Review

Diversity of potato genetic resources

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A considerable number of highly diverse species exist in genus *Solanum*. Because they can adapt to a broad range of habitats, potato wild relatives are promising sources of desirable agricultural traits. Potato taxonomy is quite complex because of introgression, interspecific hybridization, auto- and allopolyploidy, sexual compatibility among many species, a mixture of sexual and asexual reproduction, possible recent species divergence, phenotypic plasticity, and the consequent high morphological similarity among species. Recent researchers using molecular tools have contributed to the identification of genes controlling several types of resistance as well as to the revision of taxonomical relationships among potato species. Historically, primitive forms of cultivated potato and its wild relatives have been used in breeding programs and there is still an enormous and unimaginable potential for discovering desirable characteristics, particularly in wild species Different methods have been developed to incorporate useful alleles from these wild species into the improved cultivars. Potato germplasm comprising of useful alleles for different breeding objectives is preserved in various gene banks worldwide. These materials, with their invaluable information, are accessible for research and breeding purposes. Precise identification of species base on the new taxonomy is essential for effective use of the germplasm collection.

Key Words: *Solanum* sp., genetic resources, potato wild species, breeding, taxonomy.

Taxonomic description of cultivated potato and its wild relatives: a complex task

The family *Solanaceae* is comprised of 3,000–4,000 species placed within about 90 genera. Potato (*Solanum tuberosum* L.), tomato (*S. lycopersicum* L.), aubergine or eggplant (*S. melongena* L.), chili pepper (*Capsicum* sp.), and husk tomato (*Physalis* sp.) are the well-known and most cultivated crops in the *Solanaceae* family. Besides, a number of species are locally cultivated for their edible fruits, tubers, or leaves, as well as for horticultural purposes.

Cultivated potato and its wild relatives belong to the genus *Solanum*, the largest genus with 1,500–2,000 species (PBI Solanum Project 2014). Within the genus *Solanum*, over a thousand species have been recognized (Burton 1989). Generally, tuber-bearing *Solanum* species are grouped in the *Petota* section. This section is subdivided into two subsections, *Potatoe* and *Estolonifera* (Hawkes 1990). The subsection *Potatoe* contains all tuber-bearing potatoes, including common potato (*S. tuberosum*, belonging to series *Tuberosa*). Two non-tuber-bearing series (*Etuberosa* and *Juglandifolia*) are placed in subsection *Estolonifera*. However, a number of molecular studies suggest that the series *Etuberosa* and *Juglandifolia* do not belong to the *Petota* section (Bohs and Olmstead 1997, Olmstead and Palmer 1997, Peralta and Spooner 2001, Spooner *et al.* 1993).

Potato has an extremely large secondary gene pool consisting of related wild species. Therefore, its taxonomy has been a subject of study for many years. Consistency of names assigned to species and higher ranks, identification of identical materials, and the classification of materials reflecting genetic similarities are major objectives in potato systematics (Spooner and Bamberg 1994). Given the importance of taxonomic consistency, different taxonomic classifications of wild and cultivated potatoes have been presented by several authors (Huamán and Spooner 2002, Ovchinnikova *et al.* 2011, Spooner and Hijmans 2001). This complication of potato taxonomy at the species level may have arisen by introgression, interspecific hybridization, auto- or allopolyploidy, sexual compatibility among many species, a mixture of sexual and asexual reproduction, recent species divergence, phenotypic plasticity and consequently high morphological similarity among species (Spooner 2009, Spooner and Bamberg 1994). Currently, 228 species are recognized by Hawkes (1990), 196 species by Spooner and Hijmans (2001), and approximately 110 species by Spooner (2009). Many authors have attempted to clarify the taxonomic relationships among species belonging to the potato gene pool [Bryan *et al.* 1999 (cpSSR),

Hosaka *et al.* 1984 (cpRFLP), Kardolus *et al.* 1998 (AFLP), Spooner and Castillo 1997 (cpRFLP), Volkov *et al.* 2003 (cpSSR)]. Various researches in recent years, using large number of samples covering a wide range of species and implementations of advanced molecular tools, have suggested reconsideration of taxonomic classifications (Jacobs *et al.* 2008, 2011, Spooner 2009). However, it seems that, as yet, people researching on potatoes worldwide have not reached on an agreement.

Cultivated potato species

Cultivated potatoes can be classified as landraces, native varieties still grown in South America today, or improved varieties, grown worldwide. Potato landraces are highly diverse with a variety of tuber shapes and skin and flesh colors (**Fig. 1**). They are grown in the upland Andes from western Venezuela south to northern Argentina and in the lowlands of south-central Chile, where they are concentrated in the Chonos and Guaitecas Archipelagos (Contreras *et al.* 1993) and are adapted to middle to high elevations (3000–4000 m altitude). Cultivated potato species have a base chromosome number of $n = 12$ and may be diploid ($2n = 2x = 24$), triploid ($2n = 3x = 36$), tetraploid ($2n = 4x = 48$), or pentaploid ($2n = 5x = 60$).

Fig. 1. Potato landraces with a variety of tuber shapes and skin colors (Copyright: International Potato Canter 2014).

The taxonomic treatment of cultivated potato is still under discussion. Bukasov (1971) and Lechnovich (1971) [both cited by Huamán and Spooner (2002)] recognized 21 species. Hawkes (1990) stated that there are seven cultivated potato species, whereas Ochoa (1999) identified only nine species and 141 infraspecific taxa. The most recent suggestion was made by Spooner *et al.* (2007). They genotyped 742 landraces of all cultivated species and wild progenitors with SSR and chloroplast markers, and suggested reclassification of cultivated potatoes into the following four species: (i) *S. tuberosum*, with two cultivar groups (the Andigenum group of upland Andean genotypes containing diploids, triploids, and tetraploids and the Chilotanum group of lowland tetraploid Chilean landraces); (ii) *S. ajanhuiri* (diploid); (iii) *S. juzepczukii* (triploid); and (iv) *S. curtilobum* (pentaploid) (Spooner *et al.* 2007). However, a practical concern is that many Web-searchable databases of world potato germplasm collections, including the International Potato Center, Peru; the Leibniz Institute of Plant Genetics and Crop Plant Research, Germany; the Centre for Genetic Resources, The Netherlands; the Germplasm Resources Information Network, USA, continue to use the classifications and descriptions of Hawkes (1990) for their databases. Recently, the germplasm collection of the Vavilov Institute of Plant Industry, Russia was assessed for their collection based on modern taxonomy, including morphological characters, chromosome number, and SSR genotyping (Gavrilenko *et al.* 2010). Updating taxonomic classification and reevaluation of the materials stored in the gene bank is essential for managers as well as the depositors of the gene bank to assure consistency of their genetic materials.

