A Test of Taxonomic and Biogeographic Predictivity: Resistance to *Potato virus Y* in Wild Relatives of the Cultivated Potato

X. K. Cai, D. M. Spooner, and S. H. Jansky

First author: College of Horticulture and Forestry, Huazhong Agricultural University, Wuhan, Hubei, China; second and third authors: United States Department of Agriculture–Agricultural Research Service, Department of Horticulture, University of Wisconsin, Madison, 53706-1590.

ABSTRACT

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A major justification for taxonomic research is its assumed ability to predict the presence of traits in a group for which the trait has been observed in a representative subset of the group. Similarly, populations in similar environments are expected to be more alike than populations in divergent environments. Consequently, it is logical to assume that taxonomic relationships and biogeographical data have the power to predict the distribution of disease resistance phenotypes among plant species. The objective of this study was to test predictivity in a group of widely

distributed wild potato species, based on hypotheses that closely related organisms (taxonomy) or organisms from similar environments (biogeography) share resistance to a simply inherited trait (*Potato virus Y* [PVY]). We found that wild potato species with an endosperm balance number (EBN) of 1 (a measure of cross compatibility) shared resistances to PVY more than species with different EBN values. However, a large amount of variation was found for resistance to PVY among and within species. We also found that populations from low elevations were more resistant than those from high elevations. Because PVY is vectored by aphids, we speculate that the distribution of aphids may determine the level of selection pressure for PVY resistance.

Potato virus Y (PVY) is the most important viral pathogen in potato worldwide (10,26). Yield losses of up to 40% have been documented (30). Disease symptoms include necrosis, mottling, chlorosis, leaf drop, and premature plant death. PVY is a member of the *Potyviridae* family, the largest group of plant viruses. It can cause disease in many members of the plant family *Solanaceae*, as well as some members of the families *Chenopodiaceae* and *Leguminosae*. The virus can be mechanically spread but aphid vectors are the most important mechanism for transmission in the field. In all, >50 species of aphids are able to act as vectors of PVY (34). In recent years, PVY has emerged as a serious disease problem in many potato production areas in North America. Previously, seed certification programs effectively controlled the disease. One explanation for the increase in incidence of PVY in certified seed is that cultivars such as 'Russet Norkotah', 'Shepody', and 'Silverton Russet' have become popular. These cultivars are susceptible to PVY but express mild or no symptoms, preventing effective rouging of infected plants during seed production (12,30).

The development of cultivars with improved levels of PVY resistance provides a logical strategy to minimize losses to PVY. There are ≈100 wild potato species distributed from the southwestern United States to Chile, with two centers of diversity, in central Mexico and in the central Andes (39). Collectively, these species represent a more diverse and accessible germplasm resource than in any other major crop (13,16,33,36). Wild potato

species are found in a wide array of environments, including the high grasslands of the Andes, humid temperate mountain rain forests, mossy branches of trees, and cultivated fields. The wild species contain genes encoding numerous traits not found in cultivars and represent an especially rich source of disease resistance genes (13,20,41). The U.S. Potato Genebank (NRSP-6) maintains a collection of ≈5,000 accessions of wild and cultivated potato (*Solanum* L. section *Petota* Dumort.) species. This is a significant resource for potato breeders and researchers but the task of searching for specific traits in such a large collection is daunting. A systematic strategy to search for phenotypes of interest is needed. Taxonomic relationships are regularly used by breeders when choosing potential sources of disease-resistant germplasm for cultivar improvement.

Major dominant genes that confer PVY resistance have been identified in wild *Solanum* relatives and in cultivated *Solanum tuberosum* Andigenum Group and Chilotanum Group germplasm (38,44). The two main types of resistance in potato are extreme resistance (ER), which protects against all strains of PVY by suppressing virus accumulation in infected cells, and hypersensitive resistance (HR). ER has been identified in the wild potato species *S. chacoense*, *S. hougasii*, *S. stoloniferum*, and the *S. tuberosum* Andigenum Group (6,29,37), while HR to PVY ordinary (O) strain group (PVY[O]) has been reported in *S. chacoense*, *S. demissum*, *S. megistacrolobum*, *S. polyadenium*, *S. sparsipilum*, *S. stoloniferum*, and the *S. tuberosum* Andigenum and Chilotanum Groups (3,7,44). Resistance in other *Solanum* spp. has been identified but the physiological basis is not known. For example, high levels of resistance have been reported in the non-tuber-bearing species *S. etuberosum* (31,32,45).

