Wide Phenotypic Diversity for Resistance to *Phytophthora infestans* Found in Potato Landraces from Peru

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Abstract

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The wild and cultivated species of potato have been utilized in potato breeding to good effect but only a very small sample of the available biodiversity has been exploited. In total, 468 accessions of wild and cultivated species of potato were assessed for resistance to the oomycete pathogen *Phytophthora infestans* using greenhouse assays. Wide phenotypic variation for resistance was found within a species (i.e., among accessions) but not among species which, on average, were

similar. Nineteen accessions had resistance levels better than or similar to the variety Chucmarina, which is routinely used by the International Potato Center as a resistant control. Surprisingly, a number of accessions were significantly more susceptible than the susceptible control, Tomasa Condemayta. Frequency histograms of species indicated continuous variation for resistance with little evidence for functional resistance genes.

Agriculture is the economic base for rural smallholders in the developing world. Smallholder farmers at mid-elevations and highlands often have limited options for increasing their incomes in agricultural subsectors. Under these conditions, potato is an ideal crop because of its high potential productivity and high nutritive value (22). Over the last decades, potato production has increased in developing countries, where more than half of the global production now occurs (14). Unfortunately, most of this growth in potato production has come from increased land use and not increased productivity (14).

In developing countries, several diseases consistently constrain productivity of potato. One of the most important of these is potato late blight (PLB), which is caused by the oomycete pathogen *Phytophthora infestans*. Annual losses due to PLB, in both yield reduction and fungicide use, has been estimated to be near U.S.\$10 billion (14). PLB is present in all major areas where potato is grown (15), although disease intensity depends on local weather conditions and host plant susceptibility. In the highland tropics, PLB is particularly difficult to manage because of year-round potato production (10) and low farmer capacity to understand and manage the disease (1).

PLB can generally be effectively managed with fungicides; however, many of these chemicals pose environmental or health hazards (17), particularly in developing countries where farmers spray by hand and seldom, if ever, use personal protective equipment (23). The most sustainable way to manage the disease is with host plant resistance but this strategy has had very limited success (8). Of the reasons given for this limited success, one of the most important is pathogen evolution, which leads to selection of new strains that are pathogenic on previously resistant potato varieties.

Host plant resistance against *P. infestans* can be found in several wild and native *Solanum* spp. (3,7); however, two phenotypic expressions of host plant resistance to *P. infestans* have been described. One is associated with major genes (resistance [*R*] genes), which confer near immunity against certain races of the pathogen (31). This resistance is referred to as vertical, qualitative, or race

specific. The other type of resistance, referred to as horizontal, quantitative, or race nonspecific, is believed to be based on the presence of multiple genes of relatively small effect that, in theory, render the host partially resistant to all races of the pathogen (18,30). However, quantitative resistance is often masked by qualitative resistance, making selection for the former difficult. Recently, an interval scale was developed to facilitate measurement of quantitative resistance and comparison of resistance measurements across experiments (33).

In the search for more durable sources of resistance, the International Potato Center (CIP) has initiated a program to evaluate some of its 3,500 potato landraces collected from farming communities in the Andes. These potato landraces of unknown origin and age have been selected by Andean farmers over millennia for their good taste, resistance to the adverse climatic conditions of the Andes, and resistance to pests and pathogens. The objective of the present work was to quantify and, to the extent possible, characterize the phenotypic expression of resistance to *P. infestans* in 468 accessions of potato landraces from the CIP germplasm collection.

Materials and Methods

Plant material. In total, 468 *Solanum* accessions distributed across seven species were evaluated for resistance to *P. infestans*. One breeding line (CIP 399076.12), belonging to the CIP population B1C5 derived from *Solanum tuberosum* subsp. *andigena*, and three Peruvian varieties (Yungay, Chucmarina, and Tomasa Condemayta) with different levels of putative horizontal resistance were used as controls. At the beginning of the experiment, all materials were propagated from in vitro mother plants free of known potato pathogens to ensure a similar high level of health. Six cuttings from each accession and control were transplanted into commercial substrate (Jiffystrips, Product 300522; Jiffy Products) mixed with organic soil and sand, which had been previously steam pasteurized for 2 h during 2 days consecutively. The plants were grown for 45 days until preflowering stage in 16.5-cm-diameter pots containing the above-mentioned substrate. Insecticide (Lambda-cyhalothrin) was applied to control potato flea beetles when necessary. Plants were protected with a systemic fungicide (Benomyl) for the first 15 days after transplanting. No fungicides effective against *P. infestans* were used.