Table 1 shows a synopsis of taxonomic treatments of the cultivated potatoes, describing the classifications provided by Hawkes (1990), Ochoa (1990, 1999), and Spooner *et al.* (2007). Here, with the aim of practical utility, species descriptions by Hawkes (1990) with their relationship to the most recently proposed classifications by Spooner *et al.* (2007) are described below.

S. ajanhuiri Juz. and Bukasov (Hawkes 1990, Spooner *et al.* 2007)

This diploid species was formed by natural hybridization

Table 1. Taxonomic treatments of cultivated potatoes by Hawkes (1990), Ochoa (1990, 1999) and Spooner *et al.* (2007)

Hawkes (1990)	Ochoa (1990, 1999)	Spooner *et al.* (2007)
Solanum ajanhuiri	*S. ×ajanhuiri*	*S. ajanhuiri*
S. curtilobum	*S. ×curtilobum*	*S. curtilobum*
S. juzpeczukii	*S. ×juzepczukii*	*S. juzepczukii*
S. tuberosum	*S. tuberosum*	*S. tuberosum*
subsp. *andigena* Hawkes	subsp. *andigena* Hawkes	Andigenum Group
subsp. *tuberosum*	subsp. *tuberosum*	Chilotanum Group
	S. hygrothermicum	
S. chaucha	*S. ×chaucha*	*S. tuberosum* (Andigenum Group)
S. phureja	*S. phureja*	*S. tuberosum* (Andigenum Group)
	S. stenotomum	
S. stenotomum	*S. goniocalyx*	*S. tuberosum* (Andigenum Group)

between diploid cultivars of *S. tuberosum* Andigenum group [classified as *S. stenotomum* Juz. and Bukasov by Hawkes (1990)] and the tetraploid wild species *S. bolivense* (*S. megistacrolobum*). Some clones of *S. ajanhuiri* are likely F$_1$ hybrids backcrossed to *S. tuberosum* (PBI Solanum Project 2014). DNA sequence data of the *waxy* gene supported a hybrid origin for this species from the *S. tuberosum* Andigenum group and *S. megistacrolobum* (Rodríguez *et al.* 2010). This landrace possesses frost resistance (Condori *et al.* 2014) and is distributed in the high Andean Altiplano between southern Peru and Central to North Bolivia, at elevations between 3700 m and 4100 m (Ochoa 1990, Ovchinnikova 2011, Spooner *et al.* 2010).

S. juzepczukii Bukasov (Hawkes 1990, Spooner *et al.* 2007)

S. juzepczukii Bukasov is a triploid (2n = 3x = 36) cultivar formed by hybridization between a diploid cultivar of *S. tuberosum* L. Andigenum group, and the tetraploid wild species *S. acaule* Bitter (Rodríguez *et al.* 2010). It can be found from central Peru to southern Bolivia and can grow at an altitude of 4000 m (Spooner *et al.* 2010). *S. juzepczuki* is highly tolerant to frost (Condori *et al.* 2014) and farmers cultivate it in the frost affected areas of Altiplano (Hijmans 1999). This species contains high levels of glycoalkaloids, and local people prepare detoxified processed potato "chuño" by freeze drying (Irikura 1989). This process makes the bitter variety edible by reducing the glycoalkaloid content from about 30 mg/100 g to 16 mg/100 g. These processes also preserve the tuber for a long period of time (Woolfe and Poats 1987).

S. curtilobum Juz. and Bukasov (Hawkes 1990, Spooner *et al.* 2007)

S. curtilobum (2n = 5x = 60) likely formed by hybridization between tetraploid forms of *S. tuberosum* L. Andigenum group (synonym for *S. tuberosum* subsp. *andigenum*), and *S. juzepczukii* Bukasov (Hawkes 1990, Rodríguez *et al.* 2010). It possesses frost hardiness as strong as that of *S. juzepczukii* and is cultivated in the Andean Altiplano at an altitude range of approximately 4000 m (Spooner *et al.* 2010). Because the tubers are bitter, owing to high glycoalkaloid content, the species is also used to prepare "chuño" (Irikura 1989, Woolfe and Poats 1987).

S. tuberosum L.

The Origin

The most popular cultivated potato is *S. tuberosum*, which is also known as "common potato" in most parts of the world. Spooner *et al.* (2005a) assumed a single origin, from a wild species progenitor present in the *S. brevicaule* complex, in southern Peru. However, multiple origins of cultivated potatoes have been suggested by different authors

(Grun 1990, Hawkes 1994, Huamán and Spooner 2002). Recently, Rodríguez *et al.* (2010) described the hybrid origins of cultivated potatoes.

The origin of potato in Europe has been controversial. Juzepczuk and Bukasov (1929, cited in Huaman and Spooner 2002) proposed that potatoes were originally introduced into Europe from the Chiloé region in Chile. In contrast, Hawkes (1994) suggested that common potato descends from potatoes widely cultivated in the Andean highlands of Bolivia, Peru, and northern Argentina. Molecular analysis has revealed that the Andean potato predominated in the 1700s, and later the Chilean potato was introduced into Europe and became predominant long before the late blight epidemics (Ames and Spooner 2008, Ríos *et al.* 2007, Spooner *et al.* 2005b).

Potato landraces cultivated in Mexico and Central America have been considered to be the result of repeated introduction in the post-Columbian era (Hosaka 2004, Spooner *et al.* 2007, Ugent 1968).