A major justification for taxonomic research is its assumed ability to predict the presence of traits in a group for which the trait has been observed in a representative subset of the group. Jansky et al. (24) summarized the history and theory of taxonomic predictivity, and the general theoretical constraints of using

Corresponding author: S. H. Jansky; E-mail address: shelley.jansky@ars.usda.gov

disease as a trait to be associated with taxonomy. For example, complex inheritance can reduce predictivity with taxonomy or geography, because the phenotype (disease resistance) may be caused by diverse and nonhomologous genes. The genetic bases of resistance traits in previous predictivity studies are not well established. In fact, it is likely that multiple physiological, morphological, and genetic mechanisms contribute to a complex array of resistance phenotypes. However, a single dominant gene has been found to confer PVY resistance in each of several *Solanum* spp. Consequently, we wished to test whether predictivity strategies may be more effective for simply inherited PVY resistance genes.

In addition to associations of disease resistance to species, we tested associations to series (groups of putatively interrelated species as determined by intuitive methods as inferred by Hawkes [16]), ploidy, crossability groups, geographic distance, climatic parameters, and plastid-based molecular clades. A summary of plastid-based restriction site phylogenetic studies (as a phylogenetic tree) of section *Petota* as discovered by several combined studies (2,35,40,42) is shown in Figure 1. Ploidy levels of wild *Solanum* spp. range from diploid ($2n = 24$) to tetraploid to hexaploid ($2n = 72$) (18). In addition, wild and cultivated potato species have been assigned endosperm balance numbers (EBNs) based on their ability to hybridize with each other, as evidenced by endosperm breakdown in EBN-incompatible species (14). Ploidy (EBN) combinations in potato include 2x(1EBN), 2x(2EBN), 4x(2EBN), 4x(4EBN), and 6x(4EBN).

Another screening strategy might use biogeographic parameters to identify potential regions of high selection pressure for the trait. Because PVY is vectored by aphids, climatic factors that influence aphid distribution may predict where plants with resistance have evolved.

The objective of our study was to determine whether PVY resistance in wild potato germplasm is associated with taxonomic species, series, clade, ploidy, crossability group (EBN), latitude, longitude, or altitude.

MATERIALS AND METHODS

Plant material. The potato accessions in NRSP-6 were originally collected in 12 countries in the Americas, covering most of the distribution area of wild potato that occurs from Colorado (United States) south to Chile, Argentina, Uruguay, and southern Brazil. Species richness is high in central Mexico at 20°N, and in the southern hemisphere, particularly in the Andean highlands at 8 to 20°S (17). Our study included 136 accessions (populations) of 39 wild *Solanum* spp., representing 13 of the 19 tuber-bearing series of Hawkes (16) and all four clades of section *Petota*. The species included 37 ingroups (section *Petota*) and two outgroups (section *Etuberosum*, including *S. etuberosum* Lindl. and *S. palustre* Poepp.) (Table 1). For the 136 accessions evaluated, 97 (71.3%) were diploid, 22 (16.2%) were tetraploid, and 17 (12.5%) were hexaploid. Accessions were chosen to represent the majority of the range of the species (Fig. 2). Because interaccession phenotypic variation in species is high, two to five accessions per species were evaluated. Accessions examined and raw screening data are available in Supplemental Table 1.

Virus isolates. Virus inoculum (PVY^O) was kindly provided by Professor Amy Charkowski, Department of Plant Pathology University of Wisconsin–Madison. It was maintained and propagated in *Nicotiana tabacum* L. 'Xanthi'.