Pathogen isolate. The isolate POX67 belonging to the EC-1 lineage (32), which indiscriminately attacks both wild and cultivated tuber-bearing solanaceous hosts in Peru (11), was used in the assays. The isolate was recovered from storage in liquid nitrogen

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and multiplied on tuber slices of Huayro potato (*S. chaucha*) at 18°C in a moist chamber to promote sporulation. Inoculum was prepared as described by Perez et al. (24) and Villamon et al. (32). The sporangial concentration used in each inoculation was 3×10^3 sporangia/ml.

Whole-plant tests. The experiments were carried out in a greenhouse in CIP's highland station at Huancayo, Peru (3,200 m above sea level, 11°56'S, 75°15'W). The greenhouse was equipped with overhead sprinklers to ensure leaf wetness during critical times. Shade cloth was placed around the structure to keep the temperature between 15 and 20°C. A plastic cover was placed over the plants at night to maintain high relative humidity for disease development. The plants were inoculated with the sporangial suspension until run-off with a hand-held sprayer; the absolute volume per plant ranged between 20 and 40 ml and depended on the amount of foliage of each inoculated plant.

Owing to the large number of plants to be assessed, three assays were done; however, the same protocols were used in each assay and the environmental conditions were similar. Each plant was considered to be an experimental unit and three plants (replicates) of each genotype were inoculated. A complete set of the controls described above was used in each assay. Pots of each replicate and controls were randomized in the greenhouse for each assay.

Evaluations. The percentage of leaf area affected of each plant was evaluated three times at 2-day intervals beginning on the third day after inoculation. From these readings, the relative area under the disease progressive curve (rAUDPC) was calculated for each

individual plant from the ratings of foliar infection (2). The rAUDPC values were then used to calculate susceptibility scale values for each accession, as proposed Yuen and Forbes (33). The proposed scale has ascending numbers for increasing susceptibility, and calculation of scale values requires a common susceptible control; thus, a scale value of 9 was assigned to Tomasa Condemayta, known for its susceptibility to PLB.

Data were analyzed using the Scott and Knott multiple comparison method ($P < 0.05$) after an analysis of variance (ANOVA) using the statistical program R (R Foundation for Statistical Computing).

Results

Resistance to potato late blight. Infection was severe in all three experiments, with the overall average severity (for all three assays) being 0.7, 32.3, and 83.51% for the three reading dates, respectively. There were no significant differences in scores of controls among the three assays (*data not shown*). A high degree of phenotypic diversity for resistance was found among the accessions tested; however, most of this variability was found within species. When resistance was assessed at the species level, the results of the ANOVAs using the scale values and considering experiments as repeated tests showed no significant differences among species and susceptible controls Tomasa Condemayta and Yungay. However, all species were significantly more susceptible than the resistant genotypes CIP 399076.12 and Chucmarina (Table 1).

Analyses of individual accessions demonstrated much greater diversity because some were more resistant than the resistant control

Table 1. Susceptibility to *Phytophthora infestans* of 468 accessions belonging to eight potato landrace species tested under greenhouse conditions in Huancayo, Peru

Potato landraces, species, and control varieties	Number of accessions per species	Ploidy	Scale value mean ^y	Standard deviation	Scott Knott Test ($\alpha = 0.05$) ^z
Tomasa Condemayta		2n=4x=48	9.00	0.37	a
<i>Solanum phureja</i> Juz. et Buk.	124	2n=2x=24	8.21	1.82	a
Yungay		2n=4x=48	7.60	0.73	a
<i>S. goniocalyx</i> Juz. et Buk.	37	2n=2x=24	7.33	2.44	a
<i>S. stenotomum</i> Juz. et Buk.	112	2n=2x=24	7.17	2.07	a
<i>S. tuberosum</i> subsp. <i>tuberosum</i> L.	31	2n=4x=48	7.16	2.42	a
<i>S. curtilobum</i> Juz. et Buk.	5	2n=5x=60	6.73	1.90	a
<i>S. tuberosum</i> subsp. <i>andigena</i> Juz. et Buk.	120	2n=4x=48	6.49	2.03	a
<i>S. chaucha</i> Juz. et Buk.	26	2n=3x=36	6.40	1.95	a
<i>S. juzepczukii</i> Buk.	13	2n=3x=36	5.90	2.98	a
CIP 399076.12	...	2n=4x=48	4.11	0.25	b
Chucmarina	...	2n=4x=48	3.02	0.44	b
Total	468	...	...	...	...

^y Susceptibility scale proposed by Yuen and Forbes (33).