Classification by Hawkes (1990)

Hawkes (1990) divided *S. tuberosum* into the following two subspecies: *tuberosum* and *andigena*; both are tetraploid (2n = 4x = 48). The subspecies *tuberosum* is the cultivated potato used worldwide, whereas the subspecies *andigena* is restricted to Central and South America (Hawkes 1990). Hawkes (1990) described these two subspecies as follows:

(1) *S. tuberosum* subspecies andigena (tetraploid): The species is cultivated over a broad range in the Andes of South America and displays a wide range of morphological variations, including diversity in the colors of the flower and tuber shapes. Theories about the origin of the species, include natural hybridization events between *S. stenotomum* and *S. sparsipilum*, followed by chromosome doubling (Cribb and Hawkes 1986) or simple chromosome doubling of *S. stenotomum*, and later hybridization between *S. stenotomum* and *S. chacoense* (Hawkes 1994).

(2) *S. tuberosum* subspecies tuberosum (tetraploid): This is the most popular cultivated species of potato and now is distributed worldwide. The geographical origin of *S. tuberosum* subsp. *tuberosum* is in Chiloé Island, the largest island in the Chiloé Archipelago off the coast of Chile. The species evolved from the subsp. *Andigena*, introduced into southern Chile followed by adaptation to longer day lengths (Hawkes 1994).

Revised classifications of S. tuberosum

Huamán and Spooner (2002) reexamined the morphological support for classification of potato landraces. They concluded that formally recognized cultivated potato species should be treated as a single species, *S. tuberosum*, with eight cultivar groups: Ajanhuiri, Andigenum, Chaucha, Chilotanum, Curtilobum, Juzepczukii, Phureja, and Stenotomum. Later, Spooner *et al.* (2007) suggested a classification of four species based on the morphological

and molecular evidence following the *International Code of Nomenclature for Cultivated Plants*: *S. tuberosum* divided into the Andigenum group (including diploids, triploids and tetraploids) and Chilotanum group (including tetraploids) of lowland tetraploid Chilean landraces, from which modern cultivars were selected.

Three species listed below were described as independent by Hawkes (1990), but Spooner *et al.* (2007) suggested including them into the *S. tuberosum* Andigenum group.

S. chaucha (Hawkes 1990) to S. tuberosum L. Andigenum group (Spooner et al. 2007)

S. chaucha is a cultivated triploid species that supposedly originated from natural hybridization between *S. tuberosum* subsp. *andigena* and *S. stenotomum* (Hawkes 1990) distributed from 2100 m to 4100 m throughout Peru, with lower frequency in Bolivia, and rarely found in Ecuador and Colombia. Taxonomic identification of this species relies largely on the chromosome number ($2n = 3x = 36$). Huamán and Spooner (2002) recommended the placement of this species in the *S. tuberosum* Chaucha group. Although the group includes different ploidies, Spooner *et al.* (2007) described it as the *S. tuberosum* L. Andigenum group.

S. phureja (Hawkes 1990) to S. tuberosum L. Andigenum group (Spooner et al. 2007)

This species was cultivated from central Peru to Ecuador, Colombia, and Venezuela since the pre-Spanish era and is believed to have originated from *S. stenotomum* (Hawkes 1990). The species was identified based on its adaptation to shorter day lengths, low tuber dormancy, and diploid ($2n = 2x = 24$) nature. However, Ghislain *et al.* (2006) reported that over 30% of the CIP collection is polyploid. Huamán and Spooner (2002) studied the morphological characters of the species and suggested that this species should be placed in the *S. tuberosum* L. Andigenum group.

S. stenotomum (Hawkes 1990) to S. tuberosum L. Andigenum group (Spooner et al. 2007)

Hawkes (1990) divided this species into the following two subspecies: *stenotomum* and *goniocalyx*. The species is diploid and cultivated from Central Peru to Central Bolivia. It is believed to be the most primitive form of cultivated potato. *S. stenotomum* shows the diversity within species, suggesting it to be the first domesticated potato derived from diploid wild species and is also believed to have been involved in the establishment of other cultivated potato species. Huamán and Spooner (2002) suggested that this species is a cultivar group of *S. tuberosum*, in view of the common morphological characteristics with other species within the group (polythetic support) and later it was included in the *S. tuberosum* Andigenum group by Spooner *et al.* (2007).

Wild potato species

Wild potato species are highly complex groups. As afore-

mentioned, taxonomic classification of wild species is controversial and continues to be refined. Wild potatoes are widely distributed in most parts of America, from southwest USA to Mexico and Central America. In South America, they occur in almost every country, mainly in the Andes of Venezuela, Colombia, Ecuador, Peru, Bolivia, and Argentina (Hijmans *et al.* 2002).

In America, two centers for diversity in wild potatoes have been recognized; one in North and Central America, with its center in Mexico, and the other in South America, with its center in the Andes, extending from Venezuela to Chile. This wide range of distribution along with a broad range of altitudinal distribution, from sea level to 4500 m, indicates adaptation to a wide range of habitats (Hijmans and Spooner 2001, Hijmans *et al.* 2002, 2007). Some species can withstand subzero temperatures (*S. acaule* and *S. megistacrolobum*), whereas others are adapted to hot, dry, and semidesert conditions (*S. berthaultii*, *S. neocardenasii*, and *S. gracilifrons*) (Hawkes 1990). These adaptations to a wide range of habitats have made the wild species tolerant to different environmental stresses and resistant to a broad range of pests and diseases (Hawkes 1994).

Genetic diversity and value of primitive cultivars and wild species in potato breeding

The value of germplasm is determined by its genetic diversity, availability, and utility. In this sense, potato stands out among all other crops (Bamberg and del Rio 2005). Primitive forms of cultivated potato and their wild relatives provide a rich, unique, and diverse source of genetic variation, which could be a source of various traits for potato breeding. This may be because of their adaptation to a broad range of habitats and niches such as latitude (from southwest United States to Argentina), altitude (from coasts to Andean mountains), habitat (in cloud forests, in cultivated fields, on cliffs, as epiphytes, in deserts, in forests, and on Pacific islands), soil (from forest floors to sandy soils, from volcanic soils to rich, loamy soils), and precipitation regimes. They are equally diverse in morphological traits (i.e. plant height, leaf and leaflet shape, flower color, stolon length, and size, color, and shape of tubers) (Hanneman 1989).