Disease resistance screening. Seed were soaked in gibberellic acid at 1,500 ppm for 24 h to break dormancy. In all, ≈100 seeds of each of 159 accessions were then sown in flats in a peat-based potting mix (Pro-Mix) on 10 September 2008, and grown in a greenhouse with an 18-h photoperiod. Night and day temperatures were 18 to 20°C and 20 to 25°C, respectively. Twenty-three accessions were eliminated from the trial due to poor seed germination or low seedling vigor. On 1 October, 15 seedlings of each accession were transplanted to individual peat pots. Leaves of each plant were mechanically inoculated at six points with a Paasche model H airbrush (Chicago) at 40 psi using carborundum power as an abrasive. The inoculum was made by extracting sap from leaves of infected tobacco plants (3 g of leaf per 100 ml of 0.1 M potassium phosphate buffer, pH 7.0). Plants were inoculated at the seven- to eight-leaf stage (4 to 6 weeks after transplanting). Four weeks after inoculation, plants were visually evaluated for virus symptoms (leaf chlorosis, lower leaf necrosis, and leaf drop). Uninoculated leaves from asymptomatic plants were tested for the presence of PVY using a double-antibody sandwich enzyme-linked immunosorbent assay (ELISA) (5). ELISA kits were obtained from Agdia (Elkhart, IN). Absorption at 405 nm was measured with an ELISA reader (Bio-TEK, ELx800). Absorbance values of uninoculated control samples were 0.00 to 0.01. PVY is not transmitted through true potato seed; therefore, all uninoculated seedlings were virus-free. Values >0.1 were regarded as positive for PVY^O, according to Sato et al. (37).
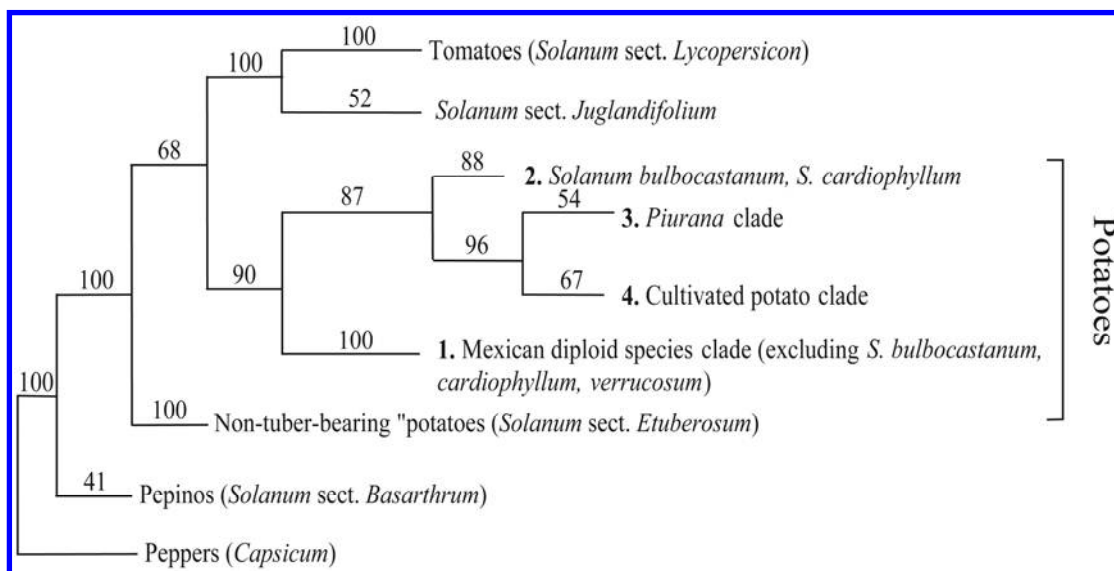

Fig. 1. Cladistic relationships (phylogenetic tree) of potato, tomato, and outgroups, sensu Spooner and collaborators as described in text, showing the four clades in potato (1 to 4) and outgroups. The numbers above the branches are bootstrap values, with higher numbers representing greater support of the branches.

In order to address the possibility of escapes in the 2008 trial, on 12 April 2009, cuttings from plants with ELISA values <0.1 were established in individual peat pots in a greenhouse. Rooted cuttings were transplanted into each of two replications in a randomized complete block design. Individual plants were inoculated and scored as in 2008.

Statistical analyses. ELISA absorbance values were 0.0 to 3.0. Plants were considered resistant if they exhibited scores <0.1 in the initial screen and after reinoculation. Plants were considered susceptible if they exhibited symptoms or if any leaf samples had ELISA scores ≥0.1. Data from the ELISA tests were censored because 3.0 was the maximum ELISA absorbance value recorded. Because of this scoring system, a binary data set was analyzed. Plants with absorbance values consistently <0.1 were given a value of 0 (resistant) and all others were given a value of 1 (susceptible). The PROC GLIMMIX procedure in SAS was used to analyze variation in this binary data set, based on species, series, clade, ploidy, and EBN. Individual plants in each accession were considered replications. Means separation was carried out using a protected least significant difference test. Pearson correlation coefficients were calculated to identify potential relationships between percent resistant plants (ELISA absorbance value <0.1) and biogeographic data (latitude, longitude, and elevation). Further refinement of biogeographic data was carried out using χ^2 tests.

