habitat, spatial distribution, ecology, geography, and surroundings, such as threats and conservation efforts, is

also critical. Ongoing evolution, mediated by gene flow between cultivated and wild species, occurs in the Andean center of potato origin and should be more thoroughly documented (Celis et al., 2004; Scurrah et al., 2008). Little is known about what happens after gene flow has occurred between wild and cultivated relatives in agricultural settings. Offspring must pass a series of critical natural and human selection steps to become viable new land race cultivars. Indeed, lessons may be learned from the study of successful cases of spontaneous farmer-mediated “pre-breeding” by selection resulting in the influx of wild species genes into the cultivated gene pool (Brush et al., 1981).

It would be useful to have a systematic strategy to characterize the value of CWR phenotypic variation for crop improvement. In 1920, the Russian scientist Nikolai Vavilov proposed the Law of Homologous Series in Variation to explain the significance of genetic diversity in relatives of crops (Vavilov, 1922). Basically, he proposed that knowledge of traits in one species can be used to predict the presence of similar traits in related species. This concept is useful for some traits and some species in potato (Jackson, 1990). A series of recent studies has attempted to predict the distribution of useful phenotypes in potato wild relatives based on taxonomic and biogeographic data (Jansky et al., 2006, 2008, 2009b; Spooner et al., 2009; Chung et al., 2010; Cai et al., 2011). However, predictivity success has been weak at best. Specifically, biogeographic data for potato have usually no or very low value for predicting resistance levels due to high intra-accession variability (e.g., Jackson, 1990; Jansky et al., 2008). This implies probably a higher genetic variability of potato than can be inferred from geographic distribution but possibly also that the biogeographic predictors used may not adequately capture the microhabitat characteristics. In conclusion, biogeographic analyses for predicting traits need to be handled on a case by case basis and should be complemented with genetic or high resolution genomic data.

As indicated above, one important limitation for predictivity analyses is that passport data from collecting expeditions are sparse. Consequently, local environmental stresses and habitats cannot be elucidated. In the future, comprehensive and standardized collecting protocols should be developed that include precise information from the collecting locality, including soil type, the presence of disease and pests, population size, species diversity, habitat disturbance, and location relative to agricultural activity.

An important element of passport data is accurate information about latitude and longitude, preferably using a global positioning system device. This allows geographical information systems to complement additional data, such as climate data, from global spatial databases and to infer biogeographic and vegetation indices, which are usually not measurable during a collection visit. While spatial datasets are not as precise as habitat data observed in situ,

the data will support three main uses: (i) to expand local environment characterization data, (ii) to detect broad-scale patterns of genetic diversity, and (iii) to identify sites with similar habitats, with the potential to orient additional collections aimed at filling gaps.

The genetic structure of populations and their spatial distribution must be taken into consideration during collecting. It is important to record the number of individuals sampled to subsequently be able to estimate gene frequencies in individual accessions. Ideally, a collector would use different sampling strategies depending on the mating system and distribution of the taxon. Especially with the genomics era, scientists may begin to treat each accession in a gene bank as a collection of genes and therefore pool individuals for genetics and breeding efforts (Maxted et al., 2012).

In addition to filling gaps in collections, it will be important to expand efforts to characterize and use potato CWR. We propose a three-pronged approach to systematically develop a use strategy. First, in the short term, diploid populations would be developed and shared among breeders who focus on germplasm enhancement. Second, sexual polyploidization would be used to create tetraploid clones that combine traits from both parents. Finally, an international multisite evaluation network for prebred materials would be launched. This final step would preferably apply a genomewide selection approach and be implemented in conjunction with a centralized high-throughput hub for quantitative phenotyping using controlled environments when feasible. Germplasm enhancement, unlike varietal breeding, should focus on new intermediate products rather than the end product of improved varieties. Attention is required to recognize valuable “unexpected” phenotypes while targeted traits are assembled from CWR combinations. It will also be important to incorporate mechanisms that will facilitate further use of diploid germplasm. For example, as mentioned above, $2n$ gamete production would allow sexual polyploidization of selected diploid germplasm (DenNijs and Peloquin, 1977). Exploitation of this mechanism allows the direct transfer of desirable traits from diploid CWR to cultivated tetraploid germplasm (Herriott et al., 1990; Hayes and Thill, 2002; Bisognin et al., 2005; Frost et al., 2006).