Wild potatoes have been used for disease resistance in breeding programs for over 100 years (Hawkes 1958). Potato has many wild relatives and primitive cultivars and these genetic resources have proven to be valuable in breeding programs in addition to disease resistance, environmental tolerance, and other agronomic traits and processing qualities of interests (Bamberg and del Rio 2005, Barker 1996, D'hoop *et al.* 2008, Hawkes 1958, 1990, Hijmans *et al.* 2003, Jansky 2010, Ochoa 1999, Spooner and Bamberg 1994). Sources of resistance have been screened, identified, and listed by several authors (Hanneman and Bamberg 1986 cited in Hawkes 1994, Irikura 1989). Hawkes and Hjerting (1989) discovered resistance to all pests and diseases known at that time in Bolivian potato species. **Table 2** shows a list

Table 2. A list of wild and cultivated potato species of reported useful traits

Species name	Status (Wild/Cultivated)	Ploidy and EBN	Country	Late blight	Wart	Common scab	Bacterial wilt	Soft rot; blackleg	Potato virus X	Potato virus Y	Potato leaf roll virus	Spindle tuber viroid	Colorado beetle	Myzus persicae, Macrosiphum euphorbiae (aphids)	Globodera rostochiensis, G. pallida (potato cyst nematode)	Meloidogyne incognita (root-knot nematode)	Frost	Heat	Drought	Lack tuber blackening
				Fungus resistance			Bacterial resistance		Virus resistance				Insect resistance		Nematode resistance		Physiological characters			
S. acaule	W	4x (2EBN), 6x	AR, BO, PE		++		+		++	+	++	+	+		+	+	++	+	+	
S. ajanhuiri	C	2x	BO, PE						+	+		+	+	+			+	+	+	
S. berthaultii	W	2x (2EBN)	BO		+				+	+		+	+		+	+	+			
S. boliviense	W	2x (2EBN)	BO	+											+	+	+			
S. brachistotrichum	W	2x (1EBN)	MX														+			
S. brachycarpum	W	6x (4EBN)	MX		+				+		+				+	+	+	+	+	
S. brevicaule	W	2x (2EBN)	BO														+			
S. brevicaule (=) *S. gourlayi*	W	2x, 4x	PE		+								+							
S. bukssovii	W	2x (2EBN)	PE		+	+				+			+	+	+	+	+	+	+	
S. bulbocastanum	W	2x (1EBBN)	MX	++	+		+	+						++	+	+	+	+	+	
S. candolleanum (=) *S. canasence*	W	2x (1EBN)	BO, PE	+	+	+		+		+			+	++	+	+	+			
S. candolleanum (=) *S. multidissectum*	W	2x (1EBN)	BO, PE	+	+									+	+	+	+	+	+	
S. cardiophyllum	W	2x (1EBN), 3x	MX	++	+				+	++			+			+	+			
S. chacoense	W	2x (2EBN)	AR, BO, PE, UY	+	+	+	+	+	+		+		+	+	+	+	++	+	+	
S. chomatophilum	W	2x (2EBN)	EC, PE								+									
S. circaeifolium	W	2x (2EBN)	BO	+																
S. circaeifolium (=) *S. capsicibaccatum*	W	2x (2EBN)	BO	+	+								+	+	+	+	+		+	
S. clarum	W	2x	MX, GT				+							+	+					
S. colombianum	W	4x (2EBN)	CO, EC, VE	+	+								+				++			
S. commersonii	W	2x (1EBN)	AR, BR, UY	+	+	+		+	+				+		+	+	+	+	+	
S. curtilobum	C	4x (4EBN), most 5x	BO, PE						+								++		+	
S. demissum	W	6x (4EBN)	GT, MX	++	+			+	+	++	+		+		+	+	+	+	+	
S. ediense	W	5x	MX	+									+							
S. etuberosum	W	2x (1EBN)	CH						++	++	+		+	+			+			
S. fendleri	W	4x (2EBN)	MX, US	+	+						+		+			+	+		+	
S. guerreroense	W	6x (4EBN)	MX									+								
S. hjertingii	W	4x (2EBN)	MX					+												+
S. infundibuliforme	W	2x (2EBN)	AR, BO		+						+		+	+	+		+			
S. jamesii	W	2x (1EBN)	MX, US		+						+		+		+		+	+	+	
S. juzepczukii	C	3x	BO, PE						+								+			
S. kurtzianum	W	2x (2EBN)	AR		+			+	+		+		+	+	+	+	+	+	+	
S. leptophyes	W	2x (2EBN), 4x (4EBN)	BO, PE		+			+	+						++	+	+	+		
S. lignicaule	W	2x (1EBN)	PE									+								+
S. lycopersicoides	W	2x	PE, CH, PE										+	+						
S. marinasense	W	2x (2EBN)	PE											+			+		+	
S. medians	W	2x (2EBN), 3x	PE										+	+			+	+	+	

Table 2. (continued)

