

## **Insect resistance in potatoes: sources, evolutionary relationships, morphological and chemical defenses, and ecogeographical associations**

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### **Summary**

The past 25 years, 1686 potato accessions, representing 100 species in the genus *Solanum* L., subgenus *Potatoe*, section *Petota*, were evaluated for field resistance to one or more of the following insect pests: green peach aphid, *Myzus persicae* (Sulzer); potato aphid, *Macrosiphum euphorbiae* (Thomas); Colorado potato beetle, *Leptinotarsa decemlineata* (Say); potato flea beetle, *Epitrix cucumeris* (Harris); and potato leafhopper, *Empoasca fabae* (Harris). Accessions highly resistant to green peach aphid were identified within 36 species, to potato aphid within 24 species, to Colorado potato beetle within 10 species, to potato flea beetle within 25 species, and to potato leafhopper within 39 species. Resistance levels were characteristic within *Solanum* species. Insect resistance appears to be a primitive trait in wild potatoes. Susceptibility was most common in the primitive and cultivated *Tuberosa*. Insect resistance was also characteristic of the most advanced species. The glycoalkaloid tomatine was associated with field resistance to Colorado potato beetle and potato leafhopper. Other glycoalkaloids were not associated with field resistance at the species level. Dense hairs were associated with resistance to green peach aphid, potato flea beetle, and potato leafhopper. Glandular trichomes were associated with field resistance to Colorado potato beetle, potato flea beetle, and potato leafhopper. Significant correlations between insect score and altitude of original collection were observed in six of thirteen species. Species from hot and arid areas were associated with resistance to Colorado potato beetle, potato flea beetle, and potato leafhopper. Species from cool or moist areas tended to be resistant to potato aphid.

**Abbreviations:** EBN – Endosperm Balance Number

### **Introduction**

The tuber-bearing *Solanum* species and their immediate relatives comprise a bewildering number of species (some 235 by present reckoning) from

diverse geographic regions and habitats. In this study, we attempt to associate resistance to five potato pests with characteristics of the potato species themselves, using the proposed evolutionary scenario of Hawkes (1990), and data on climatic

adaptation, as well as chemical and physical features of the potato species.

Potatoes occur from the southwestern USA southward through Mexico and Central America into southern South America. However, most species are restricted to the western Andes. Seven species are cultivated, the rest are 'wild'. In the latest classification (Hawkes, 1990), the genus *Solanum*, subgenus *Potatoe*, section *Petota* is divided into two subsections, *Estolonifera*, which do not form tubers, and *Potatoe*, which are tuber-bearing. The subsections are further divided into a total of 21 series.

Potatoes occur in a very wide range of habitats, ranging from hot, dry semideserts to cold wet upland and lowland forests, grasslands, and even ocean beaches. Thus, it is not surprising that within various adaptive ranges resistances to pests and pathogens and adaptations to environmental extremes vary greatly (Rowe, 1969).

Exotic potato germplasm has and continues to be used as a source of desirable traits for improvement of *Solanum tuberosum* cultivars (Plaisted & Hoopes, 1989). The prerequisite to such plant breeding programs is identification of suitable germplasm in potato collections. Potato germplasm is presently held in nine major potato genebanks, one of which is the Inter-Regional Potato Introduction Project in Sturgeon Bay, Wisconsin, the sole genebank for wild and cultivated potatoes in the United States (Hanneman, 1989).

During the past 25 years, approximately 125,000 plants from 2128 potato accessions were screened in Minnesota for field resistance to one or more of the following potato insect pests: green peach aphid, *Myzus persicae* (Sulzer) (Homoptera: Aphididae); potato aphid, *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae); Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae); potato flea beetle, *Epitrix cucumeris* (Harris) (Coleoptera: Chrysomelidae); and potato leafhopper, *Empoasca fabae* (Harris) (Homoptera: Cicadellidae). This paper discusses the results from the 1686 wild potato accessions for which taxonomic identification has been verified by one of us (J.G.H.). The extensive data collected

identify germplasm possibly useful as sources of insect resistance in potato breeding programs.

## Materials and methods

The insect resistance rating data reported here were collected from 1966 to 1986 by the Minnesota authors. Material evaluated was primarily from the Inter-Regional Potato Introduction Project, although some commercial potato cultivars and advanced breeding lines were included. Data on response of individual potato accessions to green peach aphid or potato aphid can be obtained from Radcliffe et al. (1981, 1988) and Radcliffe & Lauer (1971). Data on response of an individual potato accession to Colorado potato beetle, potato leafhopper, and potato flea beetle can be obtained from Flanders & Radcliffe (1992) and Radcliffe & Lauer (1968). Details on experimental methods used can also be obtained from these papers. Partial results of these screenings have been incorporated into the Inter-Regional Potato Introduction Project inventory (Hanneman & Bamberg, 1986) and interpreted by Rowe (1969) and Gould (1983).

Procedures followed in Minnesota resistance trials were as follows: plants were started from true potato seed in mid-April to early May and seedlings were transplanted into the field in mid-June. A randomized complete block design with 3–6 plants per plot was used throughout these experiments. Three to five replications were used, depending upon the experiment. For a few accessions, vegetatively propagated materials were used in the aphid screenings. Aphid trials were run in Grand Rapids and Rosemount, Minnesota, and were treated with insecticides to enhance aphid populations and eliminate competing pests. Colorado potato beetle experiments were run in the Red River Valley of the North (Crookston, Minnesota and Grand Forks, North Dakota) using local beetle populations. Pressure from other potato insect pests was not consequential in the Colorado potato beetle experiments. Potato flea beetle and leafhopper trials were run in Rosemount, Minnesota, and were protected from Colorado potato

beetle defoliation with foliar applications of *Bacillus thuringiensis* var *san diego*. Aphids were of little consequence in the latter experiments as *Bacillus thuringiensis* does not enhance aphid populations.

#### *Data collection and analysis*

The goal of our field screening trials was to determine the average insect response to a particular accession. Repeated evaluations and testing multiple plants per evaluation characterized such a response, but at the expense of data on within-accession variation.

Resistance to aphids was evaluated with timed counts of 20–45 seconds, usually 30 seconds, duration per plant. In the sampling times used it was not possible to count all the aphids except on the smallest plants, thus results were largely independent of plant size. An upper ceiling of 100 aphids was used, so there was little difference in results in timed counts of varying lengths. Each evaluation represented a single timed count. Twenty-one percent of accessions evaluated for green peach aphid resistance were evaluated only once during 1966–1979, 58% were evaluated 2–5 times, and 21% were evaluated more than 5 times (the maximum number of evaluations was 55). Each evaluation, replicate means were averaged to determine overall accession means. Nine accessions were included as resistant standards in nearly all green peach aphid evaluations, allowing for comparisons across evaluations. The standards were each included in 95% of the trials. Missing values were estimated in the few previous trials in which one or more of these standards were not represented. Mean number of green peach aphids per plant per evaluation ranged from 0.32 to 58.32. Although insect pressure varied widely between evaluations, relative resistance within an evaluation was remarkably stable (Radcliffe et al., 1981). For each evaluation, the mean number of green peach aphids per plant over the nine standards was set equal to 1.0. In a given trial, mean aphid counts for each entry were expressed as ratios relative to that denominator. After standardization, a mean ratio ( $x$ ) over all evaluations

was calculated for each entry. Ratios were transformed to  $\log_{10}(x + 0.01)$ .

For potato aphid, 26% of accessions were evaluated only once during 1966–1979, 55% were evaluated 2–5 times, and 19% were evaluated more than 5 times (the maximum number of evaluations was 42). The same nine resistant standards were used to compensate for variation between evaluations. Means for the nine standard accessions ranged from 0.04 to 25.8 potato aphids per plant. Overall mean ratios were calculated and transformed as with green peach aphid.

Colorado potato beetle resistance was evaluated using defoliation and beetle abundance on a 0–3 scale, with 0 indicating no defoliation and 3 indicating more than 90% defoliation. Plants were evaluated three times in 1983 and twice in 1984, with 22% of accessions common to both years. Mean defoliation rating for the common accessions was 1.35 in 1983 and 1.64 in 1984. Overall mean defoliation rating was calculated for each accession (2–5 evaluations).

Leafhopper data from 1966 were timed nymphal counts of 30 sec duration per plant. In 1985–1986, plants were vacuumed to determine number of potato flea beetle adults and potato leafhopper nymphs present per plant. One evaluation was made in 1966, four in 1985, and three in 1986, with 17% of accessions evaluated in more than one year for potato flea beetle, and 25% of accessions evaluated in more than one year for potato leafhopper. Twenty-eight accessions were common for all potato leafhopper trials. Mean number of potato flea beetle adults per plant per evaluation for the 28 common accessions was 0.48 in 1986, and 1.44 in 1985. Mean number of leafhopper nymphs per plant per evaluation for the 28 common accessions was 0.74 in 1966, 0.27 in 1985, and 0.82 in 1986. The timed counts from 1966 compensated for differences in plant size. The season totals from 1985 and 1986 were adjusted by dividing by a measure of plant size using data collected in that year. Accession means were summed over evaluations within each year. The flea beetle and leafhopper data were transformed to the logarithmic scale as before. Adjustment for plant size varied between

years, so data for an accession screened in more than one year could not be pooled directly (Flanders & Radcliffe, 1992). Instead, for potato leafhopper and potato flea beetle, data were pooled following cluster analysis, with data presented from the year of highest insect population pressure, i.e., 1986 leafhopper data used in preference to 1985 data and 1966 data, and 1985 flea beetle data used in preference to 1986 data.

Some *Solanum* species did not grow well, so we excluded their data from statistical analysis. Species tested for one or more insects, but for which we do not present data here were: *S. clarum*, *S. chiquidenum*, *S. colombianum*, *S. fernandezianum*, *S. morelliforme*, *S. oxycarpum*, *S. paucisectum*, *S. sandemanii*, *S. tuquerrense*, and *S. violaceimarmoratum*. Results for these species are presented in Radcliffe & Lauer (1971) and Radcliffe et al. (1981, 1988), and Flanders & Radcliffe (1992).

K-means cluster analysis (Dixon et al., 1983) was used to identify groupings within the data for each insect. The basic unit of observation for cluster analysis was the individual accession. We used 1567 accessions for green peach aphid, 1195 accessions for potato aphid, 754 accessions for Colorado potato beetle, 709 accessions for 1985 leafhopper and flea beetle data, 705 accessions for 1986 flea beetle and leafhopper data, and 378 accessions for 1966 leafhopper data. By convention, clusters were numbered in order of field resistance, and cluster ranks are treated as resistance scores. Thus, a score of 1 indicates an accession was in the cluster most resistant to that particular insect.

Only those accessions for which taxonomic identification has been verified by one of us (J.G.H.) are included (1686 total accessions, representing 100 potato species). Green peach aphid data are presented for 1289 accessions, potato aphid data for 1004 accessions, Colorado potato beetle data for 609 accessions, potato flea beetle data for 992 accessions, and potato leafhopper data for 1176 accessions. Assistance of J.B. Bamberg (Project Leader, Inter-Regional Potato Introduction Project) in verifying the identity of certain accessions is gratefully acknowledged. Two of the species included in our trials have not yet been described in

publication. Therefore, they are referred to in the text and tables as *S. n.sp.* # 1, represented by PI 473203, PI 473204, PI 473205, PI 473207, PI 473208, and PI 498405, and *S. n.sp.* # 2, represented by PI 473209 and PI 473210.

