REVIEW & INTERPRETATION

Are We Getting Better at Using Wild Potato Species in Light of New Tools?

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ABSTRACT

Potato (*Solanum tuberosum* L.), mankind's third most consumed food crop, originated as an interspecific hybrid in the Andean highlands. More than 100 species closely related to potato exist throughout Central and South America. Potato was introduced to Europe, Asia, and North America in the 16th and 17th centuries, but most cultivars were destroyed by late blight epidemics in the mid-19th century. Late blight resistance genes from the wild relative *Solanum demissum* Lindl. were subsequently introduced into cultivated potato. Thus, a precedent for the use of wild relatives in potato genetic improvement was established a century ago. Intensive efforts have been made to collect and maintain wild relatives of potato in public germplasm repositories. Genetic diversity in these species is high, and most are sexually compatible with cultivated potato. Perhaps more than any other vegetable crop, potato can benefit from the introgression of genes for valuable traits from wild relatives. However, a century of breeding has realized that potential on only a few notable occasions. Important examples include improved processing quality and resistance to viruses and nematodes. Substantial barriers prevent the facile incorporation of genetic material from wild relatives into potato cultivars. Overcoming these barriers may require an expansion of germplasm collections to include well-characterized individuals as a complement to population-based accessions. To be most useful for potato improvement, individual wild species plants will need to be cataloged by allelic composition, haplotype, biochemical properties, and physiological responses to stress. Effectively using the genetic diversity in wild relatives is likely to rely heavily on alternative methods of potato breeding, augmenting reassortment, and selection at the tetraploid level with diploid breeding and genetic modification using biotechnology.

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Abbreviations: BSP, bilateral sexual polyploidization; CIP, International Potato Center, Lima, Perú; EBN, endosperm balance number; SGN, SOL Genomics Network; USP, unilateral sexual polyploidization.

The potato (*Solanum* spp.) germplasm resource is composed of 107 wild relatives, four landrace (indigenous) cultivated species, and modern cultivars (Spooner et al., 2007, 2014). Although most cultivated potatoes are tetraploid, nearly three-fourths of wild species relatives are diploid. Wild potatoes are distributed from the southwestern United States southward to central Chile and Argentina (Spooner et al., 2014). Species richness is greatest in central Mexico and in the Andean highlands (Hijmans and Spooner, 2001). Among the world's 10 most important crops, potato (*S. tuberosum* L.) has the largest number of wild relatives (Vincent et al., 2013). In addition, potato germplasm is considered to be more accessible to breeders than relatives of most other crops (Ross, 1986; Hanneman, 1989; Peloquin et al., 1989; Hawkes, 1990).

Wild potato species are found in highly diverse habitats, including cloud forests, cactus deserts, scrub vegetation, mountain pastures, high grasslands, and pine forests (Hawkes, 1990). They carry genes for traits that have not been identified in cultivated potato and are a rich source of stress resistance and tuber quality genes (Hanneman, Jr., 1989; Hawkes, 1990; Spooner and Bamberg, 1994; Ortiz, 1998; Jansky, 2000). Reports of disease and pest resistance in wild and cultivated relatives of potato are abundant (Jansky, 2000; Gebhardt and Valkonen, 2001; Spooner et al., 2009; Machida-Hirano, 2015).

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Wild potato populations are often isolated by geographical or ecological niches, rather than reproductive barriers (Hawkes and Hjerting, 1969). For example, one population may be found in a valley in the Andes Mountains, whereas another population of the same species is in a distant valley, where it may be exposed to different stresses as a result of differences in altitude, temperature, rainfall, and insect pest and pathogen populations. Gene flow occurs through insect pollinators, typically bumble bees (*Bombus* spp.) and through seed dispersal via water, soil movement, and animals that consume wild potato berries (Camadro, 2012). These mechanisms effectively promote local gene flow but are less effective over long distances, especially between populations that are geographically isolated.

It has been assumed that most wild potato relatives are highly heterozygous as a result of outcrossing. Although polyploid potato species are self-compatible, most diploid *Solanum* species are self-incompatible due to a gametophytic self-incompatibility system (Pushkarnath, 1942; Pandey, 1962). Recent genomic studies, however, have revealed surprisingly high levels of homozygosity in wild relatives obtained from genebanks (Hirsch et al., 2013; Aversano et al., 2015a). Several explanations are possible. Small wild populations may be necessarily inbred, sample sizes during collection may have been small and inbreeding occurred during genebank maintenance, or self-incompatibility may not be as effective or as widespread as we have believed. Self-compatible diploid cultivated potatoes have been identified (Olsder and Hermsen, 1976; de Jong, 1977; Hermsen, 1978; Eijlander et al., 2000), and self-compatible individuals have been found in self-incompatible species (Cipar et al., 1964). A dominant self-incompatibility inhibitor gene (*Sli*) has been identified in the wild species *S. chacoense* Bitter (Hosaka and Hanneman, 1998a, 1998b).

Diversity within landraces offers another source of genetic variation for potato improvement. The International Potato Center maintains >600 clones of potato landraces. Several surveys have found phenotypic variability within landraces for traits important for potato (Ritter et al., 2008), including tuber quality (Cuesta-Subia et al., 2012), resistance to late blight [caused by *Phytophthora infestans* (Mont.) de Bary] (Delgado et al., 2013; Pérez et al., 2014), drought tolerance (Cabello et al., 2012), and the presence of nutritional compounds (Andre et al., 2007). There are three notable examples of contributions of cultivated potato relatives to crop improvement in North America and Europe. These are discussed in more detail below. Briefly, tetraploid *S. tuberosum* Andigenum group (the set of Andean cultivars) has been an important source of resistance to *potato virus Y* (Munoz et al., 1975). Diploid *S. tuberosum* Andigenum group (Phureja) has been used for over a half century as the pollinator for dihaploid induction (Hougas and Peloquin, 1957). Dihaploids formed the foundation for analytic breeding schemes in the late 20th century (Carputo and Barone, 2005; Ortiz et al., 2009). Group Phureja has contributed different tuber color and flavor traits to modern yellow-fleshed potato cultivars.

A fundamental postulate in plant breeding is that cultivated relatives should be accessed before wild relatives when searching for useful genes. In potato, however, a number of negative traits are introduced when cultivated relatives are used in breeding. These include rough tuber shape, short tuber dormancy, and male sterility (Jansky and Peloquin, 2005).

EX SITU CONSERVATION OF POTATO GERMPLASM

Genebanks worldwide maintain wild potato relatives along with potato cultivars and genetic stocks. These facilities provide a rich resource for potato breeders and other plant and crop scientists. Potato genebanks include the International Potato Center (CIP, Lima, Perú), the USDA Potato Genebank (Sturgeon Bay, WI), the Dutch German Potato Collection (CGN, Wageningen, the Netherlands, and BGRC, Braunschweig, Germany), the Institute of Plant Genetics and Crop Plant Research (GLKS, Groß Lüsewitz, Germany), the Commonwealth Potato Collection (CPC, Dundee, Scotland), the N.I. Vavilov Institute (VIR, St. Petersburg, Russia), the Instituto Nacional de Tecnología Agropecuaria (INTA, Balcarce, Argentina), and Cenargen (Embrapa, Brasilia, Brazil). A complete list of organizations that maintain potato germplasm is provided by (Machida-Hirano, 2015). An intergenebank potato database is hosted by CIP and can be found online at http://germplasmdb.cip.cgiar.org.