Species name	Status (Wild/Cultivated)	Ploidy and EBN	Country	Fungus resistance			Bacterial resistance		Virus resistance				Insect resistance		Nematode resistance		Physiological characters			
				Late blight	Wart	Common scab	Bacterial wilt	Soft rot; blackleg	Potato virus X	Potato virus Y	Potato leaf roll virus	Spindle tuber viroid	Colorado beetle	Myzus persicae, Macrosiphum euphorbiae (aphids)	Globodera rostochiensis, G. pallida (potato cyst nematode)	Meloidogyne incognita (root-knot nematode)	Frost	Heat	Drought	Lack tuber blackening
S. megistacrolobum	W	2x (2EBN)	AR, PE, BO		+			+			+		+	+	+	+	++	+	+	
S. microdontum	W	2x (2EBN), 3x	AR, BO		+		+	+			+		+	+	+	+	+	+	+	
S. morelliforme	W	2x	MX, GT, HN	+									+				++			
S. moscopanum	W	6x (4EBN)	CO	+													+	+		
S. oplocense	W	2x (2EBN), 4x (4EBN), 6x (4EBN)	AR, BO		+						+		+		+	+			+	
S. oxycarpum	W	4x (2EBN)	MX	+									+							
S. palustre (=) S. brevidens	W	2x (1EBN)	AR, CL								+			++			+	+	+	
S. papita	W	4x (2EBN)	MX								+						+		+	
S. phureja	C	2x (2EBN)	AN	+	+	+	+	+	+	+							+	+	+	
S. pinnatisectum	W	2x (1EBN)	MX	++	+		+	+		+			+		+	+	+	+	+	
S. polyadenium	W	2x	MX	+	+		+				+		+	+	+	+	+	+	+	
S. polytrichon	W	4x (2EBN)	MX	+	+										+	+	+		+	
S. raphanifolium	W	2x (2EBN)	PE		+						+								+	
S. sanctae - rosae	W	2x (2EBN)	AR											+		+	++	+	+	
S. semidemissum	W	6x	MX	+													+			
S. sparsipilum	W	2x (2EBN)	BO, PE		+		+		+						+	+	+	+	+	
S. spegazzinii	W	2x (2EBN)	AR											+	+	+	+	+	+	
S. stenotomum	C	2x (2EBN)	BO, PE				+						+				+		+	
S. stoloniferum	W	4x (2EBN)	MX	++	+			+	+	++				+	+	+		+	+	
S. sucrense	W	4x (4EBN)	BO	+	+				+						+		+			
S. tarijense	W	2x (2EBN)	AR, BO	+	+				+	+			+	++			+	+	+	
S. megistacrolobum var. toralapanum (=) S. toralapanum	W	2x (2EBN)	AR, PE, BO	+													++			
S. trifidum	W	2x (1EBN)	MX	+	+								+	+			+	+	+	
S. tuberosum subsp. andigenum*	C	2x, 4x	AN	+	+			+	++	+	+		+		+	+	+	+	+	
S. tuquerrense	W	4x (2EBN)	CO, EC											+						
S. vernei	W	2x (2EBN)	AR	+			+	+					+	+	+	+	+	+	+	
S. verrucosum	W	2x (2EBN)	MX	+					+				+	++	+	+	++	+	++	
S. violaceimarmoratum	W	2x (2EBN)	BO										+				+		+	
S. yungasense	W	2x (2EBN)	BO, PE			+														

Source: Hawkes 1994; Irikura (1989); Spooner and Hijmans (2001). (=): synonyms. Name of the species are written as appeared in original sources. * S. tuberosum subsp. andigenum includes S. goniocalyx (2x). Synonyms were identified The Plant List (2013). W, Wild; C, Cultivated. AN, wide spread in Andes; AR, Argentine; BO, Bolivia; BR, Brazil; CH, Chile; CO, Colombia; EC, Ecuador; GU, Guatemala; HN, Honduras; MX, Mexico; PE, Peru; US, United States; UY, Uruguay; VE, Venezuela. ++, specie include individuals possesses immunity, high resistance, high tolerance, or high quality; +, specie include individuals possesses resistance, tolerance, or good quality.

of wild and cultivated potato species reported to carry useful traits.

Although most wild relatives of potatoes are not adapted for cultivation at higher altitudes, numerous wild species have been integrated into the parentage of potato cultivars in Europe and North America, owing to their disease-resistance traits (Plaisted and Hoopes 1989). For example, Ross (1986) mentioned that germplasm from only six of its wild relatives is frequently incorporated into European cultivars, namely *S. demissum* [late blight (LB) and potato leafroll virus (PLRV)]; *S. acaule* [potato virus X (PVX), PLRV, potato spindle tuber viroid (PSTV), wart, *Globodera*, and frost), *S. chacoense* [potato virus A (PVA), potato virus Y (PVY), LB, Colorado beetle, tuber moth]; *S. spegazzinii* (*Fusarium*, wart, *Globodera*); *S. stoloniferum* (PVA, PVY); and *S. vernei* (*Globodera*). *S. microdontum*, *S. sparsipilum*, *S. verrucosum*, *S. phureja*, *S. tuberosum* subsp. *andigena*, *S. commersonii*, and *S. maglia* have also been used occasionally as breeding materials (Hawkes 1994). Studies of major contributing ancestors in North American potato cultivars have shown that the frequency of the presence of the German *S. demissum* × *S. tuberosum* population ranged from 61 to 100% in the 44 most prominent North American cultivars (Love 1999).

Most of the wild potato species grow in the Andes, but the United States, Mexico, and Central America contain about 30 diploid taxa as well as tetraploid and hexaploid species (Lara-Cabrera and Spooner 2005). These include *S. demissum* and *S. bulbocastanum*, which are highly resistant to LB. A recent study discovered the pathogen that caused potato LB (responsible for the great Irish famine of the 1840s) in the Toluca Valley of central Mexico (Gossa *et al.* 2014). Niederhauser (1992) reported that Mexican national potato germplasm contains high levels of durable resistance to LB, so that farmers in central parts of Mexico can grow it without applying fungicides. Recently, cultivation of two wild potatoes in the state of Jalisco, Mexico has been reported (Villa-Vázquez and Rodríguez Contreras 2011). Several *Solanum* sp. are newly registered in central Mexico (Rodríguez Contreras and Vargas Ponce 2001). These Mexican potato species are among the most promising plant materials for potato breeding. There remains an enormous, unimaginable potential to encounter desirable characteristics, not only blight resistance but for other agronomical traits as well.

Disease resistance

Potato late blight

The potato LB disaster in Ireland during 1845 and 1846 and subsequent epidemics in Britain and Europe have advanced disease-resistance breeding of potato. LB is the main potato disease worldwide (CIP 2013), and the use of fungicides to control LB is still the norm even with the most resistant cultivars. The potato breeders of the world have put much effort into assessing and using wild potato species in

search of resistance to this disease caused by *Phytophthora* (Hawkes 1958, 1994). In 1849, *S. demissum* was introduced by Mexico with the aim of achieving *Phytophthora* resistance (Hawkes 1958). Since then, improvement of potato LB resistance has been one of the most important research areas for the potato breeders of the world (CIP 2013). Although the use of disease-free seeds and fungicide has controlled damage in potato production worldwide (Fry 2007, Struik and Wiersema 1999), LB remains the primary disease.