RESULTS

PVY resistance was identified in 17 of the 39 species tested (Fig. 3). Of the 1,443 plants tested, 136 (9.4%) appeared to be escapes but 160 (11%) were resistant to PVY. Significant differences in mean percent susceptible plants were detected among species (Table 2). The two outgroup species *S. etuberosum* and *S.*

Fig. 2. Distribution of *Potato virus Y*-resistant and susceptible accessions (triangles are resistant accessions, circle are susceptible accessions).

TABLE 1. Number of accessions and number of plants, ploidy, endosperm balance number (EBN), clade, and series of *Solanum* spp. evaluated for *Potato virus Y* resistance

Species	Number of accessions	Number of plants	Ploidy	EBN	Clade	Series
Solanum acaule	2	30	4×	2	4	*Acaulia*
S. agrimonifolium	3	21	4x	2	4	*Conicibaccata*
S. albicans	3	22	6x	4	4	*Acaulia*
S. albornozii	3	32	2x	2	3	*Piurana*
S. andreanum	2	21	2x	2	3	*Tuberosa*
S. boliviense	5	57	2x	2	4	*Magistacroloba*
S. brevicaule	4	44	2x	2	4	*Tuberosa*
S. bukasovii	4	40	2x	2	4	*Tuberosa*
S. bulbocastanum	4	39	2x	1	2	*Bulbocastana*
S. cardiophyllum	3	34	2x	1	2	*Pinnatisecta*
S. chacoense	4	48	2x	2	4	*Yungasensia*
S. chomatophilum	3	22	2x	2	3	*Conicibaccata*
S. colombianum	3	34	4x	2	4	*Conicibaccata*
S. commersonii	3	24	2x	1	4	*Commersoniana*
S. demissum	4	50	6x	4	4	*Demissa*
S. ehrenbergii	3	31	2x	1	1	*Pinnatisecta*
S. etuberosum	3	26	2x	1	O	*Outgroup*
S. hjertingii	4	30	4x	2	4	*Longipedicellata*
S. infundibuliforme	4	42	2x	2	4	*Cuneoalata*
S. iopetalum	4	29	6x	4	4	*Demissa*
S. jamesii	5	43	2x	1	1	*Pinnatisecta*
S. kurtzianum	4	54	2x	2	4	*Tuberosa*
S. lesteri	3	26	2x	1	1	*Polyadenia*
S. megistacrolobum	3	25	2x	2	4	*Magistacroloba*
S. microdontum	4	44	2x	2	4	*Tuberosa*
S. moscopanum	3	22	6x	4	4	*Conicibaccata*
S. palustre	3	18	2x	1	O	*Outgroup*
S. paucijugum	3	29	4x	2	3	*Conicibaccata*
S. pinnatisectum	4	44	2x	1	1	*Pinnatisecta*
S. polyadenium	4	34	2x	1	1	*Polyadenia*
S. raphanifolium	4	49	2x	2	4	*Magistacroloba*
S. schenckii	3	31	6x	4	4	*Demissa*
S. sparsipilum	3	45	2x	2	4	*Tuberosa*
S. stenophyllidium	4	55	2x	1	1	*Pinnatisecta*
S. stoloniferum	5	74	4x	2	4	*Longipedicellata*
S. tarijense	4	59	2x	2	4	*Yungasensia*
S. tuquerrense	2	30	4x	2	3	*Piurana*
S. verrucosum	4	45	2x	2	4	*Tuberosa*
S. violaceimarmoratum	3	40	2x	2	4	*Conicibaccata*