A recent gap analysis of 73 potato wild species assigned 32 species as high priority for collection (Castañeda-Álvarez et al., 2015). Four (*S. ayacuchense* Ochoa, *S. neovavilovii* Ochoa, *S. olmosense* Ochoa, and *S. salasianum* Ochoa) are not represented in any genebank, and the others are not adequately represented. Priority for collection was based on analyses that considered whether or not current collections are likely to capture variation attributable to population size, geographic distribution, and ecosystem diversity. Some of the high-priority species are narrowly distributed, and their habitats are threatened by development and climate change, so the collection need is urgent. The low-priority species, and those for which no further collection is needed, include those that have been widely used in breeding, such as *S. bulbocastanum* Dunal, *S. kurtzianum* Bitter & Wittm., *S. microdontum* Bitter, *S. raphanifolium* Cárdenas and Hawkes, and *S. vernei* Bitter & Wittm.

Considering the cost of maintaining large numbers of accessions in a genebank, efforts to identify redundancies can be productive. A study evaluating 314 accessions of *S. acaule* Bitter found that 15 were redundant according to analysis of amplified fragment length polymorphism (AFLP) markers (van Treuren et al., 2004). Accessions collected near each other sometimes had quite different genotypic patterns, whereas redundant germplasm was found in accessions that were geographically distant. Current and emerging technologies to analyze thousands of genetic markers simultaneously, or resequence entire genomes, will enhance our ability to detect redundancy within potato genebanks.

Interspecific hybridization can occur in wild populations, and this leads to one of the challenges with potato genebank collections—samples collected from the field may carry introgressions from other species. Several studies have demonstrated that natural hybrids exist and that collected specimens carry genes from other species (Camadro, 2012; Spooner et al., 2014). In addition, passport data do not typically provide information on population and sample size, so it is impossible to know how well an accession represents the population from which it was collected (Camadro, 2012). The collection of genes in an accession represents a snapshot in the life history of a population, taken at the time of collection and likely not complete. Additional information on responses to biotic and abiotic stresses is typically not provided in passport data, and more importantly, there are no data on the stresses under which the population evolved. This limitation was also reported by van Treuren et al. (2004).

Potato genebanks seek to preserve the diversity found within wild species, but quantifying diversity is challenging. Phenotypic variability may not reflect underlying genetic variability of a population because not all of the alleles carried by a plant are reflected in its phenotype (Tanksley and McCouch, 1997). In addition, segregation of a small number of major genes can lead to a large number of phenotypes in subsequent generations. For example, when a single inbred line–derived diploid F_1 hybrid of potato was self-pollinated, the resulting F_2 population exhibited a range of phenotypic variability for tuber appearance that was similar to that in large landrace collections (Jansky et al., 2015). Furthermore, Camadro (2012) warned of the dangers of assuming that phenotypic variation mirrors genetic variation, because the environment can have a large effect on phenotype in potato. Consequently, a single clone can look quite different in different environments.

Genebank users must realize the limitations of ex situ collections, which are samples of wild populations that may or may not be representative of the diversity present within a species. Due to limited propagule availability during collection, an accession may not adequately represent the natural population in the wild. In addition, although each wild population continues to evolve (del Rio et al., 1997a), genebank managers focus on preventing genetic change during sexual propagation. Consequently, an accession does not serve as a duplicate of a natural population. It is necessary to periodically generate new seed populations of genebank accessions, and this raises the concern that genetic drift will occur over time. Studies at the US Potato Genebank, however, determined that seed increase and seedling selection for vigor did not lead to changes in genetic diversity, according to molecular markers (del Rio et al., 1997b; Bamberg and del Rio, 2006). Finally, rare alleles in an accession may be lost during maintenance. Bamberg and del Rio (2009), however, have found that an allele that is rare in one population is usually common in another.

INTROGRESSION OF WILD SPECIES INTO CULTIVATED POTATO

Potato breeders have turned to wild relatives as sources of disease resistance and improved tuber quality 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). An understanding of hybridization barriers and the development of strategies to overcome these barriers have allowed breeders to access the potato germplasm resource. Potato breeding methods are typically divided into those for tetraploids and those for diploids. For the past several decades, breeders have focused on introgressing diploid wild germplasm into cultivated potato at the diploid level, with the goal of returning to the tetraploid level for cultivar development. At present, there is growing interest in remaining at the diploid level and creating diploid cultivars (Lindhout et al., 2011; Jansky et al., 2016).

In this section, we describe genetic barriers and ways that breeding techniques are used to successfully introgress traits from wild species relatives into cultivated potato.

Endosperm Balance Number Considerations

The potato genetics community routinely uses a bookkeeping system called endosperm balance number (EBN) to determine whether interspecific crosses will be successful, producing viable seeds (Johnston et al., 1980; Ortiz and Ehlenfeldt, 1992). Endosperm balance number is a biological isolating mechanism that affects endosperm development. Endosperm balance number values must match if the endosperm is to develop normally and viable seeds are to be produced. The values match when crosses are made within a species. Conversely, EBN does not match in most interploidy crosses, the endosperm fails to develop normally, and inviable seeds are produced. Johnston et al. (1980) proposed that a 2:1 maternal:paternal ratio of endosperm balance factors, rather than genomes, is necessary for normal endosperm development. Subsequently, *Solanum* species have been assigned EBN numbers based on their ability to hybridize with each other (Hanneman, 1994). Barring other crossing barriers, successful hybridization is expected when male and female gametes have matching EBN values, resulting in a 2:1 maternal:paternal ratio after fertilization of the central cell to produce endosperm. Ploidy, EBN combinations in wild potato relatives include 6*x*, 4EBN; 4*x*, 4EBN; 4*x*, 2EBN; 2*x*, 2EBN; and 2*x*, 1EBN. Designations of ploidy and EBN values for wild potato relatives are provided by Spooner et al. (2014).

Bradeen and Haynes (2011) proposed a potato genepool concept based on EBN. Primary genepool species are cultivated potato, which are 4*x*, 4EBN. The secondary genepool is the largest and contains wild relatives that are easy to cross to cultivated potato directly or after ploidy manipulations. Tertiary genepool species have an EBN value of 1. These species do not cross directly to cultivated potato but may be introgressed through bridge crosses, embryo rescue, or somatic fusion, as described below. Figure 1 illustrates the composition of the potato germplasm resource according to the Bradeen and Haynes definitions of potato genepools and the most current taxonomy, as summarized by Spooner et al. (2014). Endosperm balance number has not been determined for some potato species, and they are not included in the illustration.