Dominant resistance genes were initially identified in the Mexican wild species *S. demissum* and introgressed by crossing and backcrossing into cultivated potato. To date, eleven resistance (*R1* to *R11*) genes in potato have been identified in *S. demissum* (Black *et al.* 1953, Malcolmson and Black 1966). However, their durability was proved to be limited owing to the rapid appearance of compatible races of the pathogen after market introduction (Wastie 1991). Strategies to prevent rapid evolution of compatible races have been proposed. *R* gene pyramids, combining multiple resistance genes isolated from diverse sources, seem to be a promising strategy for durable and broad spectrum resistance against LB (Haverkort *et al.* 2009, Kim *et al.* 2012, Tan *et al.* 2010). In recent years, development of durable and extreme resistance to LB disease, using resistance genes from several wild potato species collected from Central America and Andean South America, has been attempted. So far, some potentially more long-lasting, broad-spectrum *R* genes such as *RB*/*Rpi-blb1* (Song *et al.* 2003, van der Vossen *et al.* 2003), *Rpi-blb2* (van der Vossen *et al.* 2005), *Rpi-blb3* (Lokossou *et al.* 2009, Park *et al.* 2005) from *S. bulbocastanum*, *Rpi-sto1* from *S. stoloniferum*, *Rpi-pta1* from *S. papita* (Vleeshouwers *et al.* 2008), and *Rpi-vnt1.1* from *S. venturii* (Foster *et al.* 2009, Pel *et al.* 2009), have been identified and cloned. Additional *R* genes have been described in other potato wild relatives from *S. berthaultii* (Ewing *et al.* 2000, Rauscher *et al.* 2006), *S. capsicibaccatum* (Jacobs *et al.* 2010), *S. microdontum* (Sandbrink *et al.* 2000, Tan *et al.* 2008), *S. mochiquense* (Smilde *et al.* 2005), *S. paucissectum* (Villamon *et al.* 2005), *S. phureja* (Śliwka *et al.* 2006), *S. pinnatisectum* (Kuhl *et al.* 2001), *S. ruizceballosii* (Śliwka *et al.* 2012), *S. schenckii* (Jacobs *et al.* 2010), *S. sparsipilum*, *S. spegazzinii* (Danan *et al.* 2009), *S. stoloniferum* (Wang *et al.* 2008), and *S. verrucosum* (Jacobs *et al.* 2010, Liu and Halterman 2006).

Resistance to potato virus Y

Potato virus Y (PVY), one of the most important diseases of potato, can reduce yield by 80% (Hane and Hamm 1999). The *Ry_{adg}* gene, conferring extreme resistance to all known PVY strains, has been mapped and cloned from *S. andigena* (Hamalainen *et al.* 1997). Kasai *et al.* (2000) developed sequence-characterized amplified region (SCAR) markers to detect PVY resistance of the gene *Ry_{adg}*. Other wild species are also known to carry *Ry* genes (Cockerham 1970), including *S. stoloniferum* (Cockerham 1943), *S. phureja* (Ross 1986), *S. brevidens* (Pehu *et al.* 1990), and *S. chacoense*

(Hosaka *et al.* 2001). Recently, a hypersensitive response gene, *Ny*, conferring resistance was also identified and mapped (Szajko *et al.* 2008, 2014).

Bacterial wilt

Bacterial wilt (BW) caused by *Ralstonia solanacearum* is considered to be one of the most important potato diseases in hot and humid tropical regions (French *et al.* 1998). Resistance to BW has been found in *S. phureja* (Fock *et al.* 2000), *S. stenotomum* (Fock *et al.* 2001), *S. commersonii* (Kim-Lee *et al.* 2005, Laferriere *et al.* 1999), and *S. chacoense* (Chen *et al.* 2013). The resistance genes have been transferred to cultivated potato by protoplast fusion (Fock *et al.* 2001, Kim-Lee *et al.* 2005, Laferriere *et al.* 1999) or somatic hybrids (Chen *et al.* 2013, Fock *et al.* 2000).

Pest resistance

A wide range of pest resistance has been identified in wild species. Various studies indicate that resistances to insects are due to glycoalkaloids, glandular trichomes, and other undetermined mechanisms (Flanders *et al.* 1992, Pelletier *et al.* 2013). Flanders *et al.* (1992) evaluated 100 species of wild potato for resistance to various insect and reported that resistance was associated with glycoalkaloid tomatine, dense hairs, and glandular trichomes. Jansky *et al.* (2009) reported resistance to Colorado potato beetle was confirmed in species characterized by high levels of glycoalkaloids (*S. chacoense*) or dense glandular trichomes (*S. polyadenium* and *S. tarijense*). *S. hougasii* showed high levels of resistance to Columbia root-knot nematode (Brown *et al.* 1991). Cyst nematode resistance has been identified in the Argentinian wild species *S. vernei* and *S. acaule* (Hawkes 1994).

Environmental stress tolerances

Many primitive forms of cultivars and wild relatives of potato can tolerate environmental stress conditions in their habitats (Watanabe *et al.* 2011). Frost tolerance may be one of the oldest breeding objectives of potato breeding. Reddick (1930) studied frost resistance or tolerance using hybrids between *S. demissum* and other susceptible species. Frost tolerance also occurred in certain accessions of *S. commersonii* and its hybrids. Bukasov (1933) evaluated the frost resistance of several wild potato species and hybrids in the winters of the years 1930–31 and 1931–32. *S. demissum*, *S. acaule*, and *S. juzepczukii* were not affected by frost of –6°C, *S. demissum* and *S. ajanhuiri* showed different reactions in different plants, and *S. andigenum* perished entirely under the same conditions, with the exception of one variety "Pacus," which proved to be resistant.

As potato has gained importance as a food source in developing countries (CIP 2013), the breeding target has shifted to adaptation to the conditions of these countries, generally hot and dry environments. Screening for drought tolerance in potato landraces has been performed by Cabello *et al.* (2012, 2013). A high proportion of accessions combining drought tolerance with high irrigated yield were found in Andean landraces, particularly in the species *S. curtilobum* (Juz. & Bukasov) in the *S. tuberosum* L. cultivar groups Stenotomum, Andigenum, and Chaucha. Watanabe *et al.* (2011) identified *S. chillonanum*, *S. jamesii*, and *S. okadae* as potential drought-tolerant species by screening 44 accessions of wild species selected based on their drought habitats derived from GIS information.