^z In the column, averages followed by the same letter belong to a common group, because they don't differ for the Scott-Knott grouping method to 5% of significance.

Table 2. Potato landraces accessions with *Phytophthora infestans* susceptibility scale values less than or equal to control variety Chucmarina

CIP code, accession	Collecting code	Species	Local name	Country	Scale value mean ^z
CIP 703765	HUA 935	<i>Solanum chaucha</i> Juz. et Buk.	Chaucha Cunvicana	Peru	2.63
CIP 703831	OCH 5685	<i>S. goniocalyx</i> Juz. et Buk.	Pampina	Peru	2.85
CIP 704270	CUA 534	<i>S. goniocalyx</i> Juz. et Buk.	Wira Pasña	Peru	2.85
CIP 704414	OCH 5272	<i>S. juzepczukii</i> Buk.	Mullu Winku	Peru	1.58
CIP 704777	HJA 1238	<i>S. juzepczukii</i> Buk.	Jancko Kaisalla	Bolivia	2.69
CIP 702619	HHCH 4932	<i>S. juzepczukii</i> Buk.	Jancko Kaisalla	Bolivia	1.43
CIP 701310	PPP 1310	<i>S. tuberosum</i> subsp. <i>andigena</i> Juz. et Buk.	Chungolonga	Peru	2.06
CIP 703652	JAK 15	<i>S. tuberosum</i> subsp. <i>andigena</i> Juz. et Buk.	Tarmeña	Peru	3.01
CIP 703957	OCH 8544	<i>S. tuberosum</i> subsp. <i>andigena</i> Juz. et Buk.	Siwayllus	Peru	1.66
CIP 704024	OCH 9870	<i>S. tuberosum</i> subsp. <i>andigena</i> Juz. et Buk.	Oqe Choqollo	Peru	1.19
CIP 704378	OCH 4733	<i>S. tuberosum</i> subsp. <i>andigena</i> Juz. et Buk.	Kashpa Ploma	Peru	2.69
CIP 704590	OCH 9248	<i>S. tuberosum</i> subsp. <i>andigena</i> Juz. et Buk.	Puka Imilla	Peru	1.19
CIP 705363	OCH 10216	<i>S. tuberosum</i> subsp. <i>andigena</i> Juz. et Buk.	Unknown	Ecuador	2.85
CIP 704176	UACH 1046	<i>S. tuberosum</i> subsp. <i>tuberosum</i> L.	Unknown	Chile	1.43
CIP 704332	UACH 1057	<i>S. tuberosum</i> subsp. <i>tuberosum</i> L.	Camota	Chile	1.39
CIP 704140	OCHS 11801	<i>S. stenotomum</i> Juz. et Buk.	Unknown	Bolivia	3.01
CIP 705476	CUA 286	<i>S. stenotomum</i> Juz. et Buk.	Yana Cambru	Peru	1.43
CIP 705554	CUA 728	<i>S. stenotomum</i> Juz. et Buk.	Kamarita Papa	Peru	2.53
CIP 703446	OCH 8852	<i>S. stenotomum</i> Juz. et Buk.	Yuraq Choqollo	Peru	1.54

^z Susceptibility scale proposed by Yuen and Forbes (33).

but, in addition, a number of accessions were significantly more susceptible than the susceptible control, which had been assigned a scale value of 9. Nineteen accessions, spread across all species, had scale values equal to or less than Chucmarina (scale value = 3.02) and, thus, were identified for their resistance and potential as sources of resistance for breeding (Table 2). In all, 32 were more resistant than breeding line CIP 399076.12 (scale value = 4.11) and 286 accessions were more resistant than Yungay (scale value = 7.60), which is the second most popular variety grown in the Peruvian highlands (20). However, 97 accessions were also more susceptible than the control Tomasa Condemayta (scale value = 9.00; Fig. 1).

The distribution pattern of resistance levels was generally similar and unimodal among the potato landraces species, indicating little evidence for the presence of major *R* genes effective against the inoculum used in the tests (Fig. 1).