The genetic basis of EBN is not known, although hypotheses for a mechanism have been proposed (Ehlenfeldt and Hanneman, 1988; Camadro and Masuelli, 1995). Given transcriptome data from inter- and intra-EBN crosses, Cornejo et al. (2012) hypothesized that microtubule assembly at the cell plate is disrupted during mitosis in young seeds. The identification of the genes responsible for the hybridization barriers imposed by EBN could lead to strategies to overcome those barriers.

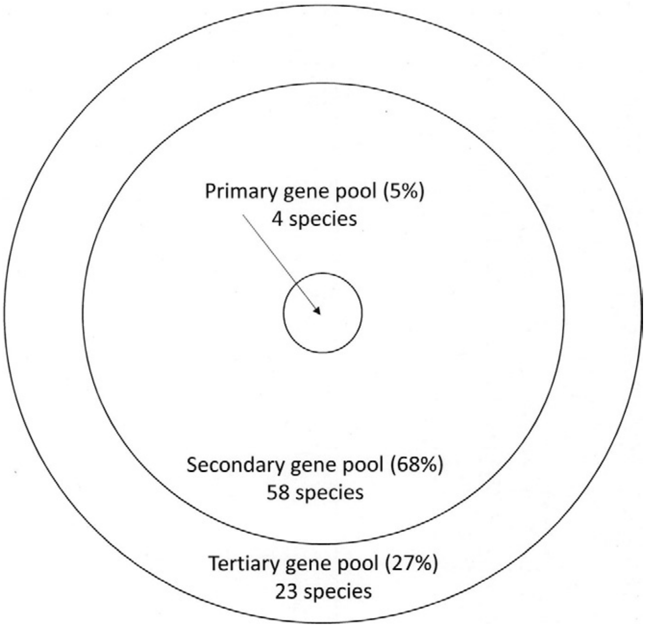

Fig. 1. Genepool composition of potato germplasm. The primary genepool is comprised of cultivated potato and is 4 endosperm balance number (EBN). The secondary genepool contains 2EBN and 4EBN species that can be crossed to cultivated potato. The tertiary genepool contains 1EBN species that are sexually incompatible with cultivated potato.

Ploidy Manipulations

Ploidy manipulations can be used to cross 2*x* with 4*x* individuals and bypass crossing barriers imposed by differences in EBN. An illustration of ploidy manipulations using somatic doubling to provide matching EBN values is provided in Fig. 2. Doubling the chromosome number doubles both ploidy and EBN. Thus, somatic doubling of 2*x*, 1EBN individuals results in 4*x*, 2EBN plants that can be crossed to other 2EBN plants. The pentaploid final product in Fig. 2 will hybridize with cultivated potato, producing generally fertile aneuploids. Several variations of this scheme have been published (Ehlenfeldt and Hanneman, 1984; Camadro and Espinillo, 1990; Adiwilaga and Brown, 1991; Carputo et al., 1997; Carputo and Barone, 2005; Caruso et al., 2008). Ploidy reduction can also be used to manipulate EBN.

As an alternative to somatic doubling, a 2*n* gamete also doubles ploidy and EBN. In this way, 2*n* gametes can substitute for somatic doubling, and diploid individuals that produce 2*n* gametes can be crossed with tetraploid potato. The 2*n* gametes result from the failure of meiosis to reduce chromosome number and are produced by plants homozygous recessive for naturally occurring meiotic mutations (Peloquin et al., 1999; Carputo et al., 2000). Mutant alleles for 2*n* gamete production are common in wild and cultivated potato (Camadro and Peloquin, 1980; Iwanaga and Peloquin, 1982). Meiotic mutants produce 2*n* eggs, (Stelly and Peloquin, 1986; Werner and Peloquin, 1990), whereas 2*n* pollen is produced by others (Quinn et al., 1974; Mok and Peloquin, 1975).

Dihaploids (2*x*, 2EBN) of cultivated potato are commonly used to access the germplasm of wild *Solanum*

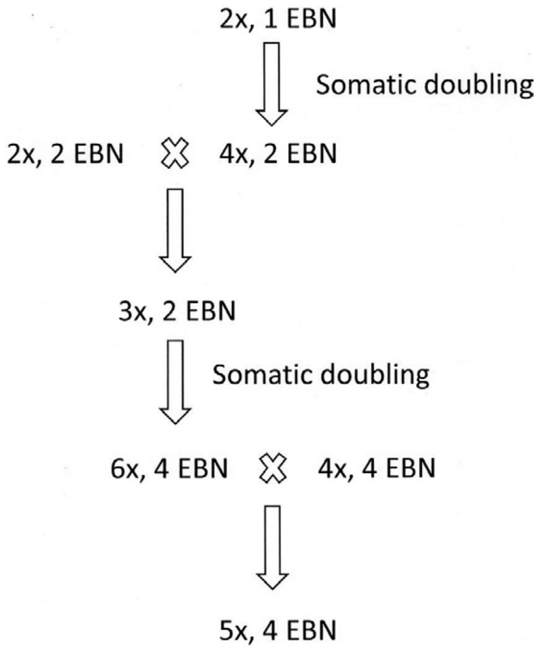

Fig. 2. Ploidy manipulation scheme to introgress tertiary (1 endosperm balance number [EBN]) germplasm into the cultivated germplasm pool using somatic doubling.

species (Jansky et al., 1990). Dihaploid induction through parthenogenesis creates 2*x*, 2EBN clones from 4*x*, 4EBN cultivars. These dihaploids readily cross with 2*x*, 2EBN species, resulting in fertile interspecific hybrids (Leue, 1983; Hermundstad and Peloquin, 1985). Nearly all wild *Solanum* species require a short critical photoperiod for tuberization; they produce stolons rather than tubers under the long day conditions of summer in North Temperate regions (Rudorf, 1958; Kittipadakul, 2010). Dihaploid wild species hybrids are often adapted to long photoperiods, producing high yields of tubers in the field (Hermundstad and Peloquin, 1985; Hermundstad and Peloquin, 1986; Yerk and Peloquin, 1989).

Dihaploid wild species hybrids can be used to evaluate wild species contributions to tuber characteristics and other valuable traits (Yerk and Peloquin, 1989; Jansky et al., 1990). The hybrids are highly variable for tuber traits but occasionally produce large and smooth tubers (Hermundstad and Peloquin, 1986; Yerk and Peloquin, 1989; Serquen and Peloquin, 1996; Santini et al., 2000). Variation for disease resistance has been observed in the hybrids on many occasions (Carputo et al., 1996; Jansky and Rouse, 2000, 2003; Oltmans and Novy, 2002; Weber and Jansky, 2012).