Breaking barriers for the use of wild relatives for breeding

As discussed above, promising genetic resources are available over the broad range of primitive cultivars and wild relatives of potato. Hawkes (1979) emphasized the importance of the incorporation of wild species in potato breeding programs. The potential for using these genetic resources in conventional breeding depends on their crossability with the commonly cultivated potato *S. tuberosum*. There are some barriers to cross-species compatibility, such as differences in the endosperm balance number (EBN) and ploidy level. The EBN hypothesis was first published by Johnston *et al.* (1980) to explain the success or failure of intraspecific crosses. It relates to a strong isolating mechanism present in the section *Petota*. In potato, exist 2x (1EBN), 2x (2EBN), 4x (2EBN), 4x (4EBN), and 6x (4EBN) (Spooner and Hijmans 2001). The EBN is independent of ploidy level and is determined based on cross compatibility using standard EBN test crosses. Crosses between species with different EBNs are very often unsuccessful, whereas crosses between species with the same EBN number are frequently successful, even if they have different ploidy levels (Johnston and Hanneman 1980).

People conducting research on potatoes have developed methods for overcoming this hybridization barrier, such as ploidy manipulations, bridge crosses, auxin treatments, mentor pollinations, and embryo rescue (Jansky 2006). The manipulation techniques for modifying ploidy levels include haploid extraction to reduce EBN (Hermundstad and Peloquin 1985, McHale and Lauer 1981) and 2n gamete production (2n egg and 2n pollen) to increase EBN (Camadro *et al.* 1990, Iwanaga *et al.* 1989). These techniques are complemented by treatments aimed at obtaining fertile interspecific hybrids, including mentor pollination, embryo rescue, hormone treatments, reciprocal crosses, selection of cross-compatible genotypes, and somatic fusion (Jansky 2006). In some cases, a trait of interest may not be present in the 2x (2EBN) and 2x (1EBN) gene pools; however, a broad range of genetic diversity present in wild potato species could be used for breeding purposes. There are several reports of the successful use of this strategy (Iwanaga *et al.* 1991, Watanabe *et al.* 1994, 1995). Using these effective tools, potato breeders can gain access to the promising characteristics present in wild potato species.

Molecular tools and information for systematic studies and breeding

The inherent genetic complexity of potato has made breeding time-consuming and often with unpredictable results. Polygenes are believed to underlie quantitative resistance, which is difficult to maintain intact during the breeding process. Thus, it is desirable to identify sources with high heritability and robust screening procedures (Pérez *et al.* 2000). The selection cycle, from initial crosses to variety release, requires approximately 10 years or sometimes more than 30 years (Gebhardt 2013, Haverkort *et al.* 2009). The transfer of resistance genes from wild potatoes directly into widely adapted potato varieties is currently the most promising strategy for developing long-lasting resistance to LB (Haverkort *et al.* 2009).

Efficiency and precision in plant breeding can be enhanced by use of diagnostic DNA-based markers and has been applied to potato breeding (Gebhardt 2013). Numerous genetic mapping experiments have been performed using potato and have identified DNA-based markers linked to genes for resistance to different diseases (D'hoop *et al.* 2008, Hamalainen *et al.* 1997, Kuhl *et al.* 2001, Szajko *et al.* 2014). DNA-based markers have also been used to study the relationships of species with different marker systems [Gavrilenko *et al.* 2010 (microsatellites), Gebhardt *et al.* 1991 (RFLP), Hosaka *et al.* 1994 (RAPD), Kim *et al.* 1998 (AFLP), Provan *et al.* 1996 (microsatellites), Spooner *et al.* 2007 (microsatellites)]. Cytoplasmic genome studies of potato have also been used for phylogenetic studies (Hosaka *et al.* 1984, Hosaka and Sanetomo 2009, Spooner and Castillo 1997). The genome sequence of potato has recently been completed. The sequence information of the 844 Mb genome revealed 39,031 protein-coding genes in potato and suggested a paleohexaploid duplication event during the genome evolution (The Potato Genome Sequencing Consortium 2011). Genome sequence information will be a platform for genetic improvement of potato as well as for phylogenetic research on the genus *Solanum*.

The world potato germplasm collection

The high utility of wild and landrace potatoes has led to a series of collection expeditions in the centers of origin,

Table 3. List of holders of *ex situ* collections of potato germplasm (*Solanum* sp.) (FAO 2010)

Name of institute*	Accessions		Types of accession (%)				
	No.	%	WS	LR	BL	AC	OT
INRA-RENNES, France	10,461	11	6	2	84	8	
VIR, Russian Federation	8,889	9		46	3	26	25
CIP, Peru	7,450	8	2	69	2	<1	27
IPK, Germany	5,392	5	18	37	7	32	6
NR6, USA	5,277	5	65	21	9	5	<1
NIAS, Japan	3,408	3	3	1	31		65
CORPOICA, Colombia	3,043	3					100
CPRI, India	2,710	3	15		85		
BNGTRA-PROINPA, Bolivia	2,393	2	26	74			
HBROD, Czech Republic	2,207	2	5	1	29	52	13
BAL, Argentine	1,739	2	85	15			
CNPH, Brazil	1,735	2					100
SASA, UK	1,671	2					100
ROPTA, Netherland	1,610	2	3	1		1	95
PNP-INIFAP, Mexico	1,500	2					100
TARI, Taiwan	1,282	1					100
SamAI, Uzbekistan	1,223	1					100
IPRBON, Poland	1,182	1			8	92	
RIPV, Kazakhstan	1,117	1	26	2	15	57	
SVKLOMNICA, Slovakia	1,080	1	1	2	47	41	9
Others (154)	32,916	33	19	15	3	16	46
Total	98,285	100	15	20	16	14	35