Discussion

Resistance to PLB has been reported previously for some of the species tested in this study. Accessions belonging to *S. juzepczukii* (BOL 1465 and BOL 3395) had adequate levels of field resistance in studies done in Bolivia (9). Ritter et al. (27) found one landrace accession, Chimi Lucki (CIP 702305, *S. juzepczukii*) with complete resistance to PLB and two accessions with partial resistance: Poluya (CIP 703421, *S. stenotomum*) and Camusa (CIP 703461, *S. tuberosum* subsp. *andigena*). Resistance in *S. tuberosum* subsp.

andigena, used either directly as landrace varieties or as a resistance source in crosses, has been reported in Peru (12,13) and Bolivia (9,25). Cañizares and Forbes (4) and Revelo et al. (26) reported high levels of horizontal resistance in the Ecuadorian national collection of *S. phureja* subsp. *phureja* Juz. & Buk. Coca (5) found resistance to PLB in Bolivian *S. phureja* varieties Jaspe, Cordillera, and Chota ñawi; however, in a subsequent study, they found different levels of resistance among *S. phureja* potato (6). In Bolivia the national potato program, PROINPA, reported field resistance to *P. infestans* in *S. tuberosum* subsp. *S. andigena*, *S. stenotomum* and *S. juzepczukii* (16).

In the development of the scale used in this study, Yuen and Forbes (33) suggested that the value 9 should be assigned to highly susceptible control genotypes. In the scale, ascending values were used to indicate increasing susceptibility because resistance is limited at immunity and, thus, can equal a value of 0 on the scale. However, there is no known limit to susceptibility; thus, the scale allows for the occurrence of genotypes more susceptible than the control. Nonetheless, Tomasa Condemayta was given 9 in this study because it was considered extremely susceptible and the much higher levels of susceptibility found among many accessions were surprising. The reasons for this are unknown. One possibility is that, for any variety to succeed in agriculture, some level of resistance is needed, whereas many of these accessions grow in areas where PLB does not occur. As a partial test of this hypothesis, we

Fig. 1. Frequency distributions of accessions belonging to eight potato landraces for susceptibility to *Phytophthora infestans* tested under greenhouse conditions. Susceptibility is expressed as scale values of Yuen and Forbes (33). The position of the control varieties are indicated by arrows. Potato landraces: SOLPHU = *Solanum phureja* Juz. et Buk. (124 accessions), SOLGON = *S. goniocalyx* Juz. et Buk. (37 accessions), SOLSTN = *S. stenotomum* Juz. et Buk. (112 accessions), SOLCUR = *S. curtilobum* Juz. et Buk. (5 accessions), SOLTBR = *S. tuberosum* subsp. *tuberosum* L. (31 accessions), SOLADG = *S. tuberosum* subsp. *andigena* Juz. et Buk. (120 accessions), SOLCHA = *S. chaucha* Juz. et Buk. (26 accessions), and SOLJUZ = *S. juzepczukii* Buk. (13 accessions). Control varieties: C = Chucmarina, B = CIP 399076.12, Y = Yungay, and T = Tomasa Condemayta.

evaluated the association between altitude and scale value, postulating that the most susceptible accessions may be found at altitudes where it is too cold for PLB. No significant correlation was found but there may also be many areas at lower altitudes where potato can grow, possibly with irrigation, but where conditions are also not appropriate for PLB. Regardless of the underlying biological explanation, this study added to our understanding and stretched the limits of susceptibility: what had been thought to be a 0-to-9 scale was found here to be a 0-to-12 scale.

This study produced no clear evidence for the predictivity of geography or taxonomy because accessions with susceptibility scale values less than or equal to Chucmarina represented different countries and species: Peru ($n = 13$), Bolivia ($n = 3$), Ecuador ($n = 1$), and Chile ($n = 2$); and different ploidy levels, with six diploid accessions from *S. stenotomum* ($n = 4$) and *S. goniocalyx* ($n = 2$), four triploid accessions from *S. chaucha* ($n = 1$) and *S. juzepczuckii* ($n = 3$), and nine tetraploid accessions from *S. tuberosum* subsp. *andigena* ($n = 7$) and *S. tuberosum* subsp. *tuberosum* ($n = 2$). Thus, potential sources of resistance were found in diverse locations and genetic backgrounds (Table 2). Lack of taxonomic predictivity was found to be common in a bibliographic metaanalysis done by Spooner et al. (29). Nonetheless, the accessions identified here for resistance can be used to improve PLB resistance in potato breeding populations (21).

Our analysis gave some indication of the nature of resistance in the accessions evaluated. There was little evidence of bi- or multimodality in the frequency distributions of susceptibility values (Fig. 1). Some indication of additional modes did occur on the susceptible end of the distribution (Fig. 1, SOLPHU) but there was no clear indication of a clearly distinguishable group of highly resistant accessions, as has been seen in other resistance evaluations of populations of potato genotypes (19,28). In those cases, the highly resistant to near-immune phenotypes were thought to express *R*-gene-mediated resistance. We hypothesize that many of the moderately resistant phenotypes we identified were not expressing typical *R* genes but, rather, another resistance mechanism, possibly multigenic, which is potentially durable.

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