Hybridization barriers due to EBN differences can be overcome, in some cases, by combining ploidy manipulations with bridge crosses (Hermsen and Ramanna, 1973). The most commonly used bridge species is *S. verrucosum* Schltdl., a Mexican 2*x*, 2EBN species. Viable seeds from *S. verrucosum* × 2*x*, 1EBN crosses are produced at a low frequency. These inter-EBN hybrids can then be crossed to 2*x*, 2EBN species, including cultivated dihaploids. This strategy has been used to introgress germplasm into cultivated potato from several tertiary genepool species (Hermsen and Ramanna, 1976; Jansky and Hamernik, 2009; Yermishin et al., 2014)

Somatic Fusions

Somatic fusion followed by regeneration of plants in tissue culture can be used to combine sexually incompatible species. Helgeson et al. (1998) created somatic fusions between the 2*x*, 1EBN species *S. bulbocastanum* and 4*x*, 4EBN cultivated potato (Helgeson et al., 1998). These hybrids led to the identification of a major broad-spectrum late blight resistance gene (Song et al., 2003). *Solanum bulbocastanum* protoplast fusions have yielded resistance to nematodes (*Melodoidogyne chitwoodi* Golden et al.) (Austin et al., 1993), aphids (*Myzus persicae* Sulzer), and viruses (Davis et al., 2012). Somatic fusions have also been used to introgress genes from 2*x*, 1EBN species for *potato leaf roll virus* resistance (Austin et al., 1985), frost tolerance (Cardi et al., 1993), bacterial wilt [caused by *Ralstonia solanacearum* (Smith 1896)] (Laferriere et al., 1999), Colorado potato beetle (*Leptinotarsa decemlineata* Say) (Thieme et al., 2010), bacterial soft rot [caused by *Pectobacterium carotovorum* ssp. *atrosepticum* (van Hall 1902)] (Allefs et al., 1995; Tek et al., 2004), early blight [caused by *Alternaria solani* (E&M) Jones & Grout] (Tek et al., 2004; Meier et al., 2015), *potato virus Y* (Thieme et al., 2010; Tiwari et al., 2010), and common scab (caused by *Streptomyces scabiei* Lambert and Loria 1989) (Ahn and Park, 2013).

Somatic fusion has also been used to combine resistance genes from two sexually compatible parents. Dominant resistance to *potato virus X* was combined with a *potato virus Y* resistance gene to create hybrids with resistance to both viruses using fused diploids (Thach et al., 1993). Two dihaploids with different resistance to two pathotypes of potato cyst nematode [*Globodera rostochiensis* (Wollenweber) Mulvey & Stone] were fused, resulting in a high level of resistance to both pathotypes (Rasmussen et al., 1996). Fusion of a *S. brevidens* Phil. clone with a cultivated potato clone was used to develop germplasm resistant to *potato virus A*, *potato virus X*, *potato virus Y*, and *cucumber mosaic virus*, with multiple mechanisms of resistance (Valkonen and Rokka, 1998). Resistance to *potato leaf roll virus* from *S. verrucosum* was introduced through fusion with cultivated potato to combine resistance with adaptation and tuber yield from the cultivated donor (Carrasco et al., 2000). Finally, somatic fusions between potato and *S. chacoense* were used to introduce bacterial wilt resistance (Chen et al., 2013)

In some cases, resistance is reduced in somatic fusion hybrids despite the presence of the appropriate genes in fused germplasm (Simko et al., 2007). Cooper-Bland et al. (1994) produced fused hybrids of a potato cyst nematode-susceptible cultivated dihaploid with a resistant one, but the resulting plants tended toward susceptibility. Somatic hybrids created by Rasmussen et al. (1998) had lower levels of resistance to both tuber and foliar late blight than the resistant donors. Similarly, soft rot resistance present in fusions of *S. brevidens* with cultivated potato (McGrath et al., 2002) and fusions of *S. commersonii* Dunal ex Poir. with cultivated potato (Carputo et al., 2000) was reduced in backcross generations. Gavrilenko et al. (2003) reported that 6*x* somatic fusion hybrids with four doses of the resistant parent (*S. etuberosum* Lindl.) genome expressed extreme resistance to *potato virus Y*, while 6*x* hybrids with four doses of the susceptible, cultivated potato genome were susceptible. On the other hand, Zimnoch-Guzowska et al. (2003) reported that somatic hybrids from fusions of cultivated potato with *S. nigrum* L. were often more resistant than the resistant wild parent, perhaps due to complementation of resistance genes.

Sexual Polyploidization

Elite potato cultivars are tetraploid, and breeders typically increase ploidy to the tetraploid level after selecting superior dihaploid wild species hybrids. Somatic doubling will accomplish this task, but the products of doubling are often inferior to the original diploids (Rowe, 1967; Stupar et al., 2007; Aversano et al., 2015b). Instead, breeders have focused on sexual polyploidization, which often produces high-yielding progeny (Mendiburu and Peloquin, 1977a; Carputo and Barone, 2005; Ortiz et al., 2009). Schemes for unilateral and bilateral sexual polyploidization are illustrated in Fig. 3. A triploid block exists in potato (Marks, 1966), preventing the formation of triploid offspring from 4*x*, 4EBN × 2*x*, 2EBN crosses.

Examples of the transfer of disease resistance to tetraploids via sexual polyploidization are abundant. Unilateral sexual polyploidization (USP) has been used successfully to create hybrids with resistance to bacterial wilt (Watanabe et al., 1992), early blight (Herriott et al., 1990), common scab (Murphy et al., 1995), late blight (Watanabe et al., 1999), potato cyst nematode (De Maine et al., 1986; Ortiz et al., 1997), root knot nematode (*Meloidogyne* spp.) (Iwanaga et al., 1989; Watanabe et al., 1999), Verticillium wilt (caused by *Verticillium albo-atrum* Reinke & Berthier) (Frost et al., 2006), and bacterial soft rot (Carputo et al., 2000; Capo et al., 2002). Bilateral sexual polyploidization (BSP) provides an alternative to USP. Tetraploid progeny from BSP are highly heterotic and typically outyield their diploid full-sibs (Mendiburu and Peloquin, 1977b) and commercial cultivars (Werner and Peloquin, 1991). Tetraploids derived from BSP were created in crosses between diploid landrace germplasm and dihaploid wild species hybrids selected for processing quality (Hayes and Thill, 2002). The successful cultivar Yukon Gold is a product of USP. The female parent was a tetraploid cultivar, and the male parent was a hybrid between diploid landrace potato (Phureja) and a cultivated dihaploid (Johnston and Rowberry, 1981).

HISTORY OF POTATO IMPROVEMENT USING WILD SPECIES RELATIVES

As mentioned above, wild species relatives of potato encompass a wide range of phenotypic and genetic diversity. Because these species exist in diverse habitats, genes contributing to abiotic and biotic stress resistance are likely to be present. These genes can be introduced into cultivated potato using the methods described above. Decades of hybridization efforts were successful in introgressing wild germplasm into the cultivated potato genepool. Most of those efforts did not lead to documented improvements in new cultivars. In this section, we highlight instances where this approach was successful.

