POTATO GENETIC RESOURCES: SOURCES OF RESISTANCE AND SYSTEMATICS

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Abstract

The major potato of commerce, *Solanum tuberosum* L., is the fourth most important food crop in the world after rice, wheat and corn. Fortunately, the potato has many primitive cultivars and wild species relatives useful to reduce our reliance on chemical controls. These include resistances against diseases, pests, and traits for useful agronomic characters such as yield, specific gravity, chipping qualities, and suppression of enzymatic browning. This paper summarizes some of these qualities, and provides an overview of germplasm availability and taxonomy of the wild species.

The major potato of commerce, *Solanum tuberosum* L., is the fourth most important food crop in the world after rice, wheat and maize. It is grown in more countries than any other crop but maize, and forms the staple crop of many societies. Over 280 million metric tons were grown worldwide in 1989, with Eastern Europe growing 46%, Asia 22%, Western Europe 17%, North America 7%, Latin America 5%, and Africa 3% (2). It is the leading vegetable crop in acreage and farm value in the United States, with 1.2 million acres planted in 1991, with a value of sales almost two and one-half billion dollars (53). *Solanum tuberosum* is one species of a group of seven cultivated and 216 additional tuber-bearing, and nine non-tuber-bearing wild relatives, all classified by Hawkes (41) in the genus *Solanum*, section *Petota* Dumort

The purposes of this paper are threefold: 1) to provide examples of the proven and potential utility of wild and cultivated landrace members of sect. *Petota* for reducing our reliance on chemical controls for many pests and diseases that affect commercial cultivars, 2) to provide an overview of the status of germplasm availability of these species, and 3) to highlight the benefits for continuing germplasm collections and systematic studies of the group.

Compendio

Solanum tuberosum L., la principal papa en el mercado, es el cuarto cultivo alimenticio más importante en el mundo, después del arroz, del trigo y del

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maíz. Afortunadamente, la papa tiene muchos cultivares primitivos y especies silvestres relacionadas útiles para reducir nuestra dependencia en los controles químicos. Estos incluyen resistencias contra enfermedades y plagas, así como también útiles características agronómicas tales como rendimiento, gravedad específica, calidades para fritura a la inglesa y supresión del pardeamiento enzimático. Este artículo resume algunas de estas cualidades y provee una visión del germoplasma disponible y de la taxonomía de las especies silvestres.

Variability in sect. *Petota*

There is tremendous ecological, physiological, and morphological diversity in sect. *Petota.* It is widely distributed throughout the Americas from the southwestern United States to south central Chile. Although some species grow in areas over 4000 m in altitude (*e.g., S. acaule* Bitter), others grow at sea-level (*e.g., S. maglia* Schldl., *S. tuberosum* ssp. *tuberosum* native to Chile). Some species are adapted to very seasonal wet/dry climates (*e.g., S. berthaultii* Hawkes, *S. bulbocastanum* Dunal, *S. infundibuliforme* Philippi), whereas others grow in areas of more frequent rains (*e.g., S. colombianum* Dunal). Tubers vary in size from that of a pea (*S. clarum* Correll) to nearly the size of the cultivars (*e.g., S. candolleanum* Berthault), and in taste from edible and flavorful (*e.g., S. cardiophyllum* Lindley) to bitter and toxic (*e.g., S. vernei* Bitter and Wittm.). Plant habits vary from ground-hugging rosettes (*e.g., S. acaule*) to upright and well over one meter tall (*e.g., S. andreanum* Baker). Leaf margins are occasionally entire (*e.g., S. morelliforme* Bitter and Muench), but usually dissected (most of the species), with leaflets wide (*e.g., S. sparsipilum* [Bitter] Bitter and Juz.) to linear (*e.g., S. vidaurrei* Cárdenas). Most species largely lack glands, but some are highly glandular (*e.g., S. berthaultii, S. polyadenium* Greenman). Corollas vary in shape from stellate (*S. pinnatisectum* Dunal) to rotate (*S. stoloniferum* Schldl. and Bché.), and in color from white to pink to blue to purple (sometimes species specific, sometimes polymorphic for various combinations within species).