A mean insect score was calculated for each insect on each plant species. Species with a mean insect score less than the overall mean minus one standard deviation were considered resistant, and species with a mean score higher than the overall mean score plus one standard deviation were considered susceptible.

Series means were calculated from species means to avoid bias due to varying numbers of accessions screened per species. Series with a mean insect score less than one overall mean minus one standard deviation were considered resistant, and series with a mean score higher than the overall mean score plus one standard deviation were considered susceptible.

#### *Characteristics of wild potato species*

The large number of wild potato species and hybrids has naturally led to more than one alternative hypothesis regarding the evolution and interrelationships of the wild potatoes (Spooner et al., 1991). Application of new techniques and approaches results in frequent revisions of the taxonomic treatment of wild potatoes. We here use the taxonomic treatment proposed by Hawkes (1990), since it is easily accessible, and presents a complete treatment of the section *Petota*.

Data were arranged from the most primitive species to the most advanced species. The arrangement does not imply that potato species evolved linearly, one from the other, rather it indicates how, according to Hawkes' scenario, species groups (not necessarily series), occur on a relative evolutionary scale. Frequency of instances of resistance was determined within each group. For example, a potato species resistant to three insects would have three instances of resistance. Chi-square tests ( $2 \times 2$  contingency tables) were used to determine if frequency of resistance differed

among groups. Correlations between mean insect scores within superseries were tested, with the species the basic unit of observation.

Data on foliar glycoalkaloids were obtained from S.L. Sinden (personal communication; Deahl, K.L. & S.L. Sinden, 1986. Screening of IR-1 *Solanum* accessions for foliar glycoalkaloid level and composition. Report to Inter-Regional Potato Introduction Project, Sturgeon Bay, WI), Osman et al. (1976), Sinden et al. (1980), Dimock & Tingey (1985), Gregory (1984), Kuhn & Löw (1955), Tingey & Sinden (1982) and van Gelder et al. (1988). Usually, species contained more than one glycoalkaloid, and in our analysis were considered in the calculations for each of these glycoalkaloids. Glycoalkaloid categories considered were solanine and chaconine, solasonine and solamargine, tomatine, demissine, commersonine and dehydrocommersonine, and leptine. Species containing solanine and chaconine were categorized as low, < 25 mg/100 g fresh weight; medium, 26–50 mg/100 g fresh weight; and high, > 50 mg/100 g fresh weight. For each insect, Chi-square tests were used to determine if resistance was more common in species with a particular glycoalkaloid than the wild potatoes as a whole.

Data on leaf pubescence were from personal observations of J.G. Hawkes, and Dimock & Tingey (1985), Hawkes (1990), Tingey (personal communication), and Tingey et al. (1981). Leaf surface categories considered were glandular trichomes, dense hairs, intermediate hairs, sparse hairs, and glabrous. Species with more than one characteristic, such as glandular trichomes as well as nonglandular hairs, were considered in our analysis for each applicable category. For each insect, Chi-square tests were used to determine if resistance was more common in species with a particular pubescence type than the wild potatoes as a whole.

Most potato species occur only in restricted habitats. Species were classified by one of us (J.G.H.) from field notes and personal observations as to typical temperature and humidity regimes in the habitats in which they occur. Temperature categories were designated cold, mild, and hot. Humidity categories were designated moist, mesic, and

dry. Habitat classifications are to some extent approximate, but are the best that can be estimated with currently available information. For each insect, 2 × 2 contingency Chi-square tests were used to determine if resistance was more common in species from particular habitats than others.

Collection altitudes were obtained from passport data submitted with the accession (field records of J.G. Hawkes; Hawkes & Hjerting, 1969; Ochoa, 1990; and USDA ARS Plant Inventory Series). In species with many accessions screened, or whose insect scores were not homogeneous, we tested for a correlation between altitude of collection and insect scores. Altitude ranges of accessions used here may not represent the entire range at which a species occurs. Correlations were tested only where more than six accessions were screened for a given insect. Correlations were tested for all insects unless otherwise noted. Plant species and altitudes in which correlations were tested were: *S. bulbocastanum* (1880–2400 m), *S. cardiophyllum* subsp. *ehrenbergii* (1850–2100 m, green peach aphid, potato aphid, and potato leafhopper only), *S. pinnatisectum* (1600–2000 m), *S. chacoense* (30–2450 m), *S. infundibuliforme* (3100–4300 m), *S. bukasovii* (3200–4000 m), *S. kurtzianum* (1400–2700 m, green peach aphid only), *S. oplocense* (2780–3800 m, green peach aphid, potato flea beetle, and potato leafhopper only), *S. acaule* subsp. *acaule* (2900–4500 m, all insects except Colorado potato beetle), *S. fendleri* (1700–2700 m), *S. polytrichon* (1840–2200 m, potato leafhopper and potato flea beetle only), *S. stoloniferum* subsp. *stoloniferum* (2000–3100 m) and *S. demissum* (2600–3500 m).

All data discussed in this paper were entered into dBASE IV data files on an MS-DOS IBM compatible personal computer. These data files have been deposited with the Inter-Regional Potato Introduction Project. Copies of the data may be obtained by applying to J.B. Bamberg, Project Leader, Inter-Regional Potato Introduction Project, Sturgeon Bay, WI 54235. A printed listing of species and accessions used in this study is also available.

## Results and discussion

For each insect, cluster analysis identified groupings of wild potato accessions (Fig. 1). Groups were arranged in ascending order of insect density or plant damage, and each group assigned a score. Highest insect score was given to those accessions with the highest damage ratings/densities. Thus, the highest score for a given insect depended on the number of clusters appropriate for that insect. Maximum score for green peach aphid or potato aphid was 7; for Colorado potato beetle, 6; for potato flea beetle, 5; and for potato leafhopper, 4. Accessions with the greatest level of resistance to a particular insect had lowest insect scores and the most susceptible had the highest scores. Cluster analysis is designed to divide individuals into natural groupings, not arbitrary categories. Therefore, we have not assigned labels of 'resistant' or 'susceptible' to particular clusters. However, insect scores of 1 or 2 indicated an accession was in the most resistant 14th percentile to green peach aphid and the most resistant 7th percentile to potato aphid. A score of 1 placed an accession in the most resistant 8th percentile to Colorado potato beetle, the most resistant 8th percentile to potato flea beetle, and the most resistant 9th percentile to potato leafhopper. Mean insect score plus or minus one standard deviation was used to determine which species fell in the intermediate class, i.e., species with a mean insect score neither resistant nor susceptible. Species with mean insect scores below the intermediate class minimum are considered resistant. Species with mean insect scores above the maximum limit of the intermediate class are considered susceptible. Species mean scores of less than 2.79 for green peach aphid, 3.45 for potato aphid, 2.84 for Colorado potato beetle, 2.19 for potato flea beetle, and 1.81 for potato leafhopper are considered resistant. Species with mean scores greater than 5.17 for green peach aphid, 5.53 for potato aphid, 5.55 for Colorado potato beetle, 4.27 for potato flea beetle, or 3.49 for potato leafhopper are considered susceptible. Insect scores were generally consistent within a plant species making species a reliable predictor of insect score (Table 1). Within a series, resistance levels to a given insect

were usually consistent. No series contained both resistant and susceptible species to a given insect pest, unless it also contained species intermediate in resistance. Series mean scores of less than 2.65 for green peach aphid, 3.46 for potato aphid, 2.69 for Colorado potato beetle, 1.93 for potato flea beetle, and 1.63 for potato leafhopper are considered resistant. Series mean scores greater than 4.49 for green peach aphid, 5.32 for potato aphid, 4.57 for Colorado potato beetle, 3.99 for potato flea beetle, or 3.05 for potato leafhopper are considered susceptible.

Here, we discuss mean insect scores for resistant species, compare these to *S. tuberosum* subsp. *andigena* and *S. phureja*, and identify those species with the greatest number (not proportion) of accessions in the most resistant percentile. The latter species may not be resistant overall, but are included as they contain potential sources of resistant germplasm. Other sources of resistance may be found in Table 1. Species with two or fewer accessions are not discussed, but their scores are given.

### *Green peach aphid resistance*

Accessions highly resistant to green peach aphid (scores of 1 or 2) occurred in 36 of 86 species (Table 1), and in 14 of 18 series. Resistant species (mean green peach aphid score < 2.79), listed on ascending mean green peach aphid score, were *S. trifidum*, *S. brachistotrichum*, *S. tuberosum*, *S. bulbocastanum*, *S. canasense*, *S. jamesii*, *S. sanctae-rosae*, *S. marinasense*, *S. lignicaule*, *S. toralapanum*, *S. hjertingii*, and *S. infundibuliforme*. Species with the greatest number of resistant accessions were *S. bulbocastanum*, *S. tarijense*, *S. infundibuliforme*, *S. canasense*, and *S. stoloniferum*.

*Solanum phureja* had three resistant accessions and an intermediate mean score. *Solanum tuberosum* subsp. *andigena* had no resistant accessions, and a susceptible mean score.

Series with greatest resistance to green peach aphid were *Circaeifolia*, *Bulbocastana*, *Etuberosa*, and *Piurana*. The series *Tuberosa* was intermediate.