The first attempts to use wild species collections began between 1824 and 1909 with hybridization of *S. tuberosum* cultivars with *S. commersonii* and *S. maglia* Schltdl. (Hawkes, 1958). These initial attempts did not succeed, most likely because the collected clones were highly sterile triploids. In the early 20th century, resistance to the late blight pathogen *Phytophthora infestans* became a primary breeding goal. Salaman (1910) identified late blight resistance in hybrids of potato with *S. demissum* and *S. edinense* Berthault, but incorporation of resistance into a cultivar did not occur until 1951, with the introduction of Pentland Ace, which contains the *R1* gene. The cultivar Pentland Dell, which contains the *R1*, *R2*, and *R3* resistance genes from *S. demissum*, was released in 1963. Despite the presence of multiple *R* genes, new pathogen strains had overcome resistance by 1967. Late blight resistant germplasm has been released recently in the United States (Douches et al., 2001b; Novy et al., 2006; Douches et al., 2010; Novy et al., 2012). However, as is typical for many modern cultivars, the original wild species source of resistance is not known, primarily because pedigree records dating to the original introgression event are lacking.

Broad-spectrum resistance to late blight has been identified in several wild species relatives and is attributed to major genes. A decade-long project on durable resistance in potato against *Phytophthora* has resulted in the introduction of several major resistance genes into potato using cisgenesis techniques (Haverkort et al., 2016). *RB* (also known as *Rpi-blb1*) is a dominant resistance gene that provides protection against most strains of late blight (Song et al., 2003; van der Vossen et al., 2003). *Rpi-blb2*, also from *S. bulbocastanum*, confers resistance by a different mechanism (van der Vossen et al., 2005). The *Rpi-vnt1.1* gene from *S. venturii* Hawkes & Hjert. (Foster et al., 2009) was combined with *RB* and *Rpi-blb2* to form a three-*R* gene construct that is currently being used to develop germplasm for distribution in Uganda and Kenya through the 2Blades Foundation (2Blades Foundation, 2016). The transfer of late blight resistance genes into modern cultivars using biotechnology is currently the focus of several projects worldwide, including a USAID project to

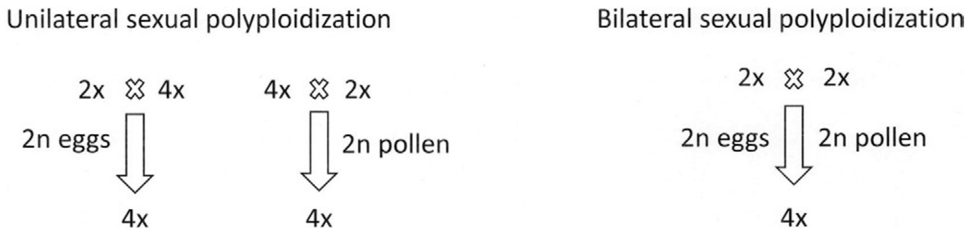

Fig. 3. Sexual polyploidization via 2*n* gamete production. Unilateral sexual polyploidization occurs when a diploid, 2*n* gamete-producing plant is crossed with a tetraploid plant to produce tetraploid offspring. Bilateral sexual polyploidization happens when 2*n* gametes from two diploid parents unite to produce tetraploid offspring.

develop resistant germplasm for Indonesia and Bangladesh (USAID, 2016). Commercially available late blight-resistant varieties containing the *Rpi-vnt1* gene from *S. venturii* will be available in the United States through Simplot Plant Sciences (http://www.simplot.com/plant_sciences/) beginning in 2018.

Breeding for resistance to *potato virus Y* began in many European breeding programs in the mid-1900s. A source of resistance, conferred by the Ry_{sto} gene from *S. stoloniferum* Schltdl. & Bouche, was originally introgressed into the widely used breeding clone MPI 61.303/34. This gene has proven quite durable and is used in breeding programs throughout the world (Ross, 1986; Barker and Dale 2006). For example, this gene provides resistance in the cultivars Bzura, Forelle, Pirola, and White Lady (Ortega and Lopez-Vizcon, 2012). A second gene for resistance to *potato virus Y* (Ry_{adg}) is derived from *S. tuberosum* Andigenum Group, the Andean landrace of cultivated tetraploid potato (Hämäläinen et al., 1997). It is found in the cultivar Tacna (Ortega and Lopez-Vizcon, 2012). An additional source of *potato virus Y* resistance from *S. chacoense* (Ry_{chc}) is found in the Japanese cultivars Konafubuki and Sakurafubuki (Hosaka et al., 2001).

Breeding for chip-processing potatoes began in the 1940s, and wild species played a significant role in improving product quality (Hirsch et al., 2013). The chipping potato cultivar Lenape, introduced in 1968, has *S. chacoense* as a grandparent. The *S. chacoense* progenitor of Lenape is thought to have contributed to increased dry matter content of tubers and decreased reducing sugar accumulation in storage (Love et al., 1998). Lenape is in the pedigree of many other successful chipping potatoes. Another wild species, *S. tarijense* Hawkes, has made a major contribution to the processing quality of chipping potatoes. The breeding clones S438 and S440 are full-sib products of USP, in which the female parent was a tetraploid *S. tuberosum* clone and the male parent was a diploid hybrid between a *S. tuberosum* dihaploid and *S. tarijense.* These clones are parents of the chip-processing cultivars Accumulator, Kalkaska, Lelah, Nicolet, Tundra, and White Pearl; S440 is the grandparent of the chip-processing cultivar Pinnacle. The diploid clone AH66-4, a hybrid between a *S. tuberosum* dihaploid and *S. raphanifolium*, is a parent of the fry-processing cultivar Dakota Russet. As is often the case, though, the wild progenitor individuals that contributed to these cultivars have been lost.

BARRIERS TO THE USE OF WILD RELATIVES

As discussed above, wild potato relatives have made notable contributions to cultivated potato. Consequently, potato is considered to be a crop for which wild relatives have been important for genetic improvement (Maxted et al., 2012). Overall, however, the use of germplasm from wild species relatives and its incorporation into new varieties has been extremely limited. To our knowledge, no cultivar carries germplasm from a somatic fusion, and only one major cultivar (Yukon Gold) is the product of sexual polyploidization. The genetic base of potato is still primarily *S. tuberosum*, despite attempts by many programs over several decades to introgress wild species germplasm into cultivars (Love, 1999; Bradshaw, 2009). Indeed, the potential value of many wild species has not been evaluated (Castañeda-Álvarez et al., 2015). Surveys of North American and European cultivars reveal 16 wild species in their pedigrees (Ross, 1986; Plaisted and Hoopes, 1989; Love, 1999; Bradshaw, 2009). In other words, 91 wild potato species have yet to contribute to cultivar development. What are the barriers that have prevented the successful use of wild species germplasm on a larger scale? Below we describe some of the biological barriers that may constitute a partial answer to this question. We will argue, however, that the problem is much deeper than biological limitations and has its root in the way we store and distribute germplasm and the data associated with that germplasm.

Biological Barriers Limiting Use of Wild Species Germplasm

The major biological barriers to the introduction of wild species traits are genetically based (Hanneman, 1999; Jackson and Hanneman., 1999; Jansky, 2006). Prezygotic barriers are common in potato, mostly in the form of stylar interactions. In some cross combinations, pollen does penetrate the style to reach the ovary (Pandey, 1962; Grun and Aubertin, 1966; Ehlenfeldt and Hanneman, 1984; Fritz and Hanneman, 1989; Novy and Hanneman, Jr., 1991; Hanneman, 1999; Jackson and Hanneman, 1999; Jansky, 2006; Weber et al., 2012). This type of barrier is typically overcome by carrying out reciprocal crosses.