Status, Consequences, and Outlook for Chemical vs. Genetic Answers to Potato Production

This diversity extends to desirable resistances against diseases, pests, and traits for useful agronomic characters such as yield, specific gravity, chipping qualities, and suppression of enzymatic browning (30, 32, 33, 38, 41, 42, 43, 45, 62, 66, 71). Current screening and breeding research are extending known resistance and agronomic traits to additional species added to the growing collection of the National Research Support Program-6 (NRSP-6, formerly known as the Inter-Regional Potato Introduction Project-1, IR-1). There is immense original literature on the useful traits of many of these species that cannot be summarized entirely here. Useful summaries

TABLE 1.—*A sample of some of the resistances found in the NRSP-6 potato collection.*[1]

	Accessions Tested					
Disease[2]	Immune or very Resistant	Resistant	Intermediate	Susceptible or very Susceptible	Total tested	Percent of collection tested
PLRV	4	162	8	2,303	2,477	58
Fungi						
LB	30	120	45	493	688	16
EB	6	44	76	550	676	16
Vert	223	164	92	761	1,240	29
Insects						
CPB	3	241	134	686	1,064	25
GPA	25	92	233	940	1,290	30
PLH	0	104	170	1,086	1,360	32
Nematodes	35	385	258	1,364	2,042	47

[1]From updated data from Hanneman and Bamberg (1986).
[2]In case of conflicting resistance scores, the accession was assigned the most common, or more susceptible score. PLRV = Potato leafroll virus; LB = Late blight; EB = Early blight; Vert = Verticillium wilt; CPB = Colorado potato beetle; GPA = Green peach aphid; PLH = Potato leafhopper.

of species-specific traits can be obtained, however, in floristic treatments (42, 43, 62), summary literature (*e.g.*, 28, 44, 48), and our summary of selected diseases resistances from (33; Table 1).

The most important diseases of potato in the U.S. today are similar to those of fifty years ago. Production of potatoes has risen dramatically despite lower acreage planted and increased disease pressures. How has this been made possible? Fifty years ago, genetic resistances were predicted to have a major impact on future potato production. However, the main factor allowing these gains has not been resistance, but chemical protection. Because chemical costs were low and effectiveness high, breeding programs have not been under much pressure to produce highly resistant varieties. Thus, the potato became the most highly chemically treated major crop (54, 76; Table 2).

The ready availability of chemical controls has lessened the apparent need for a concerted national effort to perform the pre-breeding/enhancement steps required to access natural genetic resistance. These steps include a comprehensive characterization of exotic germplasm's reproductive biology and crossing behavior, initial evaluation of raw germplasm, subsequent advanced screening to identify parents with fixed extreme resistance, and enhancement of these materials to make them adapted to cultivation—*i.e.*, fit for use in a cultivar breeding program. The use of wild species should

TABLE 2.—*1992 chemical applications to U.S. fall potatoes.*[1]

Chemical	Average % of acres treated[2]	Total application (million lb.)
Nitrogen	100	213
Herbicides	81	1.71
Insecticides	90[3]	2.83
Fungicides	90	2.99
Others[4]	43	38.90

[1]Source: "Agricultural Chemical Usage," USDA/NASS/ERS Bulletin, March 1993.
[2]Of 1.07 million acres surveyed.
[3]Not including Idaho which had a low use of 39%. With ID included the overall average would be 72%.
[4]Mostly vine killers.

not be viewed as a "magic bullet" to improve our potato crop, but as a long-term effort and investment in concert with reduced chemical treatments, cultural practices, and other methods (52).

Chemical protection is increasingly losing its ability to serve the needs of the potato industry for the following reasons. Pathogens and pests are overcoming many of our most effective chemical controls. There also is a growing concern for human health and the environment that is eliminating or restricting the use of pesticides. Thus, costs of these controls are increasing. More efforts nationally and internationally must be directed toward supporting a stepwise and coordinated effort of collection, classification, preservation, characterization, evaluation, enhancement, and breeding for genetic resistances (60, 76). We list below some major diseases of potato and discussion of some wild and landrace cultivated species that could be used to control them.