Among species most susceptible to green peach

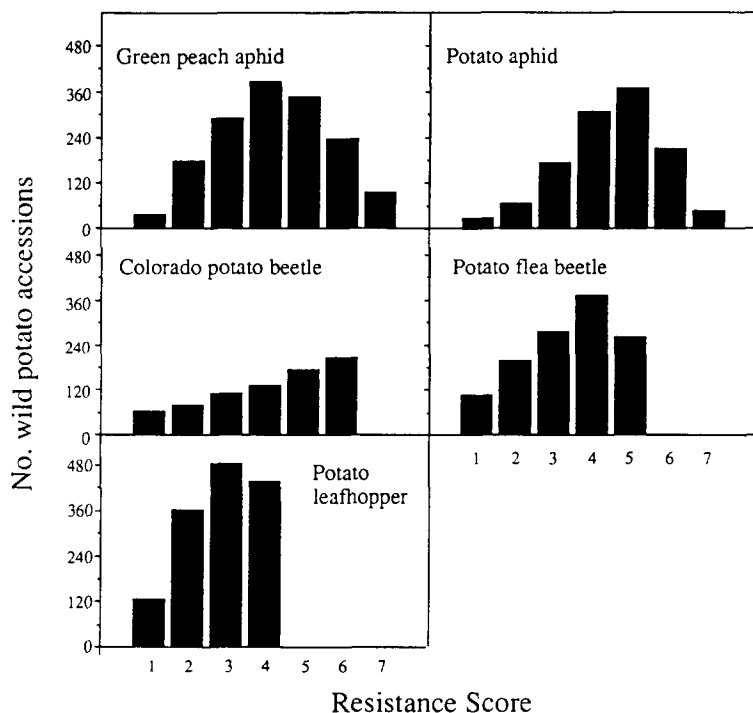


Fig. 1. Frequency distribution of number of accessions over classes of resistance to five insect pests. Numbering in descending order of field resistance (class 1 = most resistant). Seven classes were appropriate for each aphid, six for Colorado potato beetle, five for potato flea beetle, and four for potato leafhopper.  $\log_{10}$  (Mean green peach aphid resistance ratio + 0.01) were, for cluster 1, -0.43, cluster 2, 0.00, cluster 3, 0.26, cluster 4, 0.47, cluster 5, 0.69, cluster 6, 0.93, and cluster 7, 1.33.  $\log_{10}$  (Mean potato aphid resistance ratio + 0.01) were, for cluster 1, -2.00, cluster 2, -0.40, cluster 3, -0.06, cluster 4, 0.19, cluster 5, 0.42, cluster 6, 0.67, and cluster 7, 0.99. Mean Colorado potato beetle defoliation/abundance rating (0–3 scale) was, for cluster 1, 0.37, cluster 2, 0.89, cluster 3, 1.37, cluster 4, 1.75, cluster 5, 2.10, and cluster 6, 2.48. In 1985, mean flea beetles per plant were adjusted by dividing by plant size (scale of 1–4), such that  $\log_{10}$  (adjusted flea beetles per plant + 0.01) were, for cluster 1, -0.47, cluster 2, -0.07, cluster 3, 0.24, cluster 4, 0.56, and cluster 5, 0.90. In 1986, mean flea beetles per plant were adjusted for plant size by dividing by plant volume ( $\text{height} \times (\text{width}/2)^2 \times \pi = \text{m}^3$ ), such that  $\log_{10}$  (adjusted flea beetles per plant + 0.01) were, for cluster 1, -0.21, cluster 2, 1.04, cluster 3, 1.52, cluster 4, 1.97, and cluster 5, 2.51. When an accession was screened in both years, flea beetle score from 1985 (most abundant potato flea beetles) was taken in preference to 1986. In 1966,  $\log_{10}$  (mean potato leafhopper nymph timed count + 0.01) was, for cluster 1, -1.36, cluster 2, -0.49, cluster 3, 0.19, and cluster 4, 0.73. In 1985, mean potato leafhopper nymphs per plant were adjusted by dividing by plant size (scale of 1–4), such that  $\log_{10}$  (mean adjusted leafhopper nymphs per plant) was, for cluster 1, -1.83, cluster 2, -1.02, cluster 3, -0.47, and cluster 4, 0.06. In 1986, mean potato leafhopper nymphs per plant were adjusted for plant size by dividing by plant height  $\times$  width (in  $\text{cm}^2$ ), such that  $\log_{10}$  (adjusted leafhopper nymphs per plant + 0.01) were, for cluster 1, -1.59, cluster 2, -1.21, cluster 3, -0.84, and cluster 4, -0.47. When an accession was screened for potato leafhopper in more than one year, data from 1986 (most abundant leafhoppers) were used in preference to 1985 data, which were used in preference to 1966 data.

aphid were *S. kurtzianum*, *S. sparsipilum*, *S. tuberosum* (both subspecies), *S. agrimonifolium*, *S. vernei*, *S. curtilobum*, *S. huancabambense*, and *S. gandarillasii*. Susceptible series (groups) were Group iii *Tuberosa* (wild species from Bolivia and Argentina), cultivated *Tuberosa*, *Yungasensa*, *Demissa*, *Polyadenia*, and *Juglandifolia*.

#### Potato aphid resistance

Accessions highly resistant to potato aphid (scores of 1 or 2) occurred in 24 of 85 species, and in 10 of 18 series. Resistant species (mean potato aphid score < 3.45), listed on ascending mean potato aphid score, were *S. multidissectum*, *S. lignicaule*, *S. albicans*, *S. hjertingii*, *S. bulbocastanum*, *S. chomatophilum*, *S. bukasovii*, *S. hougasii*, *S. stoloniferum*, *S. verrucosum* and *S. medians*. Species with

Table 1. Resistance of exotic potato germplasm to Colorado potato beetle, green peach aphid, potato aphid, potato flea beetle, and potato leafhopper, Minnesota – North Dakota, 1967–1986

Species <sup>a</sup>	Number of accessions receiving insect score <sup>b</sup>																																									
	Green peach aphid							Potato aphid							Colorado potato beetle							Potato flea beetle							Potato leafhopper													
	1	2	3	4	5	6	7	mean	1	2	3	4	5	6	7	mean	1	2	3	4	5	6	mean	1	2	3	4	5	6	mean	1	2	3	4	mean	1	2	3	4			
<i>S. pennellii</i> <sup>c</sup>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	2.5	1	-	-	-	-	1.0	1	-	-	-	-	-	-	-	-	1.0	-	-	-	-
	Section <i>Neolycopersicon</i>																																									
	Section <i>Petota</i>																																									
	Subsection <i>Estolonifera</i> <sup>c</sup>																																									
	Series <i>Etiuberosa</i>																																									
<i>S. brevidens</i>	-	2	-	-	-	-	3.0	-	-	-	-	2	-	-	5.0	1	1	-	-	-	4.3	-	-	-	-	-	2	5.0	2	-	-	1.0	-	-	-	-						
<i>S. etuberosum</i>	-	3	-	-	-	-	2.0	-	-	-	1	2	-	-	4.7	-	2	-	-	-	3.0	-	-	-	-	-	3	5.0	1	2	-	1.7	-	-	-	-						
	Series <i>Juglandifolia</i>																																									
<i>S. lycopersicoides</i>	-	-	-	1	-	-	4.0	-	-	-	1	-	-	-	4.0	-	2	-	-	-	2.0	-	-	1	1	-	3.5	2	-	-	-	1.0	-	-	-	-						
<i>S. ochrantum</i>	-	-	-	1	-	-	5.0	-	-	-	1	-	-	-	4.0	-	-	-	-	-	4.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
<i>S. stitens</i> (= <i>rickii</i> )	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	4.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
	Subsection <i>Potatae</i>																																									
	Series <i>Bulbocastana</i>																																									
<i>S. bulbocastanum</i>	6	10	-	-	-	-	2.2	-	7	9	7	2	-	-	3.2	-	6	2	2	1	3.8	12	5	5	-	-	1.7	2	7	16	1	2.6	-	-	-	-						
subsp.																																										
<i>bulbocastanum</i>																																										
<i>S. bulbocastanum</i>	2	1	1	-	-	-	1.8	-	3	1	-	-	-	-	2.3	-	2	-	3	-	4.2	3	2	-	-	-	1.4	-	4	1	-	2.2	-	-	-	-						
subsp.																																										
<i>dolichophyllum</i>																																										
<i>S. bulbocastanum</i>	1	-	-	-	-	-	1.0	-	-	-	1	-	-	-	4.0	-	-	-	1	-	4.0	-	1	-	-	-	2.0	-	1	-	-	2.0	-	-	-	-						
subsp. <i>partitum</i>																																										
	Series <i>Pinnatisecta</i>																																									
<i>S. brachistorrichum</i>	2	5	-	-	-	-	1.7	-	-	-	2	5	-	-	4.7	-	2	4	1	1	4.1	4	2	3	-	-	1	2.2	-	6	4	2.4	-	-	-	-						
<i>S. cardiophyllum</i> <sup>c</sup>	-	3	-	1	-	-	2.5	-	-	1	-	2	-	-	4.3	-	1	1	1	-	4.0	-	2	1	1	-	2.8	1	2	1	-	2.0	-	-	-	-						
subsp.																																										
<i>cardiophyllum</i>																																										
<i>S. cardiophyllum</i>	-	5	3	3	1	-	3.0	-	-	3	3	4	2	-	4.4	-	1	4	1	-	4.0	1	3	2	1	-	2.4	1	6	4	-	2.3	-	-	-	-						
subsp. <i>ehrenbergii</i>																																										
<i>S. jamesii</i>	1	5	2	2	-	-	2.5	-	-	-	2	2	5	1	5.5	2	4	2	-	-	2.0	-	-	-	-	-	6	5	4	5	4	3	2.8	-	-	-						
<i>S. pinnatisectum</i>	-	-	1	4	3	3	4.7	-	-	1	-	5	4	-	5.2	10	-	-	-	-	1.0	-	5	6	1	-	2.7	2	6	4	-	2.2	-	-	-	-						
<i>S. trifidum</i>	6	3	1	-	-	-	1.5	-	-	2	4	1	2	-	4.3	3	4	3	1	-	2.2	-	4	4	1	-	2.7	-	3	6	1	2.8	-	-	-	-						
<i>S. × sambucinum</i>	-	-	-	-	-	1	6.0	-	-	-	-	-	1	-	6.0	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1.0	-	-	-	-						
	Series <i>Polyadenia</i>																																									
<i>S. lesteri</i>	-	-	-	1	-	-	5.0	-	-	-	1	-	-	-	4.0	-	-	-	1	-	4.0	-	1	-	-	-	2.0	1	-	-	-	1.0	-	-	-	-						
<i>S. polyadenium</i>	-	1	2	4	5	1	4.2	-	-	-	2	3	4	-	5.2	8	1	-	-	-	1.1	6	5	2	-	-	1.7	6	6	1	-	1.6	-	-	-	-						
	Series <i>Commersoniana</i>																																									
<i>S. commersonii</i>	-	-	1	2	1	1	4.4	-	1	-	2	1	-	-	3.8	-	2	1	-	-	3.3	-	2	2	-	-	3.5	-	1	1	3	3.4	-	-	-	-						
subsp. <i>commersonii</i>																																										
<i>S. commersonii</i>	-	-	2	-	-	1	4.0	-	-	-	1	1	-	-	5.3	-	1	-	-	-	3.0	-	1	-	-	-	3.0	-	1	-	-	2.0	-	-	-	-						
subsp. <i>malmeanum</i>																																										











Table 1. Continued

		Series <i>Demissa</i>																													
<i>S. brachycarpum</i>	-	-	-	4	1	-	5.2	-	2	-	3	-	4.2	-	1	1	3	5.4	-	3	3	7	4.3	7	6	-	1.5				
<i>S. brachycarpum</i> atypical	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	4.0	-	1	-	2.0				
<i>S. demissum</i>	-	4	11	15	19	-	5.0	3	2	10	12	11	2	-	2	15	29	31	5.2	-	1	9	34	10	4.0	11	30	12	3	2.1	
<i>S. guerrerense</i>	-	-	1	-	-	1	5.5	-	1	1	-	-	-	-	-	-	2	6.0	-	-	1	1	-	3.5	-	2	-	-	2.0		
<i>S. hougasii</i>	1	-	1	2	-	-	3.8	-	3	1	-	-	-	-	-	-	-	-	-	-	1	1	-	2.5	-	2	-	-	2.0		
<i>S. iopetalum</i>	-	-	2	-	-	-	4.0	-	1	1	-	-	-	-	1	1	-	3.5	-	2	-	-	-	2.0	-	1	1	-	2.5		
<i>S. schenckii</i>	-	-	1	-	-	-	4.0	-	1	-	-	-	4.0	-	1	1	1	4.7	-	1	4	1	-	3.0	-	3	3	-	2.5		
Interseries Hybrids and Crosses																															
<i>S. megistacrolobum</i> - -	-	1	-	-	-	-	3.0	-	-	-	-	-	-	-	1	1	5.5	1	1	-	-	-	-	1.5	-	1	1	-	2.5		
<i>S. infundibuliforme</i> hyb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	3.0	-	1	1	-	2.5		
<i>S. gourlayi</i> - <i>S.</i> <i>infundibuliforme</i> hyb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	3.0	-	1	1	-	2.5		
<i>S. canasense</i> - <i>S.</i> <i>raphanifolium</i> hyb.	-	1	-	-	-	-	2.0	-	1	-	-	-	3.0	-	1	-	-	3.0	-	-	1	-	-	3.0	-	-	-	1	4.0		
<i>S. gourlayi</i> - <i>S.</i> <i>megistacrolobum</i> hyb.	-	1	-	-	-	-	3.0	-	-	-	-	-	-	-	1	-	1	5.0	-	1	-	-	2.0	-	-	1	-	3.0			
<i>S. sparsipilum</i> - <i>S.</i> <i>raphanifolium</i> hyb.	-	-	-	1	-	1	5.0	-	-	1	-	1	5.0	-	-	-	-	-	-	-	-	-	1	4.0	-	-	-	1	4.0		
<i>S. berthaultii</i> - <i>S.</i> <i>tarijense</i> hyb.	-	2	4	2	2	-	3.7	-	-	-	-	1	2	6	6.6	4	3	1	1	-	1.9	2	7	5	1	1	2.5	4	9	3	1.9
<i>S. kurizianum</i> - <i>S.</i> <i>chacoense</i> hyb.	-	-	-	2	-	2	5.0	-	-	-	-	-	1	-	6.0	-	1	4.3	-	-	-	-	1	2	4.7	1	2	-	-	1.7	
<i>S. spegazzinii</i> - <i>S.</i> <i>tarijense</i> hyb.	-	-	-	-	1	-	5.0	-	-	-	-	1	-	5.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>S. vernetii</i> - <i>S. tarijense</i> hyb.	-	3	-	-	-	-	2.0	-	-	-	-	-	-	-	1	-	-	1.0	1	2	1	-	2.0	-	4	-	-	-	2.0		