Many wild potato relatives readily hybridize with cultivated potato to produce fertile hybrids (Peloquin et al., 1989, 1991; Yerk, 1989; Jansky et al., 1990). Thus, it has been generally believed that extensive genome differentiation between wild species and cultivated potato is uncommon. Ongoing research in which the genomes of multiple wild species relatives of potato are being sequenced will shed further light on the extent that genome organization or size varies among species. For example, a comparison between the genome of the 2*x*, 1EBN species *S. commersonii* and that of cultivated potato revealed that they are similar in size but exhibit sequence variation mainly in intergenic regions (Aversano et al., 2015a).

Mentor pollination and embryo rescue can be used to overcome hybridization barriers when both endosperm failure and stylar interactions are in place. Mentor pollination reduces premature fruit drop by applying pollen from a compatible species (mentor pollen) a day or two after pollinating with an incompatible species (Singsit and Hanneman, 1990). The mentor pollen fertilizes some ovules to stimulate berry development. This allows a few of the slower-growing pollen tubes from the incompatible parent to reach the ovules and carry out fertilization. The mentor pollen typically carries a dominant seed spot marker so its offspring can be identified and discarded. However, the resulting hybrids may fail to develop viable seeds due to endosperm failure. The young embryo may be rescued in tissue culture.

Unilateral incompatibility occurs when a self-incompatible species is crossed as a female to a self-compatible species. Pollen tubes fail to penetrate stylar tissue in self-incompatible × self-compatible crosses (Grun and Aubertin, 1966; Abdalla and Hermsen, 1972; Eijlander et al., 2000; Kuhl et al., 2002; Dinu et al., 2005). Although most 2*x*, 2EBN species are self-incompatible, an exception is *S. verrucosum*. Therefore, unilateral incompatibility prevents *S. verrucosum* from being used as a male in crosses to self-incompatible wild relatives.

Male sterility in interspecific hybrids is often observed (Jackson and Hanneman, 1999). Hawkes (1990) reported that sib matings of interspecific hybrids can result in unthrifty and/or sterile plants. He suggested that hybrid breakdown occurs as adaptive gene complexes that had evolved in each of the parents are broken up during meiosis. Hybrid breakdown has been reported after self-pollination or intercrossing of interspecific hybrids in other crops, as well (Li et al., 1997, 2015; Johansen-Morris and Latta, 2006; Ellison and Burton, 2008; Matsubara et al., 2015; Dai et al., 2016).

Cytoplasmic-genetic male sterility has also been reported in interspecific hybrids (Dionne, 1961; Grun et al., 1962; Grun and Aubertin, 1966; Grun, 1970). It has been hypothesized that cytoplasmic genetic factors in the female parent interact with dominant nuclear genes from the male parent, resulting in male sterility. Levels of cytoplasmic genetic male sterility are frequently variable, presumably due to genetic and environmental influences (Hanneman and Peloquin, 1981). Consequently, this type of barrier can be overcome by carrying out reciprocal crosses or by selecting parents that do not contain sensitive cytoplasm or nuclear sterility genes. For example, Iwanaga et al. (1991) identified a dominant gene (*Rt*) that restores fertility to plants with the male sterility gene (*Ms*) in the presence of sensitive cytoplasm. A male fertility restorer gene has also been identified in a cultivated dihaploid × *S. chacoense* hybrid (Tucci et al., 1996).

Barriers Attributable to Insufficient Knowledge of Wild Species Germplasm

As mentioned above, most wild relatives are infrequent components of cultivar pedigrees. It is unlikely that this situation will change in the absence of compelling information on potential benefits of using exotic potato germplasm.

Populations of wild potato relatives have been scored for the presence or absence of many traits. In some cases, such as isoenzyme banding patterns or genomic marker data, these characterizations are extensions of traditional taxonomic descriptions. Phenotypic data, often collected from a subset of species and accessions, include disease and pest resistance and biochemical analyses. In total, however, very little information with relevance to potato improvement is available for the accessions in the genebanks. This reflects, in part, the original purpose of genebanks, which was to conserve samples of natural diversity. Notably, the value of wild species for improvement of tuber traits is difficult to evaluate, as they typically produce very small tubers.

A series of studies has been performed to determine whether taxonomic or biogeographic information can be used to identify wild species likely to be enriched for disease or pest resistance traits (Jansky et al., 2006, 2008, 2009; Spooner et al., 2009; Cai et al., 2011; Chung et al., 2011; Khiutti et al., 2015). These studies included an analysis of resistance to *Sclerotinia sclerotiorum* (white mold), *Alternaria solani* (early blight), *potato virus Y*, Colorado potato beetle, *Pectobacterium carotovorum* (soft rot), and late blight. A major goal of these studies was to provide guidance to breeders regarding choices of wild species to use in introgression efforts. However, relationships between resistance phenotype and both taxonomy and geographic distribution were generally poor. Variation among accessions within a species, and even plants within an accession, was often as large as variation among species. Similarly, no consistent relationship between geographic distance and marker polymorphisms were detected in a study of 314 accessions of *S. acaule* (McGregor et al., 2002).

Despite the lack of predictive power in these experiments to identify correlations between taxonomy and disease resistance, the screens were successful in identifying species enriched in disease resistance traits, as well as species that appear to be broadly susceptible to disease (Table 1). The species listed in Table 1 were ranked within each experiment, and species ranking was averaged across all experiments. This number was multiplied by 100 to give an overall rank for disease resistance. For example, *S. bulbocastanum*, on average, ranked within the top 21% of the species used in these studies. On the other hand, *S. moscopanum* Hawkes, with a score of 91, ranked in the bottom 9% of all species across experiments. Advances in genome sequencing should allow us to probe certain species, such as *S. bulbocastanum* and *S. moscopanum,* and identify genomic regions, such as the presence or absence of novel *R* gene clusters, that could be associated with disease resistance.

Barriers Resulting from the Breeding System

As mentioned above, hybrids between diploid cultivated and wild potatoes can produce tubers that are similar to advanced material in breeding programs (Rudorf, 1958;

Table 1. Wild species relatives scored for disease and pest resistance. Species were ranked according to the presence or absence of resistance in seven studies. A low score indicates resistance to multiple biotic stresses (see text for details).