Colorado Potato Beetle—The Colorado potato beetle is the most important insect pest of potato in the U.S. (24). It has the capacity to defoliate completely the potato crop, and has demonstrated an extraordinary capacity to overcome chemical controls, having developed resistance to nearly every licensed insecticide (5). Genetic resistance is the only practical long-range solution to this problem, and several approaches are in progress. Except for transformation of potato with bacterial genes, all other genetic controls involve the use of exotic *Solanum* germplasm. Some wild potato species completely deter feeding by the Colorado potato beetle by: 1) glycoalkaloids, particularly leptines, which have the added benefit of expression only in foliage, not in tubers (22), 2) glandular hairs which inhibit feeding, growth, locomotion and reproduction of the insect (59, 67), and 3) unknown properties of species lacking glandular hairs and with low concentrations of glycoalkaloids, such as *S. acroglossum* Juz. and *S. jamesii* Torr.

(33).

Fungal Diseases—Late blight is the most important disease of potato worldwide (60), and a significant problem throughout the U.S. (68). Over 90% of U.S. potato acreage is treated with fungicides primarily to control late blight and early blight (83), secondarily to control gray mold (*Botrytis*). Loss of these fungicides without a compensatory increase in genetic resistance would result in an estimated 23% reduction in overall production, 13.5% reduction in consumption, and 36.6% increase in retail potato prices (88). Even if diligently applied, these fungicides sometimes fail to control disease, resulting in reduced yield and quality. This problem is expected to be aggravated by the spread of the A^2 mating type (and therefore the sexual cycle) of late blight throughout the range of potato production (23).

Verticillium—Verticillium wilt is influenced by host genotype and a complex of biotic and cultural factors. It is one of the most important problems in U.S. and world potato production (21, 47, 49). In some areas of intensive potato cultivation, it is the predominant yield limiting disease (49). Losses of 100 cwt./acre are common, and up to 50% loss may occur in Russet Burbank continuously cropped in highly infested soils. Tuber size and specific gravity are reduced also (20, 21, 57, 75). The most effective control measure is soil fumigation, which, at approximately $200 per acre, often is not cost effective (25). Fumigation also may destroy beneficial microbes (19). Only a few soil fumigants continue to be registered in the United States. They are being closely scrutinized by the U.S. Environmental Protection Agency. Hence, their use may be curtailed in the future. Varieties with genetic resistance produce nearly double the total yield, and 3-4 times the U.S. #1 yield of Russet Burbank in infested soils (16). Clones with genetic resistance are not only more productive, but leave less inoculum in the soil to infect the subsequent crop (47).

Leafroll—This virus disease may have the greatest economic impact of all virus diseases of potato in the U.S. Over 95% of the acreage of major production areas is treated with insecticides to counter the Colorado potato beetle and the insects that spread leafroll (50). Yield losses of 60% may occur (35), including the multimillion dollar losses each year due to net necrosis of tubers, which makes them unacceptable for chips or fries (85). Systemic infection by the leafroll virus requires sprays to control transmitting insects, and vine killers to stop infection of the tubers (84). Thus, susceptible varieties incur great costs for chemical insect control and vine killers, excluding lost yield, lost processing, cost of seed certification, and storage of tubers with net necrosis (85).

Nematodes—Nematodes are an important pest worldwide, with average estimated 10% losses in infected regions. The pest also contributes, with Verticillium wilt, to a syndrome called early dying which is more severe than either of the separate diseases (27). Repeated cropping of susceptible varieties results in buildup of nematode populations in the soil. Soil fumigation is costly, and not satisfactorily reliable or safe. The best control is long rotation with non-host crops or repeated use of resistant potato cultivars (55). Only one race is a major problem in the U.S., concentrated on Long Island, New York. This pathotype is controlled effectively with new, resistant varieties derived from *S. tuberosum* ssp. *andigena* Hawkes and strict quarantine practices. Other races endemic throughout Europe and Latin America are controlled with varieties deriving resistance from *S. tuberosum* ssp. *andigena* and *S. vernei* (6).

Past Successes in Reducing Chemical Dependency—*Solanum* germplasm has already played a major role in reducing the chemical dependency of potato. This is particularly true in Europe, where over 60% of the listed varieties have incorporated features of the wild species and landrace cultivars (30). Among twenty-two North American breeding programs surveyed by Pavek (64), the primary objective of four was breeding resistance. For the remaining eighteen programs, the first objective was yield/quality and the second was breeding for resistance.