<sup>a</sup> Arranged according to Hawkes (1990). Natural hybrids indicated with hyphen between species names, followed by 'hyb.', artificial crosses with 'x' between two species names, tentative identifications with a '?'.  
<sup>b</sup> Most resistant accessions in cluster 1. A '-' indicates no accessions in that category. A listing of individual accessions can be obtained from Project Leader, IR-1, Sturgeon Bay, WI. Data on individual accessions also reported in Radcliffe et al. (1981), Radcliffe et al. (1988), and Flanders & Radcliffe (1992).  
<sup>c</sup> Taxon of uncertain/debatable status - see text for discussion  
<sup>d</sup> *Solanum sparsipilum* occurs in both Group ii and Group iii *Tuberosa*.

the greatest number of accessions resistant to potato aphid were *S. bulbocastanum*, *S. stoloniferum*, and *S. demissum*.

*Solanum phureja* had one resistant accession and an intermediate mean score, and *S. tuberosum* subsp. *andigena* had four resistant accessions and an intermediate mean score.

Series with greatest resistance to potato aphid were *Lignicaulia*, *Bulbocastana*, and *Acaulia*. The series *Tuberosa* had an intermediate mean score.

Among species most susceptible to potato aphid were *S. chacoense*, *S. × sucrense*, *S. leptophyes*, *S. mochiquense* and *S. okadae*. The most susceptible series was *Maglia*.

#### Colorado potato beetle resistance

Accessions resistant to Colorado potato beetle (score of 1) occurred in 10 of 86 species, and in 5 of 18 series. Another 14 species contained accessions with Colorado potato beetle scores of 2. Resistant species (mean Colorado potato beetle score < 2.84), listed on ascending mean Colorado potato beetle score, were *S. pinnatisectum*, *S. polyadenium*, *S. jamesii*, *S. trifidum*, *S. capsicibaccatum*, *S. tarijense*, *S. chacoense*, *S. berthaultii*, and *S. chomatophilum*. Species with the greatest number of resistant accessions were *S. jamesii*, *S. pinnatisectum*, *S. polyadenium*, *S. chacoense*, *S. tarijense*, *S. berthaultii*-*S. tarijense* natural hybrids and *S. trifidum*.

*Solanum phureja* and *S. tuberosum* subsp. *andigena* had no resistant accessions, and susceptible mean scores.

Series with greatest resistance to Colorado potato beetle were *Circaeifolia*, *Polyadenia*, and *Pinnatisecta*. The series *Tuberosa* had an intermediate mean score.

Among species most susceptible to Colorado potato beetle were *S. vernei*, *S. medians*, *S. multiinterruptum*, *S. stenotomum*, *S. boliviense* and *S. phureja*. Series (groups) classified as susceptible to Colorado potato beetle were cultivated *Tuberosa*, *Megistacroloba*, *Longipedicellata* and *Demissa*.

#### Potato flea beetle resistance

Accessions resistant to potato flea beetle (score of 1) occurred in 25 of 90 species, and in 12 of 18 series. Resistant species (mean potato flea beetle score < 2.19), listed on ascending mean potato flea beetle score, were *S. lignicaule*, *S. pampasense*, *S. bulbocastanum*, *S. sanctae-rosae*, *S. polyadenium*, *S. berthaultii*, *S. marinasense*, *S. mochiquense*, *S. microdontum*, *S. toralapanum*, *S. polytrichon*, and *S. alandiae*. Species with the greatest number of resistant accessions were *S. bulbocastanum*, *S. polyadenium*, *S. toralapanum*, *S. berthaultii*, and *S. stoloniferum*.

*Solanum phureja* and *S. tuberosum* subsp. *andigena* had no resistant accessions, and susceptible mean scores.

Series with greatest resistance to potato flea beetle were *Lignicaulia*, *Bulbocastana*, and *Polyadenia*. The series *Tuberosa* had an intermediate mean score.

Among species most susceptible to potato flea beetle were *S. huancabambense*, *S. sparsipilum*, *S. stenotomum*, *S. etuberosum*, *S. agrimonifolium*, and *S. hondelmannii*. Series (groups) most susceptible to potato flea beetle were cultivated *Tuberosa*, *Etuberosa*, *Conicibaccata*, and *Acaulia*.

#### Potato leafhopper resistance

Accessions resistant to potato leafhopper (score of 1) occurred in 39 of 92 species, and in 15 of 18 series. Resistant species (mean potato leafhopper score < 1.81), listed on ascending mean potato leafhopper score, were *S. agrimonifolium*, *S. berthaultii*, *S. brachycarpum*, *S. polyadenium*, and *S. etuberosum*. Species with greatest number of resistant accessions were *S. berthaultii*, *S. demissum*, *S. brachycarpum*, *S. polyadenium*, *S. tuberosum* subsp. *andigena*, and *S. berthaultii*-*S. tarijense* natural hybrids.

*Solanum phureja* had no resistant accessions, and a susceptible mean score. *Solanum tuberosum* subsp. *andigena* had five resistant accessions, but overall, a susceptible mean score.

Series with greatest resistance to potato leaf-

hopper were *Juglandifolia*, *Etuberosa*, and *Polyadenia*. The series *Tuberosa* had an intermediate mean score.

Among the most susceptible species were *S. neo-rossii*, *S. tuberosum*, *S. sanctae-rosae*, *S. curtlobum*, *S. boliviense*, and *S. hondelmannii*. Series (groups) most susceptible to potato leafhopper were cultivated *Tuberosa*, Group iii *Tuberosa*, *Cuneolata*, and *Commersoniana*.

#### *Resistance within the series Tuberosa*

The series *Tuberosa* contains the largest number of potato species, 101. Hawkes (1990) identified four groups within the *Tuberosa*: Group i, from Mexico, Venezuela, Colombia, and Ecuador; Group ii, from Peru; the more primitive Group iii, from Bolivia, Argentina, and Chile; and the cultivated species.

Groups within the *Tuberosa* were intermediate or susceptible to all five insects. The cultivated potatoes were the most susceptible group in the series *Tuberosa*. This may be due to lack of resistance in their postulated ancestors, *S. leptophyes*, *S. sparsipilum*, and *S. megistacrolobum* (Hawkes, 1990), which are intermediate or susceptible to all five insects.

The lowest insect scores occurred in Group i, *S. verrucosum* and *S. andreanum*. Next lowest were the Group ii species. Group iii species had higher mean insect scores than Group ii species, with the exception of Colorado potato beetle, where scores for the two groups were similar. The cultivated species had slightly higher mean insect scores than the Group iii species.

#### *Sources of resistance to more than one insect*

We found no species or individual accessions within species highly resistant to all five insects. There were five species resistant to three insects each: *S. bulbocastanum* and *S. lignicaule* were resistant to green peach aphid, potato aphid, and potato flea beetle; *S. polyadenium*, *S. berthaultii*, and *S. pennellii* were resistant to Colorado potato beetle, po-

tato flea beetle, and potato leafhopper. All of the foregoing except *S. berthaultii* are primitive species. *Solanum pennellii* has been transferred by some authorities to the genus *Lycopersicon* (Palmer & Zamir, 1982; Miller & Tanksley, 1990), though it possesses features of both potato and tomato.

#### *Inconsistencies noted within species*

There were a few accessions within a species that were not representative of the rest of that species. *Solanum commersonii* subsp. *malmeanum* PI 414154 was susceptible to aphids, while other accessions in this species were intermediate. *Solanum lignicaule* PI 498253 was susceptible to Colorado potato beetle, while other accessions in this species were resistant. *Solanum tarijense* PI 275154 and PI 208881 were resistant to potato aphid, but the species was generally susceptible to potato aphid. *Solanum sanctae-rosae* PI 473200 was susceptible to green peach aphid, but the species was generally resistant to green peach aphid. *Solanum acroscopicum* PI 365315 was intermediate to green peach aphid, whereas the other two accessions in the species were susceptible. *Solanum marinasense* tended to be resistant to green peach aphid and susceptible to potato aphid, with three exceptions: PI 210040 was intermediate and PI 283079 was susceptible to green peach aphid, and PI 283078 was resistant to potato aphid. *Solanum spgazzinii* PI 320300 was resistant to potato aphid, but the species was generally susceptible. This last accession is hypothesized to have some *S. kurtzianum* introgression. *Solanum hougasii* PI 161741 was resistant to green peach aphid, but the other accessions were intermediate. An atypical reaction could have resulted from an error in pedigree, planting, or data collection; from uneven insect pressure; or may represent true genetic variation within the species.

#### *Summary – sources of resistance*

Numerous sources of resistance to each of the five

insects studied were identified, but usefulness of this germplasm will be dependent on ease of incorporation into potato breeding lines. Of the 128 wild potato species maintained in gene banks, only 15 have contributed germplasm to cultivars of either Europe (Ross, 1986) or North America (Plaisted & Hoopes, 1989). These species are *S. acaule*, *S. chacoense*, *S. commersonii*, *S. demissum*, *S. fendleri*, *S. kurtzianum*, *S. maglia*, *S. microdontum*, *S. raphanifolium*, *S. sparsipilum*, *S. spegazzinii*, *S. stoloniferum*, *S. toralapanum*, *S. vernei*, and *S. verrucosum*. Others are presently being used in developmental breeding lines for future cultivars.

As potato breeders are well aware, primary crosses between certain wild and cultivated species were formerly difficult if not impossible to achieve. Often this has been due to ploidy differences, as in diploid × tetraploid crosses, or to Endosperm Balance Number (EBN) differences (Johnston & Hanneman, 1980; Ehlenfeldt & Hanneman, 1984). Manipulation of these factors, and development of new techniques such as somatic hybridization (Williams et al., 1990), helped to overcome hybridization difficulties, so that most wild species can now be crossed with the cultivated ones.