Species	Score
S. bulbocastanum	21
S. etuberosum	34
S. tarijense	41
S. paucijugum	41
S. pinnatisectum	42
S. chacoense	42
S. sparsipilum	44
S. neorossii	45
S. schenckii	45
S. commersonii	46
S. demissum	47
S. albornozii	48
S. polyadenium	48
S. albicans	49
S. immite	49
S. andreanum	50
S. cardiophyllum	50
S. chomatophilum	50
S. microdontum	50
S. acaule	51
S. palustre	51
S. brevicaule	52
S. berthaultii	55
S. verrucosum	56
S. hjertingii	57
S. bukasovii	57
S. jamesii	59
S. boliviense	59
S. raphanifolium	60
S. ehrenbergii	60
S. iopetalum	61
S. megistacrolobum	63
S. violaceimarmoratum	65
S. stenophyllidum	65
S. kurtzianum	65
S. lesteri	67
S. stoloniferum	73
S. candolleanum	73
S. tuquerrense	79
S. infundibuliforme	81
S. colombianum	83
S. agrimonifolium	84
S. moscopanum	91

Jansky et al., 1990; Jansky and Peloquin, 2005; Ortiz et al., 2009). Why, then, aren't these hybrids more prominent in the pedigrees of successful cultivars? The potato breeding system can provide one explanation. When a wild species or a dihaploid wild species hybrid is crossed to a cultivated parent in a breeding program, segregation is observed in the offspring, as expected. Selection in this segregating generation is based on plant phenotype and, particularly, tuber appearance. Selection pressure is severe, with 90% or more of individuals typically discarded (Tarn et al., 1992). Among those discarded are plants that express wild species traits, such as late maturity, small tuber size, long stolons, and excessive vine vigor. The wild species germplasm was likely brought into the breeding program as the source of a specific trait, such as disease resistance. However, unless selection for that trait occurs in the first generation, which is rare, most clones that carry valuable wild species introgressions are discarded.

A solution to this problem is to carry out backcrosses so the final product is a cultivated potato clone carrying the trait of interest on chromosomal fragment(s) inherited from a wild species. The removal of unfavorable wild species traits through selective breeding typically requires at least three backcrosses to the cultivated parent (Black, 1949; Rudorf, 1958; Lauer, 1959). This process is time- and resource-intensive, since clones must be screened for both the trait being introgressed and important agronomic traits. Introgressed chromosomal regions can be large, even after several generations of backcrossing (Young and Tanksley, 1989; Hermsen, 1994). Linkage between desirable and undesirable genes from the wild species can slow progress (Swiezynski and Zimnoch-Guzowska, 1996). On the horizon, we see the potential to select for specific gene or haplotype combinations that are associated with the desired phenotypes. Thus, although the process of removing multiple negative alleles has been inefficient and costly, new genomics tools and computational methods based on data generated from high-throughput nucleotide sequencing have the potential to make the introgression of wild species genes much more efficient. DNA markers will allow scientists to follow chromosomal regions in interspecific hybrids and select plants carrying desirable wild species genes.

Are We Getting Better at Using Wild Potato Species in Light of New Tools?

A potato wild species accession is a population that has value as a genetics resource for studies of gene variation among individuals within and across accessions. As a breeding resource, though, the collection of diverse genotypes that we call an accession has little value per se. It is not stable because it changes over time and space—two seed packets from the same accession are not identical. Collections of wild species are reservoirs of allelic diversity, but that diversity is unordered, largely unexplored, and not linked to individual genotypes or phenotypes. To use wild species more effectively for potato improvement, and to make use of the computational and genomics tools that are revolutionizing breeding and genetics, it will be important to move toward collections of individuals that are propagated clonally and are associated with phenotypic and genotypic data that contribute to their utility. Nucleic acid sequences are useful to plant breeders, but entire genotypes are required to provide the necessary context for the expression of heritable traits.

AN EVOLVING ROLE FOR POTATO GENEBANKS

The mission of genebanks has always included the preservation of genetic resources and the distribution of these resources for use by scientists. These overarching goals reflect social concerns about the potential loss of species, practical concerns related to the difficulty of accessing germplasm directly from distant locations, and the well-founded belief that wild species germplasm can contribute substantially to the productivity and quality of cultivated plants and animals. How to best accomplish these goals is currently a topic of intense discussion (del Rio et al., 1997a, 1997b; Hijmans et al., 2000; Bamberg and del Rio, 2003; Ramírez-Villegas et al., 2010; McCouch et al., 2012; Jansky et al., 2013, 2015). For potato, it is clear that the current model in which wild species germplasm is distributed as seeds of individual accessions does not promote the facile use of that germplasm for 21st century breeding efforts.

Although genebanks will continue to play roles in resource preservation and utilization, we expect that new technologies will allow them to do both more effectively. Accessions of the same species may vary widely because they were collected from different habitats over a wide geographic range in which natural selection pressures vary. For example, *S. acaule* populations have been observed across a span of 3253 km (Hijmans et al., 2002). *Solanum chacoense* is found in five South American countries, and *S. acaule* and *S. commersonii* are found in four countries (Hijmans and Spooner, 2001). In addition, variability among individuals within an accession is common, and some populations have undergone interspecific hybridization (Camadro, 2012). As discussed above, the large amount of inter- and intra-accession variability observed in a series of predictive studies supports the contention that variation within a species may be as wide as that among species. Consequently, when breeders use wild species, they carry out fine-screening studies to identify wild species clones of value to their programs (Bamberg et al., 1996; Douches et al., 2001a; Ali and Jansky, 2015).

Large-scale sequencing efforts will be necessary to determine the genetic structure of wild potato species. Each accession has its own history with regard to effective population size in the wild, exposure to stresses before collection, opportunities for introgression from other wild species before collection, and sample size during collection. Consequently, the genetic makeup of each accession is unique and generalizations cannot be made regarding sampling strategies for genotyping accessions. In a large study, genotypic variation among plants was found to vary from accession to accession (van Treuren et al., 2004). In some accessions, most plants were genetically similar to each other; in others, distinct genotypes were identified. In another study with the same set of accessions, genetic differentiation was detected among samples from different collection areas, but more than half of the genetic variation was distributed within collection areas (McGregor et al., 2002). As genotyping efforts such as these get underway, a knowledge base will be created from which to make decisions about how to efficiently characterize accessions, identify redundancies, and predict the likelihood that collections of accessions adequately reflect the diversity present in wild species. McCouch et al. (2012) envision a time when genebanks are transformed from warehouses where seeds are maintained into cutting edge research centers that actively investigate the genetic potential of their holdings. A critical component of this model is the concept that an accession is a set of allele frequencies, rather than a collection of plants (Camadro, 2012; McCouch et al., 2012). The accession is thus an entity that can be maintained over time and space, even though the plants within it are ephemeral.

We believe that it is time to develop new strategies that allow us to better use germplasm collections for potato improvement. One path toward this end is to increase the number of clonally maintained genotypes in genebanks and to link each individual clone to genotypic and phenotypic data. Potato is uniquely suited for this because methods for maintaining potato clones through vegetative propagation are routine at existing potato genebanks. In the past, clonal maintenance has been restricted largely to cultivars and landraces, but there are substantial upsides to expanding this approach to individuals from wild species and to unique genotypes that are not representative of a single species but have value as a genetic resource. One example of these unique genotypes could be products of germplasm enhancement efforts in which wild germplasm has been introgressed into cultivated potato. A component of this vision could be an expansion of the core collection concept. Rather than being restricted to a subset of accessions from each species, a genotypic diversity collection would include multiple genetically diverse individuals from each species. These would be genotyped and would become a community resource that is readily screened for allelic variants, genome deletions and duplications, and copy number variants. Most importantly, phenotypic data generated from the use of these lines can be captured and linked to each genotype. In this way, the value of the collection increases without increasing its size.