Several technological advances occurred that facilitate the use of exotic germplasm for introgression of desirable traits into breeding materials. These techniques involve 2n gametes (65), Endosperm Balance Number (26, 63), protoplast fusion (3), and genetic transformation (9). These techniques have made it possible to enhance germplasm to the level of adapted breeding stocks or cultivars, thereby reducing the potato crop's dependency on chemical treatments. Glandular hairs from *S. berthaultii* and *S. tarijense* Hawkes have provided resistance to Colorado potato beetle and other insects (59). Leptines, unique forms of glycoalkaloids from *S. chacoense* Bitter, greatly deter feeding of the Colorado potato beetle, and occur only in the potato plant's foliage (77). Monogenic resistance to the golden nematode is obtained from *S. tuberosum* ssp. *andigena* (27), and Columbia root-knot nematode is countered with genes from *S. bulbocastanum*, *S. hougasii* Correll, and *S. vernei* (7). Genes from *S. demissum* Lindley and other Mexican species have been used to combat late blight (60). Extreme resistance to PLRV and *Erwinia* have been transferred from *S. brevidens* Philippi to breeding stocks (4). Virus X and Y immunity from *S. acaule* and *S. stoloniferum*, respectfully, have been used (64, 71). Bacterial wilt resistance has been obtained from *S. chacoense*, *S. sparsipilum*, and other species (87). Breeding for Verticillium resistance has made use of *S. sparsipilum*, *S. sucrense* Hawkes, and *S. tarijense* (15). The ability to chip potatoes directly from cold storage has been transferred from *S. phureja* Juz. and Buk. to cultivars (51), reducing the dependence of stored potatoes on reconditioning and chemical sprout inhibitors.

Germplasm Availability

The great proven and potential utility of wild potato species and primitive cultivars has led to many expeditions to collect them and make them available for researchers worldwide (41, 79). NRSP-6 has sponsored or conducted collecting expeditions to Argentina in 1983, 1985, and 1990; Bolivia in 1986, 1987, and 1993; Chile in 1989 and 1990; Colombia in 1992; Ecuador in 1991; Mexico in 1965, 1982, 1983, 1984, 1988; the southwestern United States in 1978; and Venezuela in 1992. The NRSP-6 collection is by far the most comprehensive regarding ongoing wild species collection, preservation, and distribution. The International Potato Center (CIP) has concentrated on the cultivated species. Other genebanks also maintain and distribute wild potato species (41). The history of the development of NRSP-6 is documented in (1, 32, 46, 72, 73, 74, 79). NRSP-6 currently maintains 4317 accessions of 157 of the 232 species listed by Hawkes (41). These collections are actively used in breeding and many other studies worldwide. Since 1950, NRSP-6 has distributed 150,000 samples of germplasm, but demand has increased so rapidly that orders within the past ten years account for nearly half this total. NRSP-6 germplasm has been used in more than 1,765 published research papers and 190 masters or Ph.D. theses.

Systematics of *Solanum* sect. *Petota*

Definition and Goals of Systematics—Because of the great use of wild species to improve the commercial potato crop, it is imperative to have a usable and reliable systematic treatment of sect. *Petota.* Systematists attempt to group populations into categories called species, and to rank the species into a hierarchical classification of nested sets of related species. For wild potatoes, the rank most commonly used above species is series, with twenty-one recognized by Hawkes (41); followed by superseries, with two recognized by Hawkes (41); section, with sect. *Petota* and eight other sections recognized by D'Arcy (17); then subgenus, including subgenus *Potatoe* [G. Don] D'Arcy and six other subgenera (17) of the genus *Solanum,* containing 1,000-1,100 species (18). See references 10, 78, 81 for alternate hypotheses regarding relationships at all of the above ranks.

Two major goals of systematics are stability and predictability. Stability includes both consistency of names assigned to species and higher ranks (using standardized rules of nomenclature), and consistency of identifications of identical material by the same or different taxonomists. Predictability assumes that the classifications reflect genetic relatedness and can be used to make inferences about traits other than those used to construct the classification, such as disease resistances. Absolute correlations between a systematic treatment and traits of interest will not always occur but, in the absence of other data, it is the most reasonable initial *a-priori* assumption.