palustre were the most resistant, while *S. lesteri* and *S. megistacrolobum* were the most susceptible, with high PVY titer detected in all plants. Significant differences were also detected for series, clade, EBN, and ploidy. The two most resistant groups were section *Etuberosum* (which contains the outgroup species), followed by series *Bulbocastana* (Table 3). The most resistant clade was the outgroup, which was composed of the two highly resistant non-tuber-bearing species (Table 4). The next most resistant clade was 2, which was more resistant than the remaining three clades. The 1EBN species were more resistant than 2EBN and 4EBN species (Table 5), while diploids were more resistant than both tetraploids and hexaploids (Table 6).
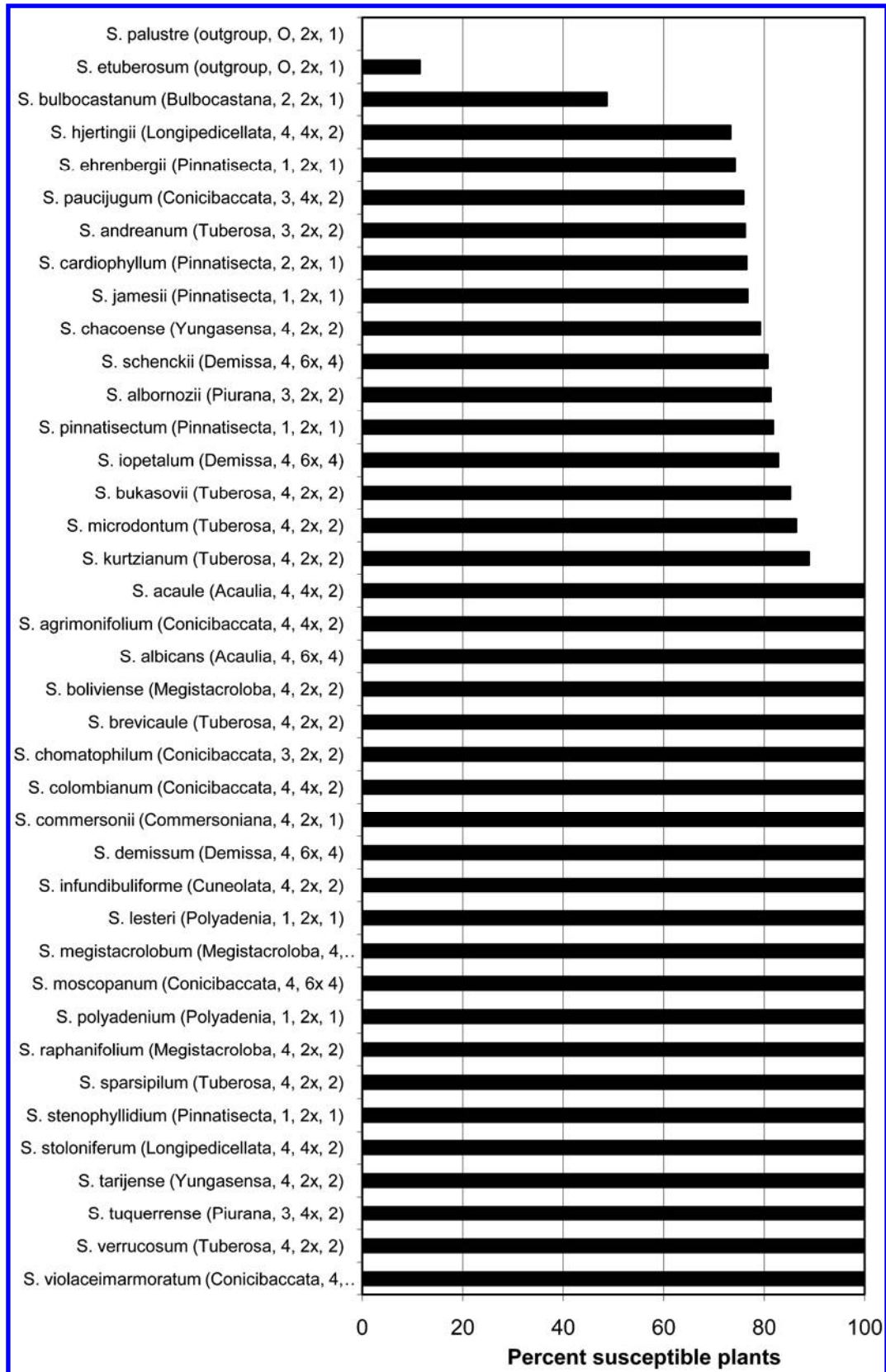
Chart — Percent susceptible plants (x-axis: 0, 20, 40, 60, 80, 100):