Filling the Information Gap with Accessible Data

As data on potato genetic resources become available through advances in genotyping and phenotyping technologies, it will be critical to link these data to individuals in potato genebanks. Making this information accessible to a range of users will be aided by the implementation of standardized descriptors, much in the same way that taxonomic information depends on the consistent use of terminology. Toward this end, a potato ontology is being developed (Shrestha et al., 2010) and data systems aimed at handling largescale datasets are also being developed (Guberman et al., 2011). A database relevant to these discussions 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.

Trait Discovery in Light of New Molecular and Bioinformatics Tools

With the advent of the genomics era, new approaches for germplasm use are emerging. For decades, efforts to characterize wild relatives of potato have focused on the screening of germplasm collections for traits of interest to breeders. However, this strategy focuses on phenotypes rather than genes, and on populations rather than individuals. This approach likely underestimates the genetic potential of wild germplasm, as valuable alleles may be hidden or linked to undesirable genes. Furthermore, individuals containing valuable traits are usually not maintained and are lost. When characterizing germplasm, it will be important to develop alternative methods that capture both the phenotype and the genotype.

Near-isogenic lines carrying wild species chromosomal regions in a domesticated background have been used to identify quantitative trait loci for improvement of yield, soluble solids content, and fruit color in tomato (*S. lycopersicum* L.) (Tanksley and McCouch, 1997). These lines outperform the original elite cultivars into which wild germplasm was introgressed. Tanksley and McCouch (1997) provide a similar case study in rice (*Oryza sativa* L.), where alleles for high yield were identified in a wild relative. In potato, we are developing inbred lines of cultivated diploids using germplasm carrying a dominant inhibitor of the self-incompatibility system. This genetic resource could be used to create introgression lines for evaluating wild germplasm. Obviously, it is not practical to generate introgression lines for all potato accessions in genebanks and it will be a challenge to identify accessions for the development of introgression lines. One strategy is to generate DNA profiles and choose accessions that differ the most from cultivated potato (Tanksley and McCouch, 1997). These accessions may carry a large number of novel alleles, some of which may have a large impact on traits of interest to breeders. As genotypes of accessions are evaluated, new accessions may be chosen for clonal maintenance on the basis of their dissimilarity to those that were already sampled.

As mentioned above, it is often difficult to identify the original sources of disease resistance in many modern cultivars due to a lack of historical information describing the germplasm used in breeding. In some cases, however, the original genes conferring the selected trait can be identified using newly developed genetic and genomic tools. For example, a recently developed approach to sequence all known major *R* genes in potato has been used to identify the genes responsible for late bight resistance (Van Weymers et al., 2016). This “diagnostic *R* gene enhancement and sequencing” method (dRenSeq) allows for the purification of genomic sequences with homology to known *R* genes, followed by high-throughput sequencing to identify functional genes. This will be a particularly useful tool to identify *R* genes toward major pathogens in germplasm with unknown or poorly documented pedigrees. The integration of this type of genomic information into the germplasm description in genebanks will be critical for the efficient use of wild germplasm in the genomics era.

Engaging the Potato Community in Genotyping and Data Collection

Potato genebanks store, maintain, and distribute germplasm. The value of that germplasm for breeding depends on the genetic, genomic, and phenotypic data associated with it. A single seed from a wild species accession has virtually no value until it is characterized. Much more valuable is an individual from that same accession that has been found to produce hybrid parents that produce progeny of high value in a breeding program. If genomic sequence data and phenotype data are also available, that individual’s worth increases further. For years, the Maize Genetics Cooperative Stock Center (http://maizecoop.cropsci.uiuc.edu/), the *Arabidopsis* Biological Resource Center (https://abrc.osu.edu/), and the Tomato Genetics Cooperative (http://tgc.ifas.ufl.edu/) have taken in, preserved, and distributed germplasm stocks. Data related to these lines are maintained in the Maize Genetics and Genomics Database (https://www.maizegdb.org/), The *Arabidopsis* Information Resource (https://www.Arabidopsis.org/), and the Tomato Genetics Resource Center (http://tgrc.ucdavis.edu/). These stocks have been contributed by researchers and industry and are used by the same clientele. Expanding potato collections to include a greater number of individual clones, especially well-characterized clones used in breeding programs or for published research, would greatly increase the utility of the collections. It is likely that, as improvements in germplasm or technologies are made, some clones donated by users will lose their value. Maintenance of clones could cease once orders for that clone fall below a minimum threshold.

CONCLUSIONS AND A CALL TO ACTION

The potato germplasm resource is abundant and highly diverse, largely due to the wide array of microenvironments in which wild potato relatives have evolved. The proportion of wild genetic diversity in modern potato cultivars is small, likely because of genetic bottlenecks that occurred during domestication, transport to Europe, photoperiod adaptation, and widespread losses to viruses and the late blight epidemics of the mid-19th century. Breeders have returned to wild relatives in genebanks, but they have tapped into only a tiny portion of the genetic variability present in potato wild relatives. The more efficient use of wild potato relatives will require a better understanding of the genetic diversity within each species. We envision a two-tiered system using modern high-throughput screening and computational tools. At the first level, the allelic composition of accessions would be characterized to identify similarities and differences within and among accessions, among species, and in comparison with potato cultivars. This is essentially a horizontal analysis of genetic diversity, with genes identified irrespective of their association with other genes or phenotypes. This analysis will aid in the identification of sources of genes for breeding and introgression studies. The second tier is a vertical analysis, considering the entire genotype of each individual and its association with phenotype. Linkages between genomic data and phenotype must be made at the level of the individual. Thus, collections of individuals from wild species will need to be maintained clonally. These collections should be augmented with clonally propagated breeding lines that carry wild species introgressions and have high value for research and breeding. In many cases, these unique genotypes will be identified and contributed by the scientific community. Introgression lines should be created to identify novel alleles in wild relatives that make a positive contribution in an adapted genetic background. In order for this system to function effectively, it will be necessary to develop an information infrastructure that expands current passport data and includes multiple descriptors of genotype and phenotype. Such a system will need to be adaptable to changing technology, as we envision a need to capture data from next-generation sequencing of DNA, RNA, microRNAs, and small interfering RNAs, as well as from DNA methylation studies, metabolomics studies, spectral and image analyses, and other phenotypic data. The encapsulation of this information will allow scientists to efficiently identify and incorporate traits related to the desired phenotype. This plan will require a large and coordinated international effort, although incremental progress will pay substantial benefits in the near term. However, there is a pressing need to begin this effort soon. Climate change models predict that global potato production will decrease by 18% by the middle of this century (Hijmans, 2003). The single most effective way to confront this predicted loss of productivity is through the development of improved genotypes of cultivated potato. Genes from wild potato relatives will be critical for this effort.

Conflict of Interest

The authors declare there to be no conflict of interest.

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