Systematics of sect. Petota—Fortunately, users of potato germplasm can draw upon collections and systematic treatments of many workers. Hawkes (41) provides the latest comprehensive systematic treatment of sect. *Petota,* complementing his earlier works (*e.g.*, 36) and earlier comprehensive treatments by Bukasov (8), Correll (13), and Gorbatenko (31). Of these treatments, Correll's (13) is the only one to provide illustrations, lists of representative species, and information on type specimens, and, therefore, is still very useful. Regional treatments, with useful details like those provided by Correll (13), occur for Argentina, Brazil, Paraguay, and Uruguay (42); Bolivia (43, 62); Chile (11, 56); Mexico (29, 37, 70); North and Central America (12); and Peru (14, 61).

Unfortunately, despite these many studies, there still are widely different opinions among systematists regarding species and series concepts, rank of infraspecific taxa, affiliations of species to series, and hypotheses of hybridization in sect. *Petota* (82). It often is difficult to use published keys effectively to identify specimens (80). Perhaps the greatest causes of these discrepancies are a lack of documentation of ranges of morphological variability within and between taxa (perhaps a result of few collections of some species), narrow species concepts, and subjective criteria for defining taxa (82). Potato systematics has problems inherent in the biology of the group, including lack of strong isolating mechanisms between species, interspecific hybridization, and vegetative reproduction that has the potential to maintain hybrids in the wild (13, 40, 41). Such problems have vexed all workers in sect. *Petota*, will be a source of continuing problems for future workers, and will make the long-term goal of an easily used system difficult. We need more precise studies to discover and quantify the morphological, geographical, and biological patterns of variation in sect. *Petota*. Continuing studies will likely reduce the number of species in the group (82).

Value of Continuing Collections and Systematic Studies in Sect. Petota—We need more collections to expand the 157 species known in genebanks to include all 232 species recognized by Hawkes (41). Additionally, it is necessary to obtain more accessions of existing but undercollected species. While the NRSP-6 collection has many accessions for some species (*e.g.*, *S. acaule* with 403 accessions, or *S. tuberosum* ssp. *andigena* with 803 accessions), 43% of the species in the collection have only one to five accessions. Some collections cover only a fraction of their entire geographic range. Such low coverage provides an insufficient statistical base for an understanding of variability within species needed for fine screening of the collection and for evaluation and systematic studies. According to a report by the National Research Council of the U.S. National Academy of Sciences (58), more than half of all species on earth are likely to become extinct by the year 2100, given the rate of ecosystem degradation in 1980. Thus, it is imperative that collection and preservation efforts continue to capture this diversity for future use. Consequently, NRSP-6 is maintaining an active collecting and research program of these species.

The value of systematic studies for breeders is documented (39). Problems in discordant systematic treatments of potato, maize, sorghum, and wheat led Harlan and de Wet (34) largely to ignore traditional systematic treatments in cultivated plants and construct the practical "gene pool" classification of cultivars and their wild relatives. They based their classification entirely on the ease of crossability, and ignore the additional systematic criteria mentioned above. Harlan and de Wet's (34) solution is reasonable with wide incongruities in existing treatments. As pointed out by Spooner and van den Berg (82), however, there are phenetically distinct groups of populations with distinct geographic ranges, ecological adaptations, and presumably distinct evolutionary histories within crossing groups in sect. *Petota*. A strict application of the gene pool concept would conceal the additional information to be obtained from a clearer interpretation of these patterns. Continuing studies in sect. *Petota* (reviewed in 82) are providing refinements to the extensive and useful prior treatments. It takes 8-15 years from the initiation of a breeding program to a release of a commercial variety (69). A refined understanding of species boundaries and interrelationships, in combination with the gene pool concept, has the potential to save time and money in breeding of potato and other crops. A better classification can guide the choice of new materials by the choice or avoidance of species based on past breeding results. The discovery and use of yet unknown traits in germplasm collections have the potential for enormous impact on reducing chemical inputs in the potato crop.

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