Unfortunately, many undesirable characters such as low yield, long stolons and poor flavors can be transferred along with useful genes. Recovery of horticulturally acceptable types may involve several generations of intermating, backcrossing, and selection. In a breeding program, overcoming such time-consuming bottlenecks as restoring acceptable flavor, yield, and market quality may deter use of wild potatoes. For this reason more prebreeding or germplasm enhancement may be necessary to expedite incorporation of traits from wild species.

#### *Wild potato evolution in relation to insect resistance*

Given the large number of wild potato species and the hybridization that can occur between them, it is not surprising that there are various classification hypotheses. We present one here, recognizing it as a hypothesis. Hawkes (1990) proposed that tuber-bearing species originated in central Mexico. The

first tuber-bearing potatoes had small, white star-shaped flowers (primitive *Stellata*), an EBN of 1 (Johnston & Hanneman, 1980; Johnston & Hanneman, 1982) and, except for *Polyadenia*, a simple immunological spectrum (Gell et al., 1960). These species, in the series *Morelliformia*, *Bulbocastana*, *Pinnatisecta* and *Polyadenia*, also stand out as a distinct group on total DNA banding patterns (Hosaka et al., 1984).

Hawkes suggests that in the early Pliocene, some 3.5 million years ago, a group of these primitive *Stellata* crossed the newly-formed isthmus from Central America into South America and left relics as they journeyed southward down the Andes. These relics are the series *Olmosiana* and *Lignicaulia* in Peru, *Circaeifolia* in Bolivia and *Commersoniana* in Argentina. These, the most primitive of the South American *Stellata*, all retain the stellate corolla (white, with the exception of part of *S. commersonii*) and an EBN of 1.

In southeastern Argentina, a switch from EBN = 1 to EBN = 2 took place, giving rise to the advanced *Stellata* (series *Yungasensa*). However, the *Yungasensa* still possess a white stellate corolla.

The primitive *Rotata* evolved from the *Yungasensa*, moving towards a 'wheel-shaped' corolla, while retaining triangular lobes. The primitive *Rotata* occur in Argentina, Bolivia and extreme southern Peru. Three conical-berried species in the series *Conicibaccata* occur here, as well as a group of round-berried species (series *Tuberosa*, Group iii, and the series *Maglia*, *Cuneolata* and *Megistacroloba*).

Finally, evolution gave rise to the advanced *Rotata*, with broad corolla lobes of a more or less circular outline: the central and northern parts of series *Tuberosa* (Group i and ii), the cultivated species in series *Tuberosa*, and the series *Acaulia*, *Piurana*, *Ingifolia*, and northern *Conicibaccata*. Some of these, and some of the conical-berried species then made a return migration to central America and to Mexico (series *Conicibaccata*, and *S. verrucosum* in the series *Tuberosa*). Some of these returning immigrants hybridized with indigenous Mexican species, forming groups of tetraploid and hexaploid species, such as the series *Longipedicellata* and *Demissa*.



Comments of D.M. Spooner and C.M. Ochoa in regard to evidence which might lead to alternative hypotheses are gratefully acknowledged. Some of the more important evidence is discussed here. The section *Estolonifera* has been reported to be paraphyletic (Spooner et al., 1990). New evidence indicates that *S. cardiophyllum* is more closely related to *S. bulbocastanum* in the series *Bulbocastana* than to other species within the series *Pinnatisecta* (Spooner et al., 1991; Spooner & Sytsma, 1992). There is evidence that *S. chomatophilum* should be moved from the *Conicibaccata* to the *Piurana* (Spooner et al., 1991). Spooner believes that intra-specific variation may limit the usefulness of corolla shape as a phylogenetic marker. Ochoa (1990) does not recognize the existence of the series *Yungasensa* and places these species in his series *Commersoniana*. *Solanum berthaultii* is also placed within the series *Commersoniana* according to Ochoa's classification hypothesis. Detailed analysis has revealed extensive morphological overlap between *S. berthaultii* and *S. tarijense*, to the point they may have to be considered as one species (Spooner & van den Berg, 1991).

Resistance at the species level to the five insects studied, and by inference to insect herbivory in general, appears to be a primitive characteristic in potato (Table 2). In the primitive *Stellata*, six species were resistant to green peach aphid, two species were resistant to potato aphid, eight species were resistant to Colorado potato beetle, four species were resistant to potato flea beetle, and three species were resistant to potato leafhopper. Only three instances of susceptibility were observed in this group: *S. jamesii* is susceptible to potato flea beetle, and *S. × sambucinum* is susceptible to both green peach aphid and potato aphid.

In the evolutionary development of the wild potato we see loss of insect resistance in transitional series and a tendency to recover resistance in advanced series. Over all species, there were 80 instances of resistance to insects, and 80 instances of susceptibility to insects (Table 2). Within the most primitive potatoes (through the primitive *Stellata*), there are 29 instances of resistance and 5 instances of susceptibility, significantly more resistant than susceptible. In the advanced *Stellata* and the prim-

itive *Rotata* (excluding the series *Tuberosa*), there were 7 instances of resistance and 9 of susceptibility, but significantly more were susceptible and fewer were resistant than occurred in the previous group. Within the primitive *Tuberosa*, there were 8 instances of resistance and 28 of susceptibility, significantly more susceptible than resistant. The cultivated *Tuberosa*, which arose from Group ii and Group iii species, had no instances of resistance and 16 instances of susceptibility, significantly more susceptible than resistant. Transition from overall susceptibility to overall resistance begins in the advanced *Tuberosa*, in which there were 15 instances of resistance and 10 of susceptibility, significantly more instances of resistance than observed in the primitive *Tuberosa* and cultivated *Tuberosa*. In series more advanced than the *Tuberosa*, e.g., *Acaulia*, *Longipedicellata*, and *Demissa*, there were 11 instances of resistance and 5 instances of susceptibility, again significantly more resistances than expected.

Resistance to green peach aphid occurs frequently in the *Stellata*, and in the primitive *Rotata* (excluding the series *Tuberosa*), as well as in the advanced *Rotata* (*Tuberosa*, Group ii, and the *Longipedicellata*). The *Longipedicellata*, one of the most advanced series of wild potatoes, contains species resistant to both green peach aphid and potato aphid. Most species resistant to potato aphid were in the most advanced groups of the series *Tuberosa*, and in the *Longipedicellata* and *Demissa*. Resistance to Colorado potato beetle was most common in the superseries *Stellata*. The series *Piurana* in the advanced *Rotata* was also predominantly resistant to Colorado potato beetle. Resistance to Colorado potato beetle was uncommon in the series *Tuberosa*. However, two species of series *Tuberosa*, *S. berthaultii* and *S. immite*, contain appreciable resistance to Colorado potato beetle. Resistance to potato flea beetle was scattered throughout the major potato taxa. Resistance to potato leafhopper was common in the primitive potatoes, and scattered throughout the advanced *Stellata* and *Rotata*.

Significant correlations ( $P \leq 0.10$ ) between mean insect scores within the superseries (*Stellata* or *Rotata*) were observed in 6 of 20 possible tests.

Table 2. Insect resistance within major potato taxa and distribution ranges, arranged from most primitive to most advanced species

Subsection, Superseries (corolla group)	Taxonomic series	Distribution	Relative resistance <sup>a</sup>					
			Species	GPA <sup>b</sup>	PA	CPB	PFB	PLH
Section <i>Neolycopersicon</i> <sup>c</sup>		Peru	<i>S. pennellii</i> <sup>c</sup>			R	R	R
Section <i>Petota</i>								
Subsection <i>Estolonifera</i> <sup>c</sup>								
	<i>Juglandifolia</i>	Peru and Chile	<i>S. lycopersicoides</i>	•	•	R	•	R
			<i>S. ochranthum</i>	•	•	•		
			<i>S. sitiens</i> (= <i>rickii</i> )	•		•		
	<i>Etuberosa</i>	Argentina and Chile	<i>S. brevidens</i>	•	•	•	S	R
			<i>S. etuberosum</i>	R	•	•	S	R
Subsection <i>Potatoe</i>								
Primitive <i>Stellata</i>	<i>Bulbocastana</i> , <i>Pinnatisecta</i> , and <i>Polyadenia</i>	Southwestern USA and Mexico	<i>S. bulbocastanum</i>	R	R	•	R	•
			<i>S. brachistotrichum</i>	R	•	•	•	•
			<i>S. cardiophyllum</i> <sup>c</sup>	•	•	•	•	•
			<i>S. jamesii</i>	R	•	R	S	•
			<i>S. pinnatisectum</i>	•	•	R	•	•
			<i>S. trifidum</i>	R	•	R	•	•
			<i>S. × sambucinum</i>	S	S			R
			<i>S. lesteri</i>	•	•	•	R	R
			<i>S. polyadenium</i>	•	•	R	R	R
Primitive <i>Stellata</i>	<i>Commersoniana</i> , <i>Circaeifolia</i> , and <i>Lignicaulia</i>	South America	<i>S. commersonii</i>	•	•	•	•	•
			<i>S. capsicibaccatum</i>	R	•	R	•	•
			<i>S. circaeifolium</i>			R	•	•
			<i>S. lignicaule</i>	R	R	•	R	•
Advanced <i>Stellata</i>	<i>Yungasensa</i> <sup>c</sup>	South America	<i>S. chacoense</i>	•	S	R	•	•
			<i>S. huancabambense</i>	S	•	•	S	•
			<i>S. tarijense</i> <sup>c</sup>	•	•	R	•	•
Primitive <i>Rotata</i>	<i>Megistacroloba</i> , <i>Cuneoalata</i> , <i>Conicibaccata</i> (partial), and <i>Maglia</i>	Southern to central regions of South America	<i>S. boliviense</i>	•	•	S	•	S
			<i>S. megistacrolobum</i>	•	•	•	•	•
			<i>S. raphanifolium</i>	•	•	•	•	•
			<i>S. sanctae-rosae</i>	R	•	•	R	S
			<i>S. sogarandinum</i>	•	•	S	•	•
			<i>S. toralapanum</i>	R	•	•	R	•
			<i>S. infundibuliforme</i>	R	•	•	•	•
			<i>S. santolallae</i>	•	S	•	•	•
			<i>S. maglia</i>	•	S			
Primitive <i>Rotata</i>	<i>Tuberosa</i> (Group iii)	Southern to central regions of South America	<i>S. alandiae</i>			•	R	S
			<i>S. avilesii</i>				•	•
			<i>S. berthaultii</i> <sup>f</sup>	•	•	R	R	R
			<i>S. brevicaule</i>	•	•	•	•	S
			<i>S. candolleianum</i>			S	S	•
			<i>S. gandarillasii</i>	S	•	•	S	•
			<i>S. gourlayi</i>	•	•	•	•	•
			<i>S. n.sp. # 1</i> <sup>c</sup>	•	S			
			<i>S. n.sp. # 2</i> <sup>c</sup>			•	R	S
			<i>S. hondelmannii</i>	S		•	S	S
			<i>S. incamayoense</i>			•	•	•
			<i>S. kurtzianum</i>	S	•	•	•	•
			<i>S. leptophyes</i>	•	S	•	•	S
			<i>S. microdontum</i>	•	S	•	R	•
			<i>S. neocardenasii</i>				R	R
			<i>S. neorossii</i>			•	•	S
			<i>S. okadae</i>	•	S	•	•	•
			<i>S. oplocense</i>	•	•	•	•	S
			<i>S. sparsipilum</i>	S	•	•	S	S
			<i>S. spegazzinii</i>	•	•	•	•	•
			<i>S. venturii</i>	•	S		•	S
			<i>S. vernei</i>	S	S	S	•	•
			<i>S. × doddsii</i>			•	•	•
			<i>S. × sucrense</i>	•	S	•	•	S
Advanced <i>Rotata</i>	<i>Conicibaccata</i> (partial)	Mexico and southern to northern regions of South America	<i>S. agrimonifolium</i>	S	•	S	S	R
			<i>S. chomatophilum</i> <sup>c</sup>	•	R	R	•	•
			<i>S. limbaniense</i>				•	S
			<i>S. moscopanum</i>	•	•	•	•	•