- S. palustre (outgroup, O, 2x, 1) — 0
- S. etuberosum (outgroup, O, 2x, 1) — ~11
- S. bulbocastanum (Bulbocastana, 2, 2x, 1) — ~48
- S. hjertingii (Longipedicellata, 4, 4x, 2) — ~73
- S. ehrenbergii (Pinnatisecta, 1, 2x, 1) — ~74
- S. paucijugum (Conicibaccata, 3, 4x, 2) — ~76
- S. andreanum (Tuberosa, 3, 2x, 2) — ~76
- S. cardiophyllum (Pinnatisecta, 2, 2x, 1) — ~77
- S. jamesii (Pinnatisecta, 1, 2x, 1) — ~77
- S. chacoense (Yungasensa, 4, 2x, 2) — ~79
- S. schenckii (Demissa, 4, 6x, 4) — ~81
- S. albornozii (Piurana, 3, 2x, 2) — ~81
- S. pinnatisectum (Pinnatisecta, 1, 2x, 1) — ~82
- S. iopetalum (Demissa, 4, 6x, 4) — ~83
- S. bukasovii (Tuberosa, 4, 2x, 2) — ~85
- S. microdontum (Tuberosa, 4, 2x, 2) — ~86
- S. kurtzianum (Tuberosa, 4, 2x, 2) — ~89
- S. acaule (Acaulia, 4, 4x, 2) — 100
- S. agrimonifolium (Conicibaccata, 4, 4x, 2) — 100
- S. albicans (Acaulia, 4, 6x, 4) — 100
- S. boliviense (Megistacroloba, 4, 2x, 2) — 100
- S. brevicaule (Tuberosa, 4, 2x, 2) — 100
- S. chomatophilum (Conicibaccata, 3, 2x, 2) — 100
- S. colombianum (Conicibaccata, 4, 4x, 2) — 100
- S. commersonii (Commersoniana, 4, 2x, 1) — 100
- S. demissum (Demissa, 4, 6x, 4) — 100
- S. infundibuliforme (Cuneolata, 4, 2x, 2) — 100
- S. lesteri (Polyadenia, 1, 2x, 1) — 100
- S. megistacrolobum (Megistacroloba, 4,..) — 100
- S. moscopanum (Conicibaccata, 4, 6x 4) — 100
- S. polyadenium (Polyadenia, 1, 2x, 1) — 100
- S. raphanifolium (Megistacroloba, 4, 2x, 2) — 100
- S. sparsipilum (Tuberosa, 4, 2x, 2) — 100
- S. stenophyllidium (Pinnatisecta, 1, 2x, 1) — 100
- S. stoloniferum (Longipedicellata, 4, 4x, 2) — 100
- S. tarijense (Yungasensa, 4, 2x, 2) — 100
- S. tuquerrense (Piurana, 3, 4x, 2) — 100
- S. verrucosum (Tuberosa, 4, 2x, 2) — 100
- S. violaceimarmoratum (Conicibaccata, 4,..) — 100

Percent susceptible plants

Fig. 3. Percent *Potato virus Y*-susceptible plants in wild *Solanum* species (series, clade, ploidy, endosperm balance number).

Considering biogeographical associations, there was no correlation between longitude and resistance ($r = -0.01$, $P = 0.93$) or between absolute latitude and resistance ($r = -0.16$, $P = 0.06$). The correlation between resistance and elevation was negative and significant ($r = -0.39$, $P < 0.001$). A χ^2 analysis revealed that the proportion of resistant plants in accessions collected at elevations <2,100 m was higher than the overall proportion of resistant plants ($\chi^2 = 20.4$, $P = 0.000006$).

DISCUSSION

Our study confirmed previous reports of PVY resistance in the species *S. chacoense* (7,37) and *S. microdontum* (7) and the outgroup species *S. etuberosum* and *S. palustre* (11,45). However, we also identified resistance in species for which PVY resistance has not been previously published: *S. albornozii*, *S. andreanum*, *S. bukasovii*, *S. bulbocastanum*, *S. cardiophyllum*, *S. hjertingii*, *S. iopetalum*, *S. jamesii*, *S. kurtzianum*, *S. paucijugum*, *S. pinnatisectum*, and *S. schenckii*. Among the resistant species, *S. chacoense*, *S. microdontum*, *S. bukasovii*, and *S. kurtzianum* are easily crossed to diploid cultivated potato; therefore, they represent the most promising sources of PVY resistance for cultivar development. Interestingly, one of the main sources of PVY resistance in potato breeding has been *S. stoloniferum* (7,9,43,44) but, despite testing 74 plants in five accessions, no resistance was found. Similarly, resistance to PVY has been reported in *S.*

demissum (7) and *S. megistacrolobum*, and *S. polyadenium* (44) but we did not find any resistant plants of these species in our assays. Intra- and interaccession variation for disease resistance is common in *Solanum* spp. (4,8,24,25). Therefore, it is likely that the accessions we tested did not contain resistance genes. The accessions used in our study were not the same as those in previous reports of resistant species. In our study, interaccession variability was observed for all tuber-bearing species in which PVY resistance was found. Alternatively, the accessions we tested may have contained resistance genes but they were present at a low allele frequency; therefore, we did not observe them in our samples.