WS: wild species, LR: landraces/old cultivars, BL: research materials/breeding lines, AC: advanced cultivars, OT: (others) the types are unknown or a mixture of two or more types. *INRA-RENNES: d'Amélioration des Plantes Institut national de la recherche agronomique/Station, VIR: N.I. Vavilov All-Russian Scientific Research Institute of Plant Industry, CIP: Centro Internacional de la Papa; IPK: External Branch North of the Department Genebank, Leibniz Institute of Plant Genetics and Crop Plant Research, Potato, NR6: Potato Germplasm Introduction Station, United States Department of Agriculture, Agricultural Research Services, NIAS: National Institute of Agrobiological Sciences, CORPOICA: Centro de Investigación La Selva, Corporación Colombiana de Investigación Agropecuaria, CPRI: Central Potato Research Institute, BNGTRA-PROINPA: Banco Nacional de Germoplasma de Tubérculos y Raíces Andinas, Fundación para la Promoción e Investigación de Productos Andinos, HBROD: Potato Research Institute Havlickuv Brod Ltd., BAL: Banco Activo de Germoplasma de Papa, Forrajeras y Girasol Silvestre, CNPH: Embrapa Hortaliças, SASA: Science and Advice for Scottish Agriculture, Scottish Government, ROPTA: Plant Breeding Station Ropta, PNP-INIFAP: Programa Nacional de la Papa, Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, TARI: Taiwan Agricultural Research Institute, SamAI: Samarkand Agricultural Institute named F. Khodjaev, IPRBON: Institute for Potato Research, Bonin, RIPV: Research Institute of Potato and Vegetables, SVKLOMNICA: Potato Research and Breeding Institute.

which are currently available for breeders and researchers through gene banks (Spooner and Bamberg 1994). Approximately 98,000 accessions are conserved *ex situ* (**Table 3**) and 80% of them are maintained in 30 key collections (FAO 2010). The major potato collections are in Latin America, Europe, North America, and a few countries in Asia. Landrace and wild relatives are found mostly in Latin American collections, whereas modern cultivars and breeding materials are found mostly in collections of Europe and North America (FAO 2010). The GCDT report (2006) stated that the most useful genetic material has already been collected and that there are currently few significant gaps in covering the total collection of the world. However, potato gene banks have several challenges pertaining to germplasm management, including the genetic drift during regeneration, inadequate evaluation of data, outdated facilities, and seed-health status.

A report on the global strategy for the *ex situ* conservation of potato (GCDT 2006) stated that wild species are the largest group represented in collections, although there is a considerable number of duplications. Native cultivars collected from centers of diversity in Latin America compose the second largest group. These materials are conserved either as botanical seeds or in vegetative form (tubers and *in vitro* plantlets) (GCDT 2006). The collections of the International Potato Center (Centro Internacional de la Papa, CIP), Czech Republic and United Kingdom are stored *in vitro* (medium-term conservation) as true seeds. Globally, 20% of accessions are in medium-term storage, 11% in short-term storage for immediate use, and 69% in unknown storage conditions (FAO 1997). The latest information and methods for long-term storage are explained in detail in the next section of this review.

These collections have been described for agromorphological traits following the descriptor lists of the International Plant Genetic Resources Institute (IPGRI) and the International Union for the Protection of New Varieties of Plants (UPOV). The UPOV list has been developed mostly for description of modern potato cultivars, whereas the IPGRI list covers all types of potato germplasm. The quality of the description data is adequate, with a few exceptions (GCDT 2006). Proper identification of the accessions held by any gene bank is critical, given that germplasm users may not be familiar enough with the species to identify them correctly. Furthermore, many potato gene banks have no direct support from a taxonomist specializing in potato species (GCDT 2006). Taking in consideration all the recent reclassifications of the genus *Solanum*, identification of the collections appears to be a priority and should be performed by an experienced taxonomist (Gavrilenko *et al.* 2010, Hanneman 1989).

Status of Potato germplasm in Japan

Currently, the National Institute of Agrobiological Sciences (NIAS) Genebank preserves and distributes potato genetic resources in Japan. The database is accessible using the NIAS Genebank databases (https://www.gene.affrc.go.jp/databases-plant_search_en.php). According to the database, a total of 1217 accessions [1076 breeders' lines (varieties), 18 landraces, 108 wild species, and 15 others/unknown] are registered. Of these, 936 accessions are available for distribution and are distributed as tubers. Eight hundred and forty nine accessions have been evaluated for plant morphology (sprout color, stem color, flower color, etc.), tuber quality (yield, color of tuber flesh and skin, number of tubers per plant, fresh type, starch value etc.), and pest and disease resistance (bacterial wilt, LB, bacterial soft rot, powdery scab, cyst nematode, leaf roll virus, Y mosaic virus, etc.).

Conservation of potato genetic resources

As described above, primitive potato cultivars and wild species are promising gene pools for crop improvement. The genetic diversity is threatened by land use change caused by urbanization, erosion, and climate change. There are many reasons diminishing the incentives for farmers to grow landraces, including the availability of improved varieties, availability of purchased inputs (fertilizer and pesticides), low cost/benefit ratio from planting traditional varieties, and opportunities to increase income by changing crops (Brush 2002). Conservation of wild species and their availability for use in breeding programs provide the foundation for future crop improvement.

Although potato germplasm has been collected widely over its distribution range and conserved in gene banks (GCDT 2006), precise identification of *in situ* populations and re-collection might be worthwhile for capturing new alleles (del Rio *et al.* 1997). Bamberg *et al.* (2003) reviewed 12 expeditions of wild potato species from United States and found that the new collections from the same collection sites were significantly different from the original collections, as though they had been collected from different sites. They also emphasized the importance of monitoring the population conservation status for further utilization.

Conclusions

Sustainably increasing productivity in a changing climate is one of the most important challenges for people conducting researches on potato worldwide to ensure food security. Many highly diverse species compose the genus *Solanum*. Primitive cultivars and wild relatives of potato have been used as sources of desirable traits, such as resistance or tolerance to diseases, pests, and environmental stresses, and of tuber qualities, for potato breeding. Tools for incorporating useful alleles from its wild relatives into cultivated potato have been developed so that there remains a broad gene pool to be more effectively exploited. Currently, large amounts of potato germplasm containing useful alleles are available in gene banks around the world; however, re-collection may reveal novel genes. *In situ* conservation of

wild populations is important for maintaining gene pool integrity and allowing evolution to occur in natural populations. Precise identification of species is essential for making decisions for effective utilization of germplasm collections; therefore, taxonomic research and updating taxonomical descriptions of the gene bank collections in potato are indispensable.

Acknowledgement

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