Table 2. Continued

Subsection, Superseries (corolla group)	Taxonomic series	Distribution	Relative resistance <sup>a</sup>						
			Species	GPA <sup>b</sup>	PA	CPB	PFB	PLH	
Advanced <i>Rotata</i>	<i>Piurana</i>	Central to northern regions of South America	<i>S. acroglossum</i>	R	S	R	•	•	
			<i>S. albornozii</i>				•	R	
			<i>S. blanco-galdosii</i>	•	•		R	S	
			<i>S. jalcae</i>			R			
Advanced <i>Rotata</i>	<i>Tuberosa</i> (Group i)	Mexico	<i>S. piurae</i>	•	•	•	R	•	
			<i>S. verrucosum</i>	•	R	S	•	•	
Advanced <i>Rotata</i>	<i>Tuberosa</i> (Group ii), <i>S. andreanum</i> (Group i)	Central to northern regions of South America	<i>S. andreanum</i>	•	•	•	R	•	
			<i>S. abancayense</i>	•	•	S	•	•	
			<i>S. acroscopicum</i>	•	•	•	S	•	
			<i>S. bukasovii</i>	•	R	•	S	•	
			<i>S. cajamarquense</i>	R	•				
			<i>S. canasense</i>	R	•	•	•	•	
			<i>S. chancayense</i>	•	R	•	•	R	
			<i>S. immite</i>	•	•	R	R	•	
			<i>S. marinasense</i>	R	•	•	R	•	
			<i>S. medians</i>	•	R	S	•	•	
			<i>S. mochiquense</i>	S	S	•	R	•	
			<i>S. multidissectum</i>	•	R	•	S	•	
			<i>S. multiinterruptum</i>	•	•	S	•	•	
			<i>S. pampasense</i>	•	•	•	R	•	
			<i>S. scabrifolium</i>	•	R	•	•	•	
			<i>S. sparsipilum</i>	S	•	•	S	•	
Cultivated	<i>Tuberosa</i>	South America	<i>S. ajanhuiri</i>	S	•				S
			<i>S. chaucha</i>	•	•				
			<i>S. curtilobum</i>	S	•	S	•	S	
			<i>S. phureja</i>	•	•	S	S	S	
			<i>S. stenotomum</i>	•	•	S	S	•	
			<i>S. tuberosum</i> subsp. <i>andigena</i>	S	•	S	S	S	
			<i>S. tuberosum</i> subsp. <i>tuberosum</i>	S	•	•	•	S	
			<i>S. acaule</i>	•	•	•	•	•	
			<i>S. albicans</i>	•	R	•	•	R	
Advanced <i>Rotata</i>	<i>Longipedicellata</i>	Southwestern USA and Mexico	<i>S. fendleri</i>	•	•	•	•	•	
			<i>S. hjertingii</i>	R	R	•	•	•	
			<i>S. papita</i>	•	•	•	•	•	
			<i>S. polytrichon</i>	•	•	•	R	•	
			<i>S. stoloniferum</i>	•	R	•	•	S	
			<i>S. × vallis-mexici</i>	R	R				
Advanced <i>Rotata</i>	<i>Demissa</i>	Mexico and Guatemala	<i>S. brachycarpum</i>	S	•	•	S	R	
			<i>S. demissum</i>	•	•	•	•	•	
			<i>S. guerreroense</i>	S	•	S	•	•	
			<i>S. hougasii</i>	•	R		•	•	
			<i>S. iopetalum</i>	•	•	•	R	•	
			<i>S. schenckii</i>	•	•	•	•	•	

<sup>a</sup> A species was considered resistant (R) to a given insect if its mean score was more than one standard deviation (sd) from the overall mean score for that insect. A species was considered intermediate (•) if its mean score was within one sd of mean insect score. A species was considered susceptible (S) if its mean score was more than one sd above mean insect score, blank within a column indicates wild potato species was not screened for that insect. Mean scores for GPA, PA, CPB, PFB, and PLH were 3.98, 4.49, 4.15, 3.23, and 2.65, respectively.

<sup>b</sup> GPA = green peach aphid, PA = potato aphid, CPB = Colorado potato beetle, PFB = potato flea beetle, and PLH = potato leafhopper.

<sup>c</sup> Taxon of uncertain/debatable status – see text for discussion.

Significant correlations within the superseries *Stellata* were between mean potato aphid score and mean Colorado potato beetle score ( $r = -0.62$ ,  $P = 0.02$ ,  $n = 14$ ), potato aphid score and potato flea beetle score ( $r = 0.46$ ,  $P = 0.10$ ,  $n = 14$ ), and potato flea beetle and potato leafhopper score ( $r = 0.56$ ,  $P = 0.03$ ,  $n = 15$ ). Significant correlations within the superseries *Rotata* (excluding the cultivated species) were between mean potato aphid score and mean green peach aphid score ( $r = 0.22$ ,  $P = 0.07$ ,  $n = 68$ ), potato flea beetle score and green peach aphid score ( $r = 0.42$ ,  $P = 0.00$ ,  $n = 63$ ), and potato flea beetle and Colorado potato beetle score ( $r = 0.31$ ,  $P = 0.01$ ,  $n = 66$ ). Within the primitive *Rotata*, green peach aphid scores and potato flea beetle scores were positively correlated ( $r = 0.59$ ,  $P = 0.00$ ,  $n = 24$ ). All other correlations within the primitive *Rotata* were nonsignificant. Within the advanced *Rotata*, green peach aphid and potato leafhopper scores were negatively correlated ( $r = -0.50$ ,  $P = 0.00$ ,  $n = 34$ ). All other correlations within the advanced *Rotata* were nonsignificant. Within the seven cultivated species, tests of correlation were limited by sample size but a significant negative correlation was observed between potato leafhopper and potato flea beetle scores ( $r = -0.97$ ,  $P = 0.00$ ,  $n = 5$ ).

Lack of a greater number of significant correlations is not surprising. Characters thought to be of high adaptive value, such as insect resistance, could have arisen in parallel through different genetic pathways, and may not be good phylogenetic markers. Where they occur, significant positive correlations may indicate germplasm useful for plant breeding schemes.

#### *Host-insect association*

In their long history of association, plants have influenced the evolution of insects, and insects the evolution of their host plants. The interaction between a particular plant and a particular insect depends upon the age of the association and the diversification of each during the association (Mitter et al., 1991), as well as on chemical composition and surface characteristics of the plant. All plants

contain secondary plant metabolites, often imparting a chemical defense against pests. Similarly, a leaf surface characteristic such as dense hairs may be a direct defense against an insect, but could have evolved to prevent water loss or for some other purpose.

The length of association between the 100 wild potato species and the five insects evaluated in this study varies. Resistance of a wild potato species to a particular insect may be the result of long association with the particular pest or a similar herbivore, or it may be incidental, due to the presence of particular secondary chemicals or surface characteristics.

Green peach aphid has been considered to be a native of Asia, from areas where its primary host, *Prunus persica*, is native (Blackman & Eastop, 1984), and therefore of relatively recent association with tuber-bearing *Solanum* species. Jones (1981) recently postulated that green peach aphid has been associated with wild potatoes over a long period of time. Aphids tend to be a greater problem in temperate regions, and therefore, selection pressure for aphid resistance may be greater at medium to high altitudes, where climatic conditions are similar to temperate regions. In Peru and Bolivia, green peach aphid is common below 3000 meters, and scarce at cooler and higher altitudes (Jones, 1981).

The potato aphid is generally accepted to be of North American origin (Blackman & Eastop, 1984). It is a cool-weather aphid favored by humid conditions. Solanaceous hosts are the most common secondary hosts of the potato aphid, suggesting a long association with potato species. Resistance might be expected in North American species based on prior association. Indeed, potato aphid resistance tends to be concentrated in accessions from Mexico, Central America, and the southwestern United States. Accessions from Argentina and Chile are among the most susceptible. There were significantly more potato aphid resistant Mexican species than Chilean and Argentinian species (Chi-square = 5.52, 1 df,  $P < 0.05$ ).

There are approximately 40 species in the genus *Leptinotarsa*, which is believed to have originated in southern Mexico (Tower, 1906). Most *Leptino-*

*tarsa* species occur in habitats in which the ground and lower stratum of air are usually moist, primarily the physiologically dry grasslands. The Colorado potato beetle has probably been in North America for hundreds of years (Neck, 1983). Host plants were other *Solanum* species, particularly *S. rostratum*. *Solanum tuberosum* became a host for Colorado potato beetle only when settlers brought cultivated potatoes into the range of *S. rostratum*. This occurred in the Great Plains around 1850, where *L. decemlineata* occurred at altitudes of 1000–2330 m (Tower, 1906; Neck, 1983). The four *Solanum* species most resistant to Colorado potato beetle, *S. pinnatisectum*, *S. polyadenium*, *S. jamesii*, and *S. trifidum* are primitive species from central and northern Mexico and the southwestern United States. However, at present, in Mexico, wild potato species and *Leptinotarsa* spp. do not have a close association, as *Leptinotarsa* spp. generally occur at lower altitudes than wild potatoes, and feed on *Solanum* species only distantly related

to potato (F.R. Drummond, Univ. of Maine, personal communication). One exception is *S. cardiophyllum*, on which Colorado potato beetles have been observed in Mexico.

Potato flea occurs primarily in the Midwest and Atlantic regions of the United States, but similar species occur throughout North and South America (Blackwelder, 1946). In Peru, at least five species of *Epitrix* feed upon potato (Bravo P. et al., 1986). Potato-feeding flea beetles occur in a wide range of environments. The flea beetles are foliage feeders in the adult stage, so generalized defense mechanisms against herbivores or foliar fungi may impart resistance. Group ii and Group iii *Tuberosa*, from South America, contain numerous sources of resistance to potato flea beetle, perhaps because of a long association with flea beetles.