TABLE 2. Number of accessions, number of plants, and mean proportion of susceptible plants for 39 *Solanum* spp. inoculated with *Potato virus Y*[z]

Species	Number of accessions	Number of plants	Mean, LSD
Solanum palustre	3	18	0.000 a
S. etuberosum	3	26	0.115 a
S. bulbocastanum	4	39	0.487 b
S. hjertingii	4	30	0.733 c
S. ehrenbergii	3	31	0.742 c
S. paucijugum	3	29	0.759 cd
S. andreanum	2	21	0.762 cd
S. cardiophyllum	3	34	0.765 cd
S. jamesii	5	43	0.767 cd
S. chacoense	4	48	0.792 cd
S. schenckii	3	31	0.807 cd
S. albornozii	3	32	0.813 cd
S. pinnatisectum	4	44	0.818 cd
S. iopetalum	4	29	0.828 cd
S. bukasovii	4	40	0.852 cd
S. microdontum	4	44	0.864 cd
S. kurtzianum	4	54	0.889 cd
S. acaule	2	30	1.000 d
S. agrimonifolium	3	21	1.000 d
S. albicans	3	22	1.000 d
S. boliviense	5	57	1.000 d
S. brevicaule	4	44	1.000 d
S. chomatophilum	3	22	1.000 d
S. commersonii	3	24	1.000 d
S. colombianum	3	34	1.000 d
S. demissum	4	50	1.000 d
S. infundibuliforme	4	42	1.000 d
S. lesteri	3	26	1.000 d
S. megistacrolobum	3	25	1.000 d
S. moscopanum	3	22	1.000 d
S. polyadenium	4	34	1.000 d
S. raphanifolium	4	49	1.000 d
S. stenophyllidium	4	55	1.000 d
S. sparsipilum	3	45	1.000 d
S. stoloniferum	5	74	1.000 d
S. tarijense	4	59	1.000 d
S. tuquerrense	2	30	1.000 d
S. verrucosum	4	45	1.000 d
S. violaceimarmoratum	3	40	1.000 d

[z] Means separation is based on a least significant difference (LSD) test at $P = 0.05$.

TABLE 3. Number of accessions, number of plants, and mean proportion of susceptible plants in section *Etuberosum* and 13 taxonomic series in section *Petota* inoculated with *Potato virus Y*[z]

Series (and section *Etuberosum*)	Number of accessions	Number of plants	Mean, LSD
Outgroup	6	44	0.068 a
Bulbocastana	4	39	0.487 b
Pinnatisecta	19	207	0.836 c
Demissa	11	110	0.900 cd
Piurana	5	62	0.903 cd
Yungasena	8	107	0.907 cd
Tuberosa	25	293	0.922 de
Longipedicellata	9	104	0.923 de
Conicibaccata	18	168	0.958 de
Acaulia	5	52	1.000 e
Commersoniana	3	24	1.000 e
Cuneoalata	4	42	1.000 e
Megistacroloba	12	131	1.000 e
Polyadenia	7	60	1.000 e

[z] Means separation is based on a least significant difference (LSD) test at $P = 0.05$.

TABLE 4. Number of accessions, number of plants, and mean proportion of susceptible plants in four clades in section *Petota* and the outgroup (O) inoculated with *Potato virus Y*[z]

Clade	Number of accessions	Number of plants	Mean, LSD
O	6	44	0.068 a
2	7	73	0.616 b
3	13	134	0.866 c
1	23	233	0.888 c
4	87	959	0.951 d

[z] Means separation is based on a least significant difference (LSD) test at $P = 0.05$.

TABLE 5. Number of accessions, number of plants, and mean proportion of susceptible plants for three *Solanum* crossability (endosperm balance number [EBN]) groups inoculated with *Potato virus Y*[z]

EBN	Number of accessions	Number of plants	Mean, LSD
1	39	374	0.746 a
4	17	154	0.929 b
2	80	915	0.941 b

[z] Means separation is based on a least significant difference (LSD) test at $P = 0.05$.