The potato research community has not focused on maximizing the effects of transgressive segregation or heterosis through the generation of a strategic set of diverse cultivar \times wild species hybrids. In wheat, new synthetics have been created on a large scale based on novel combinations of CWR and then selected for biotic and abiotic stress tolerances (Mujeeb-Kazi et al., 2008). This germplasm has provided a worldwide resource for wheat genetic improvement and illustrates the value of the introgression of CWR germplasm into adapted breeding lines. A similar strategy could be used in potato to develop populations from which to select multitrait prebred populations and clones for breeding.

The third prong in the CWR use strategy is the development of a trait observation network, similar in concept to the Group on Earth Observations Biodiversity Observation Network (GEO BON) focused on the long-term collection and curation of ecological data (Scholes et al., 2012). This facility would bring together existing evaluation data from collaborators worldwide and use these datasets to establish a network of trial sites that could be used by the community to generate new evaluation data on potato prebred materials over the long term. The germplasm included in such a network of evaluation sites would be a set that includes cultivated \times wild hybrids that are of interest to the local context of each evaluation site but also be of potential value at other locations. The set of prebred lines could include preexisting materials as well as some materials that would be created by researchers at each site using a diversity of CWR accessions and *S. tuberosum* recipient lines with traits that are useful to each program. The *S. tuberosum* recipient parent clones would likely be dihaploids or successful diploid (landrace) cultivars ($2n = 2x = 24$) that have been thoroughly characterized with robust molecular markers. Such an approach would create sets of materials that are highly diverse and that could be very useful for discovering unexpected traits in agronomically improved genetic backgrounds. Once valuable hybrids are selected and made available, the use of common, well-characterized sets of diploid and tetraploid recipient parents would facilitate monitoring of introgressed genes and traits to representatives of the cultivated gene pool. Various elements of this proposed strategy have been realized by breeding research centers lately, with noted promising contributions to ongoing cultivar development programs in their respective countries (Zimnoch-Guzowska et al., 1998). However, these efforts have been performed on a smaller scale than is proposed here.

The key to the success of this approach will be the use of standardized protocols for the evaluation of genetic resources and breeding lines. This includes the development of trait ontologies, trait dictionaries, and appropriate data management systems through which the resulting evaluation data can be shared among collaborators across locations and made available to the wider community. Such efforts are underway for potato: (i) a set of standardized protocols is available with electronic field book (Bonierbale et al., 2007), (ii) a potato ontology is being developed (Shrestha et al., 2010), and (iii) data systems aimed at handling large scale datasets are also being developed (Guberman et al., 2011). Protocols from CIP's International Cooperators Guide are currently being expanded to include drought tolerance evaluation. The ontology work for potato is performed as part of a community in an effort to maintain consistency and knowledge transfer within and across crops. The data systems currently in use at CIP as a potato breeding information platform make

use of a database developed to house genome size data to store additional phenotyping and environmental data, facilitating data integration. The standard protocol development would also include training on carrying out field phenotyping with an associated quality assurance program for repeatability and reproducibility. The resulting datasets would then become a community resource and can be "conserved" in perpetuity, independent of the career paths of individual researchers. Another relevant database is the SOL Genomics Network (SGN), which contains genetic, genomic, and phenotypic data on the Solanaceae, including potato (Bombarely et al., 2011). The long-term goal of the SGN is to create a network of resources to link genotype with phenotype to provide insights into plant adaptation and diversification.

CONCLUSIONS AND THE WAY FORWARD

Collection and Preservation

The conservation and sustainable use of CWR has become a priority on the international conservation agenda (Maxted et al., 2012). Crop wild relatives are worth preserving because they make a significant contribution to ecosystem services (Ford-Lloyd et al., 2011). Both ex situ and in situ preservation of wild potato species is essential to assure a comprehensive conservation plan. A top priority is a re-inventory of gene bank collections followed by re-collection of CWR where gaps are detected. Gene frequencies of natural populations and not genotypes ought to be conserved because genes, not genotypes, are transmitted across generations. Access to CWR genetic diversity will continue to be critical as breeders face the challenge to develop new cultivars that fit into new production systems, especially in response to climate change. With the advent of the genomics era, new visions of germplasm use strategies are emerging. For example, gene banks have the potential to evolve from collections of seeds to dynamic research centers for gene mining activities (McCouch et al., 2012).

Evaluation and Breeding

A systematic strategy is needed to evaluate CWR in gene banks for traits needed to continue breeding progress. Among adapted derivatives, characterization of a range of traits is likely to be productive (Jansky and Rouse, 2003). In addition, thorough evaluation of populations during the course of breeding, such as in backcross and marker-assisted selection programs, must be a priority to find the unexpected while evaluating the contributions of CWR in relevant genetic backgrounds. This program should be split among research centers under one global umbrella and requires joint durable funding.

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