The potato leafhopper, *Empoasca fabae*, is a tropical to semitropical insect that disperses to more temperate areas of North America in the summer months. Taxonomy of this group is diffi-

Table 3. Association of insect resistance and host plant defense mechanisms

	Percent resistant species, (n)				
	GPA <sup>a</sup>	PA	CPB	PFB	PLH
<b>Glycoalkaloids</b>					
chaconine-solanine	15% (41)	23% (40)	5% (40)	22% (41)	10% (41)
chaconine-solanine (high levels)	8% (13)	33% (12)	8% (12)	15% (13)	0% (13)
chaconine-solanine (medium levels)	22% (9)	11% (9)	0% (9)	30% (10)	20% (10)
chaconine-solanine (low levels)	17% (18)	22% (18)	6% (18)	22% (18)	6% (18)
solamargine-solasonine	8% (13)	8% (13)	15% (13)	21% (14)	14% (14)
tomatine	25% (8)	13% (8)	50% (8)**	11% (9)	44% (9)**
demissine	0% (4)	0% (4)	25% (4)	0% (4)	0% (4)
commersonine-dehydrocommersonine	0% (2)	0% (2)	50% (2)	0% (2)	0% (2)
leptines	0% (1)	0% (1)	100% (1)	0% (1)	0% (1)
no major glycoalkaloids	50% (2)	0% (2)	25% (4)	0% (4)	0% (4)
overall, where glycoalkaloid data available	15% (60)	17% (59)	14% (60)	20% (64)	14% (64)
<b>Density of hairs</b>					
glandular hairs	22% (9)	11% (9)	50% (10)**	70% (10)**	60% (10)**
dense hairs	35% (20)*	20% (20)	22% (23)	45% (22)**	32% (22)**
intermediate hairs	13% (40)	15% (40)	6% (36)*	14% (37)	3% (38)**
sparse hairs	9% (11)	0% (10)	0% (12)	15% (13)	8% (13)
glabrous/glabrescent	23% (13)	23% (15)	46% (13)**	13% (15)	19% (16)
overall, where pubescence data available	19% (86)	15% (85)	17% (86)	23% (90)	15% (92)

<sup>a</sup> GPA = green peach aphid, PA = potato aphid, CPB = Colorado potato beetle, PFB = potato flea beetle, and PLH = potato leafhopper. A species was considered resistant if its mean insect score was at least one standard deviation below the mean.

\* indicates  $P < 0.10$ , \*\* indicates  $P < 0.05$ , Chi-square tests, 1 df, with 'overall' used as expected.

cult. Seven species of Empoascans related to *E. fabae*, including *E. kraemeri* Ross & Moore, have been collected from potato in Peru (K.V. Raman, International Potato Center, Lima, Peru, personal communication). *E. fabae* has been reported in Central as well as South America (Ross et al., 1964). In Argentina, a leafhopper identified as *E. fabae* was the most abundant empoascan (Young, 1953). *E. fabae* was reported as the most common and damaging empoascan on crops in the *clima medio*, elevation 1000 to 2000 m, in Colombia (Ruppel & DeLong, 1956), but this leafhopper may actually be *E. kraemeri* (Ross & Moore, 1957). Other empoascans occur on crops at higher altitudes, but leafhoppers are serious pests only in the *clima medio*.

#### *Glycoalkaloid content*

Wild potatoes contain a variety of glycoalkaloids, often in concentrations far greater than observed in cultivated potatoes (van Gelder et al., 1988). Excessive total glycoalkaloids are associated with undesirable flavor and mammalian toxicity and teratogenicity (Gregory et al., 1981). Plant breeding programs based on enhancing total glycoalkaloid content have been largely abandoned because foliar total glycoalkaloid content is highly correlated with tuber glycoalkaloid levels, because glycoalkaloid concentration varies with environment, and because total glycoalkaloid content is polygenically inherited (Dimock & Tingey, 1985). Resistance to Colorado potato beetle may involve relatively few glycoalkaloids, hence breeding for a specific glycoalkaloid may be easier and more feasible than breeding for total glycoalkaloid content.

In wild potatoes, the most common glycoalkaloids are solanine and chaconine, followed by solamargine and solasonine. These glycoalkaloids were not associated with resistance at the species level to any of the five insects (Table 3). Solanine, chaconine, solamargine, and solasonine have been reported to have no effect on Colorado potato beetle (Dimock & Tingey, 1985). Dahlman & Hibbs (1967) observed that solanine, even at high concentration, did not affect potato leafhopper survival.

Resistance to Colorado potato beetle and potato leafhopper occurred more frequently in species containing tomatine than in the wild potatoes as a whole. Beck (1965) reported that tomatine repels Colorado potato beetle, and Stürckow & Löw (1961) observed that tomatine reduces feeding by Colorado potato beetle larvae. Dahlman & Hibbs (1967) found that tomatine reduces inhibition rates and survival of potato leafhopper nymphs.

Colorado potato beetle resistance has been associated with demissine and leptines (Kuhn & Löw, 1955), and with commersonine and dehydrocommersonine (Sinden et al., 1980), as well as with tomatine. However, of the four species containing demissine, only one, *S. chacoense*, was resistant overall to Colorado potato beetle. *Solanum chacoense* and *S. commersonii* both contain commersonine and dehydrocommersonine (Osman et al., 1976), yet only *S. chacoense* is resistant to Colorado potato beetle. The leptines are unique to a few accessions of *S. chacoense*. Dahlman & Hibbs (1967) reported that leptine I reduces leafhopper feeding and survival. Three accessions of *S. chacoense* were highly resistant to potato leafhopper, but the species as a whole was intermediate. Glycoalkaloid content varies between individual accessions within a species. This may explain lack of correlation between these glycoalkaloids and insect resistance at the species level.

#### *Glandular trichomes*

Defense due to glandular trichomes involves both physical and chemical aspects that lead to a series of modifications in insect behavior (Tingey, 1991). In potatoes, glandular trichomes are of two types, type A glandular trichomes (Gibson, 1971) are four-lobed, and contain phenolic compounds (Avé & Tingey, 1986); type B are longer trichomes which exude droplets containing sucrose esters of carboxylic acids from their tips (Neal et al., 1990). Species with glandular trichomes were more frequently resistant to Colorado potato beetle, potato flea beetle, and potato leafhopper than in wild potatoes as a whole (Table 3). Glandular trichomes did not confer field resistance to aphids more often

than might be expected of the wild potatoes as a whole. However, species with glandular trichomes had fewer green peach aphids than *S. tuberosum*, but more potato aphids.

Accessions with type A + B trichomes (most *S. berthaultii* possess both) were more resistant (lower insect ratings) to potato aphid, potato leafhopper and potato flea beetle than accessions with type A trichomes only (Table 4). However, accessions with both types of trichomes had more green peach aphids than accessions with type A trichomes alone. Type B trichomes are long, and may be more prone to damage in the field. One of us (E.B.R.) has observed that glandular trichomes often become coated with dust or otherwise damaged in the field, rendering them ineffective as defenses against insects (Fig. 2). Green peach aphid preferentially feed on older leaves where trichomes have been exposed longer and possibly rendered ineffective. Production of glandular exudate by a type B trichome is not constant (W.M. Tingey, Cornell University, personal communication), as individual trichomes start and stop production. Trichomes may also be lost, then regenerated. Accessions with type A trichomes have twice as many type A trichomes per unit area than do accessions with both type A and type B trichomes (Tingey & Sinden, 1982). Resistance to green peach aphid has been shown to increase with type A trichome density (Tingey & Laubengayer, 1981). Perhaps type B trichomes are more readily damaged in the field, resulting in accessions with effectively type A trichomes only. Such accessions would have fewer type A trichomes than the type A only accessions, and might therefore be expected to have higher aphid counts. Accessions in which some plants had type A trichomes, others both type A and type B trichomes had considerably higher aphid ratings than accessions with type A only, or those with type A + B trichomes.

Because of the presence of glandular trichomes, *Solanum berthaultii* and *S. tarijense* have received much attention as possible sources of insect resistance. The traditional classification of these two species has recently been re-examined. Hawkes & Hjerting (1989) and Ochoa (1990) map *S. berthaultii* from northern to southern Bolivia, and *S. tari-*

*jense* from central Bolivia to northern Argentina, with considerable sympatry in central Bolivia. Hawkes & Hjerting hypothesize that the many intermediate forms connecting the morphology of these two species (24% of the populations cited in their book) are interspecific hybrids between the two species and these are widely distributed from central to northern Bolivia, occupying the northern range of *S. tarijense* and almost the entire range of *S. berthaultii*. *Solanum tarijense* has been placed in series *Yungasensa*, superseries *Stellata*, and *S. berthaultii* in series *Tuberosa*, superseries *Rotata* by Hawkes (1990); both of these species have been placed in series *Commersoniana* by Ochoa (1990), who does not use the *Stellata* and *Rotata* superseries ranks. Spooner & van den Berg (1991) have proposed that *S. berthaultii* and *S. tarijense* are actually a single species because of the extensive overlap in morphological characteristics.

Among these two species and their natural hybrids as defined by Hawkes, we observed differences in insect response. Raw data, rather than insect scores, reveal similarities and differences among the three groups. *Solanum berthaultii* as a species was resistant to Colorado potato beetle, potato flea beetle, and potato leafhopper. *Solanum tarijense* as a species was resistant to Colorado potato beetle only. *Solanum berthaultii*-*S. tarijense* hybrids were resistant to Colorado potato beetle only. *Solanum tarijense* possesses more field resistance to aphids and Colorado potato beetle than *S. berthaultii* (Table 4), whereas *S. berthaultii* is more resistant to flea beetles and leafhoppers than *S. tarijense*. *Solanum berthaultii*-*S. tarijense* hybrids were more susceptible to potato aphid and potato flea beetle than either parent. One character involved in the traditional differentiation of these two species is the presence of type B trichomes in many *S. berthaultii* accessions. For each insect other than potato aphid, the difference in insect response to *S. berthaultii* vs. *S. tarijense* mirrored the difference in insect response of accessions with type A + B trichomes vs. accessions with type A trichomes only. Difference in response of the two species to potato aphid cannot be explained by trichome type.

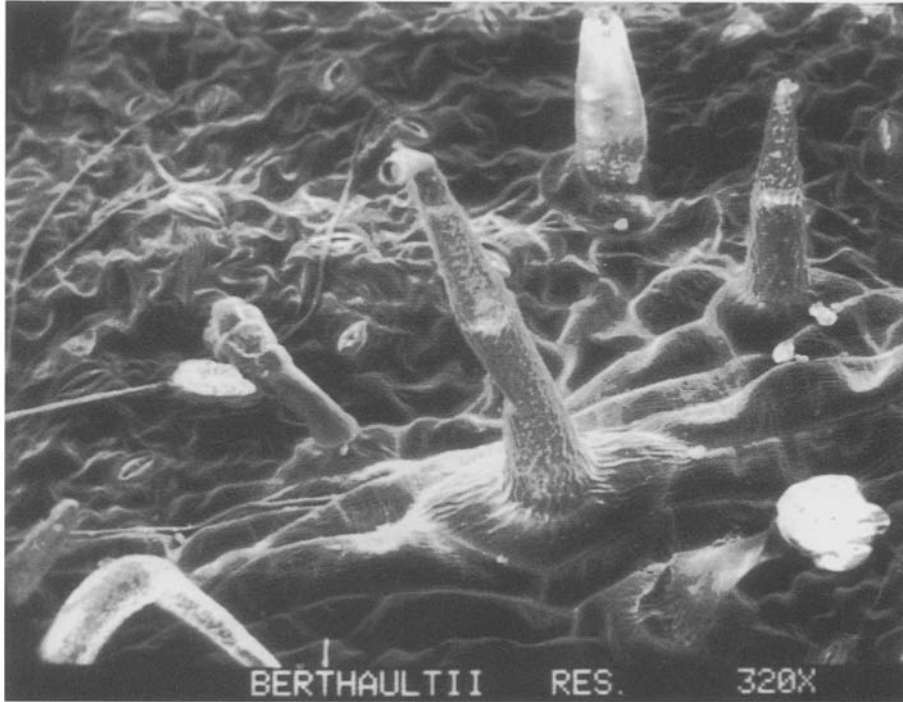


Fig. 2. Scanning electron micrograph of a leaf from *S. berthaultii* in Minnesota screening trials, showing damaged glandular trichomes possibly associated with soil splash, wind, raindrops, or foliage rubbing together in the field.