TABLE 6. Number of accessions, number of plants, and mean proportion of susceptible plants for three ploidy levels of *Solanum* spp. inoculated with *Potato virus Y*[z]

Ploidy	Number of accessions	Number of plants	Mean, LSD
2x	97	1,041	0.871 a
6x	17	154	0.929 b
4x	22	248	0.940 b

[z] Means separation is based on a least significant difference (LSD) test at $P = 0.05$.

Because resistance was identified in 9 of the 14 series represented in the study and in all four clades plus the outgroup (Figs. 1 and 3), broad taxonomic groupings do not seem to predict the distribution of PVY resistance genes. However, the species *S. bulbocastanum*, *S. chacoense*, and *S. commersonii* have been among the most resistant species in four of the five predictivity studies we have carried out to date. *S. chacoense* and *S. commersonii* are widely distributed in southern South America and *S. bulbocastanum* is found from central Mexico to Guatemala. In a previous predictivity study (4), we found that high levels of soft rot resistance are associated with phenotypic plasticity in *Solanum* spp. Perhaps this concept can be extended more broadly to biotic stresses.

In this study and many previous ones, 1EBN species have been rich sources of disease resistance (22,24,25,27,28,47). In contrast to 2EBN species, which are directly crossable to diploid forms of the cultivated potato, the 1EBN species are not sexually compatible with the cultivated potato (15). However, they can be introgressed using in vitro chromosome doubling, somatic fusion, or bridge crosses (21,23). In our study, whereas the majority of resistant species were 1EBN, several 1EBN species were susceptible (*S. commersonii*, *S. lesteri*, *S. polyadenium*, and *S. stenophyllidium*), and several 2EBN species were resistant. We found diploid species to be more resistant than tetraploid or hexaploid species (Table 6). However, the highly resistant 1EBN species are all diploid. When they are removed from the analysis, there is no effect of ploidy on resistance.

The finding in this study that resistance to a simply inherited disease, PVY, showed a lack of association to taxonomic traits similar to that of resistance with complex inheritance (in previous studies) suggests that the genetic complexity of a trait does not determine whether taxonomic predictivity will be effective. It may be more related to the complex biological histories of wild potato, including possible recent evolution, interspecific hybridization, and allopolyploidy involving species across different clades (39).

It is interesting that, in the outgroup species, all plants of S. *palustre* (formerly *S. brevidens*) and 23 of 26 plants of *S. etuberosum* were resistant to PVY. Extreme resistance to PVY has been previously reported in these species (11,45). In previous studies with these two species, virus particles were observed in microscopy studies following graft inoculations but they remained below the ELISA detection limit (45). Consequently, although they are very strong sources of PVY resistance, they do not exhibit immunity.

When accessions are plotted on a map, the lack of resistant accessions in the high Andes becomes apparent (Fig. 2). PVY is vectored by >50 species of aphids (34) and the spread of PVY is determined by the presence of the vector and the availability of inoculum (46). Temperature is the most important factor influencing aphids in moderate climates, with cool temperatures limiting movement (1). A strong negative correlation was observed between spring air temperature and PVY incidence (19). In the current study, cold temperatures at high elevations likely resulted in low virus incidence and a lack of selection pressure for PVY resistance. Additional studies are underway to determine whether the distribution of the vector corresponds to that of PVY resistance genes.

This is our fifth study designed to test the predictive component of diverse *Solanum* spp. taxonomies and biogeography using disease resistance data. Previous studies found tremendous variation within and among species for resistance to the foliar fungal disease white mold (24), the foliar fungal disease early blight (25), the defoliating insect Colorado potato beetle (22), and the bacterial tuber disease soft rot (4). No consistent associations were observed between disease or pest resistance and taxonomic series, clade, ploidy, EBN, geographic distance, or climate parameters. Species and individual accessions with high proportions of

resistant plants were identified in each study but both often exhibited extensive variation. Consequently, we have not found that taxonomic relationships or ecogeographic data can be used to consistently predict where additional sources of resistance genes are likely to be found. Based on these results, a more effective strategy than taxonomic and biogeographic prediction is probably careful screening of core collections.

ACKNOWLEDGMENTS

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