Table 4. Comparison of insect response to *S. berthaultii*, *S. tarijense*, *S. berthaultii*-*S. tarijense* hybrids, based on trichome type and species definition

Insect	Mean insect rating (n) <sup>a</sup>					
	Trichome type <sup>b</sup>			<i>S. berthaultii</i> <sup>c</sup>	<i>S. tarijense</i> <sup>d</sup>	<i>S. berthaultii</i> - <i>S. tarijense</i> hyb. <sup>e</sup>
	type A + B	type A	type A or type A + B			
Green peach aphid	1.22 (8)	1.00 (32)	2.25 (4)	1.34 (8)	0.89 (27)	1.77 (9)
Potato aphid	0.90 (8)	1.00 (14)	2.83 (4)	1.13 (8)	0.90 (11)	1.93 (7)
Colorado potato beetle	1.08 (8)	1.00 (15)	1.01 (2)	1.22 (7)	0.93 (11)	0.99 (7)
Potato flea beetle	0.39 (7)	1.00 (28)	0.41 (1)	0.55 (6)	0.85 (23)	1.19 (7)
Potato leafhopper	0.33 (8)	1.00 (22)	0.50 (2)	0.67 (7)	1.00 (17)	0.67 (8)

<sup>a</sup>Mean insect rating (not insect score), standardized by dividing by insect rating for accessions with type A trichomes. Only those accessions for which trichome data (courtesy W.M. Tingey, Cornell University) available are included. Number of accessions screened in parentheses.

<sup>b</sup>100 clones from each accession were evaluated for trichome type. Accessions were classified according to whether all individuals had type A trichomes, all individuals had type A + B trichomes, or some individuals had type A + B trichomes and some individuals had type A only.

<sup>c</sup>Six accessions identified by Hawkes as *S. berthaultii* had both type A + B trichomes, plants from two other accessions had either type A, or type A + B trichomes.

<sup>d</sup>The 29 accessions included as *S. tarijense* all had type A trichomes only.

<sup>e</sup>Five *berthaultii*-*tarijense* hybrids had type A trichomes only, two had type A + B trichomes, and plants of three accessions had either type A, or type A + B trichomes.



### Nonglandular hairs

In plants, nonglandular hairs serve various physiological functions, such as water conservation or other ecological functions including defense against phytophagous insects. Dense hairs have long been recognized as a defense mechanism against potato leafhopper on legumes (Poos, 1929). The effectiveness of nonglandular pubescence as a resistance mechanism depends on density, erectness, length, and shape of hairs. Wild potato species with dense, nonglandular hairs were more frequently resistant to green peach aphid, potato flea beetle, and potato leafhopper than expected (Table 3). Presence of dense nonglandular hairs in the wild potatoes would appear to be a generalized defense mechanism, although it is significant that Colorado potato beetles and potato aphids are apparently unaffected by dense hairs. Species with sparse or intermediate hairs were least likely to possess any kind of resistance.

There are a few potato species with glabrous leaves. Resistance to Colorado potato beetle occurred more frequently in these species, namely *S. pinnatisectum*, *S. circaeifolium*, *S. acroglossum*, *S. chomatophilum*, *S. jalcae* and *S. immite*. Perhaps species with glabrous leaves have evolved other defense mechanisms. It has been noted that plants with glabrous leaves often possess resistance to insects (Norris & Kogan, 1980).

### Habitat

Resistance to green peach aphid tended to occur more frequently in species occurring naturally in mesic and dry habits than in species in moist habitats (Fig. 3), but the differences were nonsignificant. Resistance to potato aphid tended to be most frequent in species occurring in moist habitats, or cold habitats, but again, differences were not significant. Species occurring in hot, dry areas were significantly more resistant to Colorado potato beetle and potato flea beetle. A similar, though nonsignificant trend, was observed with potato leafhopper and species from hot, dry areas.

#### Green peach aphid

	Moist	Mesic	Dry	
Cold	5/37	1/2	2/6	5/42 vs. 11/44,
Mild	0/1	4/13	0/0	$\chi^2 = 2.4$ , n.s.
Hot	0/4	0/1	4/22	

#### Potato aphid

	Moist	Mesic	Dry	
Cold	7/37	0/2	2/6	10/50 vs. 3/35,
Mild	0/1	0/13	0/0	$\chi^2 = 2.1$ , n.s.
Hot	1/4	1/1	2/21	

#### Colorado potato beetle

	Moist	Mesic	Dry	
Cold	4/38	1/2	0/6	8/65 vs 7/21,
Mild	0/1	2/13	0/0	$\chi^2 = 4.9$ , *
Hot	1/4	0/1	7/21	

#### Potato flea beetle

	Moist	Mesic	Dry	
Cold	7/39	0/3	0/6	12/68 vs. 9/22,
Mild	0/1	3/13	0/0	$\chi^2 = 5.0$ , *
Hot	2/4	0/1	9/22	

#### Potato leafhopper

	Moist	Mesic	Dry	
Cold	3/40	1/3	1/6	9/68 vs 6/23,
Mild	0/1	2/13	0/0	$\chi^2 = 2.1$ , n.s.
Hot	2/4	0/1	6/23	

Fig. 3. Association of resistance with wild potato habitat. Each category lists number of resistant species/total number of species within that category. Heavy lines indicate categories with similar resistance levels. Asterisk indicates  $P < 0.05$ , Chi-square, 1 df.

### Altitude

In those species occurring over a wide range of altitude, or in which a wide range of insect scores was observed, significant correlations ( $P \leq 0.10$ ) between insect score and altitude of collection occurred in six of thirteen species examined. Both positive correlations, indicating decreasing resist-

ance with increasing altitude, and negative correlations, indicating increasing resistance with increased altitude, were observed. For some species, the small number of accessions screened and a small altitude range may have affected the results. Mean number of accessions screened where significant correlations were found was 25.8, and 15.6 in species where significant correlations were not found. A significant correlation between green peach aphid and altitude occurred in *S. acaule* subsp. *acaule* ( $r = -0.26$ ,  $P = 0.10$ ,  $n = 41$ ), 1 of 12 species tested. A significant correlation between potato aphid and altitude occurred in *S. pinnatisectum* ( $r = 0.74$ ,  $P = 0.06$ ,  $n = 7$ ), and *S. stoloniferum* subsp. *stoloniferum* ( $r = -0.55$ ,  $P = 0.04$ ,  $n = 14$ ), 2 of 10 species tested. A significant correlation between Colorado potato beetle and altitude occurred in *S. stoloniferum* subsp. *stoloniferum* ( $r = 0.76$ ,  $P = 0.03$ ,  $n = 8$ ), 1 of 8 species tested. A significant correlation between potato flea beetle and altitude occurred in *S. fendleri* ( $r = -0.89$ ,  $P = 0.01$ ,  $n = 7$ ), 1 of 11 species tested. A significant correlation between potato leafhopper and altitude occurred in *S. pinnatisectum* ( $r = -0.77$ ,  $P = 0.04$ ,  $n = 7$ ), *S. chacoense* ( $r = 0.58$ ,  $P = 0.00$ ,  $n = 33$ ), and *S. infundibuliforme* ( $r = -0.55$ ,  $P = 0.02$ ,  $n = 17$ ), 3 of 12 species tested.

Ecogeographical variation in characters associated with host plant resistance is not surprising. Levin (1973) discusses numerous examples of intraspecific variation in trichome density relative to altitude and geographic zones. Altitudinal variation within the species could have come about from pressure by a particular insect in our screening trials or a similar insect.

A positive correlation between insect score and altitude indicates that the more resistant accessions occurred at lower altitudes. This was observed in *S. chacoense*, a low-altitude species, and might be expected because empoascan leafhoppers are more numerous at lower altitudes. *Leptinotarsa* species are also generally found at lower altitudes (under 2300 m), and pressure by these insects in the past or by other defoliators may explain greater resistance to Colorado potato beetle in lower-altitude collections of *S. stoloniferum*. Mean Colorado potato beetle score in *S. stoloniferum* accessions collected

below 2300 m was 3.4. Mean Colorado potato beetle score in *S. stoloniferum* collections above 2500 m was 5.3.

At the highest altitudes a potato species has become adapted to, plants may be under such environmental stress that they cannot tolerate substantial insect damage; thus insect defense mechanisms would be of evolutionary advantage. This could explain the altitude effects observed in *S. infundibuliforme*, *S. fendleri*, and *S. acaule*, where insect score decreased with altitude. The decreasing potato aphid scores with increasing altitudes observed in *S. stoloniferum* may also be thus explained.

The significant correlations observed in *S. pinnatisectum* (1600–2000 m, 7 accessions, positive potato leafhopper correlation, negative potato aphid correlation) may simply reflect isolation of a single accession from the rest of the population, not differences arising from altitudinally associated variation in pest pressure. PI 275236 had the highest potato leafhopper score and the lowest potato aphid score of *S. pinnatisectum* accessions included in the analysis (Table 1). It was collected at 1600 m in Jalisco province. This happened to be the lowest altitude collection of *S. pinnatisectum*, but it was also the most isolated of the accessions, the nearest *S. pinnatisectum* collection being 140 km distant.

## Conclusions

The wild potatoes provide many sources of insect resistance of potential value to plant breeders. Historically, breeders have accessed exotic species, especially the more primitive ones, only when desirable traits are not available in cultivated potatoes. However, there is justification in striving to introgress primitive genes, if only to increase diversity within breeding lines. Difficulties could arise in incorporating some of these sources into breeding lines, and in inadvertently selecting for susceptibility to one insect while selecting for resistance to another insect or in selection for some other attribute. This paper identifies insect resistant germplasm, as well as susceptible germplasm. From our data we cannot infer how many times resistance to a particular insect evolved. We sug-

gest breeders might increase the chances of obtaining valuable resistance genes by utilizing diverse sources in prebreeding schemes.

It is apparent that no one factor explains resistance to a particular insect. However, the following generalizations can be made. Resistance to one or more insects appears to be a primitive trait in wild potatoes. The cultivated species and their near relatives are susceptible to intermediate in resistance, compared to the wild potatoes as a whole. Insect resistance was also characteristic of the most advanced species. Species from hot and arid areas are significantly more resistant to Colorado potato beetle and potato flea beetle. Species from cool or moist areas tend to be more frequently resistant to potato aphid. Resistance to potato aphid occurred significantly more often in the Mexican and Central American species than in Argentinian and Chilean species. Six of eight species containing the glycoalkaloid tomatine are resistant to at least one insect. *Solanum chacoense*, with more types of glycoalkaloids than any other species, is resistant to Colorado potato beetle. Possession of dense hairs was associated with resistance to green peach aphid, potato flea beetle, and potato leafhopper. Glandular trichomes are particularly associated with field resistance to Colorado potato beetle, potato flea beetle, and potato leafhopper. Significant correlations between insect score and altitude at which an accession was collected occurred in six of thirteen species.

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